

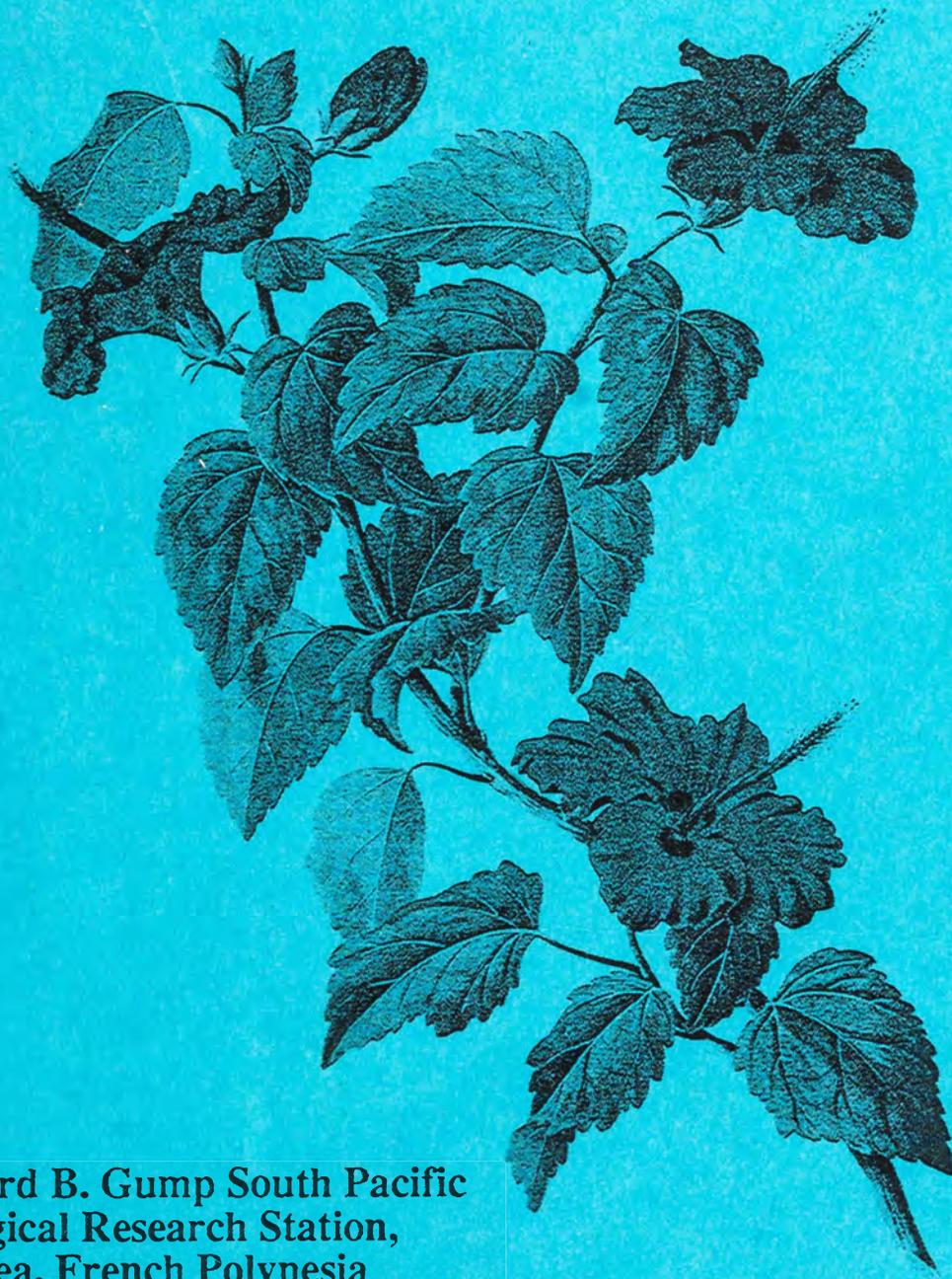
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 RESERVES

**Environmental Science Policy and Management 107,  
Geography 142, and Integrative Biology 158**

# **The Biology and Geomorphology of Tropical Islands**

**Student Research Papers, Fall 1999**



**Richard B. Gump South Pacific  
Biological Research Station,  
Moorea, French Polynesia**

**University of California, Berkeley**

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## The Biology and Geomorphology of Tropical Islands

Student Research Papers, Fall 1999

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Above: The lagoon at Tamae, Moorea, French Polynesia.

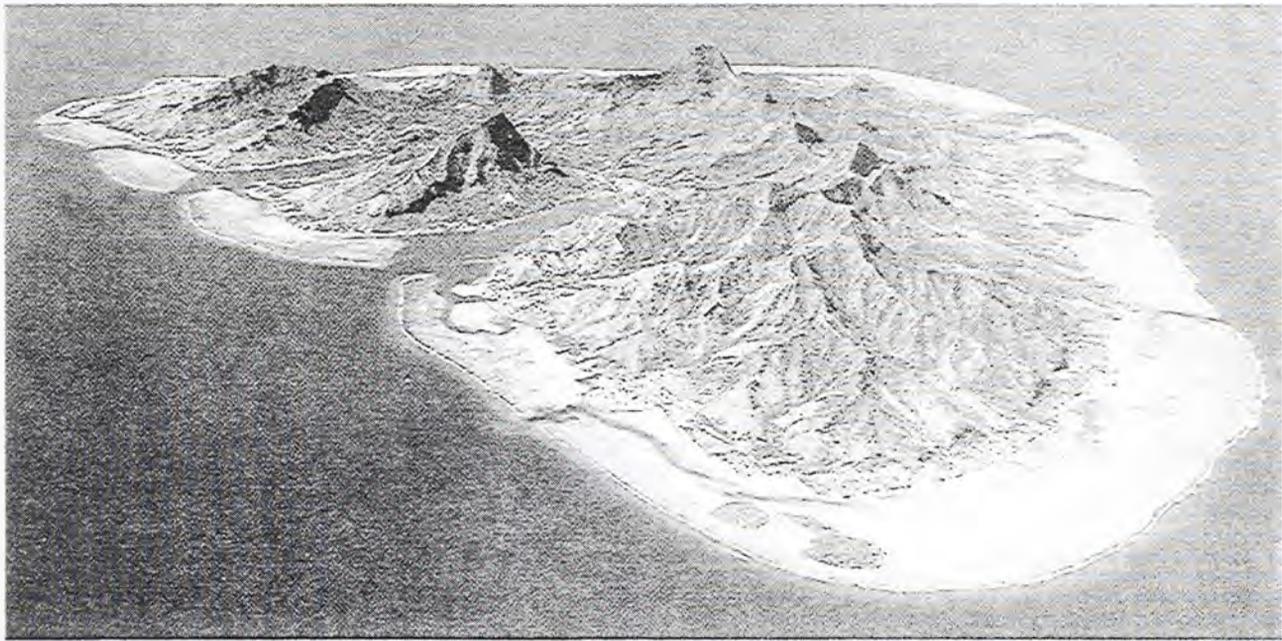
**Book cover:** One of the most common plants on Moorea, as well as the other Society Islands, is *Hibiscus*. Two species grow around the Richard B. Gump Station, *H. rosa-sinensis* and *H. tiliaceus*. *Hibiscus rosa-sinensis*, shown on the cover of this book, grows as an ornamental shrub next to the dormitory at the Station. The cover illustration was done by Sydney Parkinson on Lieutenant James Cook's first circumnavigation of the globe from 1768 to 1771 in H.M. Bark *Endeavour*. Parkinson painted and sketched not only botanical specimens, but zoological ones, coastlines, tattoos, canoes, villages, and Cook's fort at Point Venus, Tahiti. He was one of two artists brought along on the voyage by Joseph Banks, who accompanied Cook as the Royal Society's natural historian and who paid personally for Parkinson's expenses. Parkinson shared a cabin directly behind Cook's and on the opposite side of the ship from Banks. The illustration on the cover of this book was done by Parkinson in vivid color with the bright red blossoms we all know. He drew it in 1769 at Otaheite, as Tahiti was then known, along the coast facing Moorea (then known as Imaio). He worked at a table set up outdoors at Point Venus, Tahiti, under rough conditions. Flies swarmed around Parkinson while he painted, as Banks noted: "they eat the painters off the paper as fast as they can be laid on, and if a fish is to be drawn there is more trouble in keeping them off than in the drawing itself". Parkinson later died crossing the Indian Ocean in 1771, the victim of dysentery contracted at Batavia in the Dutch East Indies. The original painting is housed in the Natural History Museum (London).





*From left to right: Back row (standing):* Jere Lipps (Professor, IB), Brent Mishler (Professor, IB), Kris Wagner-Porter, Dave Des Marais, Norm Hetland (GSI), Andy Murdock, Andres Lebensohn, David Lindberg (Professor, IB), Ryan Johnson, Jennifer Williams and James Jackson (GSI). *Third row (standing):* Analise Elliot, DanTram Nguyen, Meredith Bauer (GSI), Erin Gontang, Allison Wickland, Zita Maliga, Amy Tang; *Second Row (kneeling):* Andrew Gwin, Lauren McGoldrick, Rich Brusck, Lisa Wu, Paula Roy-Burman, Christian Baker, Jillian Silva, Tobias Koehler; *Front row (sitting):* friends of the station including Jaques, Ruhama and Michael.  
Not pictured: David Stoddart (Professor, Geography)





# The Biology and Geomorphology of Tropical Islands

## Scientific Reports for 1999

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## The Moorea Course 1999

### Introduction

Twenty Berkeley Juniors and Seniors were selected based on their previous academic and field work, and studies of biology, geography, geology, and environmental sciences, to take part in the Moorea Class. The course is a very special one unmatched in most curricula at any college or university. These students, together with three Graduate Student Instructors, lived at the Gump Station on the Island of Moorea, just 11 km from Tahiti, in French Polynesia, for nine weeks. Five faculty took part in the field instruction for two or three weeks each at different times in the semester.

Our objective in this course is to make undergraduate students into professional natural scientists through the design and implementation of their own original research project. During this work, the 1999 students encountered typical field research situations. Some of these are strange and new, like the upside-down Jellyfish *Cassiopeia* or the jumping clam, *Lima*, or highly unusual like the strange Black Sea Cucumbers. Others are wonderful variations on well known themes, like the biology of Morning Glories, flowering trees and liane, or the behavior of geckos, octopuses, or reef fish. Some portended disaster, like when cages were swept away by flash floods or recalcitrant property owners stood in the way of science! All of these are common to field research in biology, geology, geomorphology and similar sciences. This class dealt successfully with all these and more in 1999.

The course has been immensely successful since its inception in 1991. Over 140 students have taken the course, done research on their own original projects, presented their results in the annual Symposium on the Biology and Geomorphology of Tropical Islands, and in written scientific papers published in books like this one. Many of the papers done by these students have also been published by them in regular scientific journals.

The Moorea Course combines many aspects of expeditionary research--scientific preparation, logistic planning, equipment and supply selection, and the development of an individual research problem. It is a complete research experience, not unlike that of

Management 107, Geography 142 or Integrative Biology 158, starts with science background, logistics and supply at Berkeley for the first four weeks of the semester, then the entire group of 20 students, several faculty and three Graduate Student Instructors moves to Moorea to begin a week of scientific field trips on Moorea and Tahiti. With the Berkeley and field background, students then develop a scientific project of their own. Although science is important, safety, logistics, cost, equipment and supplies are critical aspects of each project that requires detailed planning as well. For the next eight weeks, students pursue their own projects on Moorea, returning to Berkeley for final report preparation and oral participation in the annual Symposium.

The 1999 Class was again profoundly successful, as can be seen in the research papers in this volume. Everyone--students, GSIs and faculty--learned many new things, had new and different experiences, and had enjoyed most every minute. The projects varied from plants to animals, and took place in the waters of the reefs, the steams of the Island, to near the very top of Moorea. The variety and achievement of the projects were enormous. Perhaps, more than anything else and as in all intensive field research, they and we learned a good deal about one another and people in general. It was a thoroughly enjoyable, if at times stressful, research trip.

## **Acknowledgments**

The course is tremendously complex and it would not work without a huge amount of effort and cooperation from the students, faculty, Graduate Student Instructors, and our colleagues at Berkeley and on Moorea. The faculty and GSIs are grateful to the class for the good times and wonderful camaraderie, and for sharing their excitement with us. Those of us in the field with the students also learned a good deal from each of them, as they developed and explored their own research.

In California, a number of other faculty and staff helped us by presenting lectures and workshops on a variety of topics. These people included Carole Hickman, Roy Caldwell (Integrative Biology), Norma Kobzina (Bioscience and Natural Resources Library), David Smith and Pang Wai Chan (VLSB Visualization Center), Mark Frieberg and Brigette Bankay (UCB Environmental Health and Safety), and Jim Hayward (UCB Diving Safety Officer). We especially thank Julie Myers, Diane Leite and Dorothy Tabron (Integrative Biology), who kept the course going administratively, and Don Bain (Geography) and the Animal Use and Care Committee for advice, arrangements and assistance of various sorts. The staff of the University and Jepson Herbaria, the Museum of Paleontology, Bioscience and Natural Resources Library, and the Visualization Center provided assistance with their resources. The class field trip to the coast of Central California was made possible by the cooperation and efforts of Peter Connors and Lisa Valentine of the UC Davis Bodega Marine Laboratory.

On Moorea, we also are grateful to many people. We especially thank Debbie Woodward and John Boland, managers of the UC Berkeley Gump Research Station on Moorea and the Station staff, who kept the facilities operating so efficiently and who made our stay so very pleasant. Jim Hayward, UCB Diving Officer, conducted several

dives for the UCB Certified divers. Frank and Hinano Murphy of Moorea and Tahiti provided much assistance and interaction with the people of Moorea. We certainly enjoyed the company of many Mooreans whose names went unrecorded, including those present during the class photograph. All of these enhanced our cultural experience. Lastly, we thank Professor Vincent Resh of the College of Natural Resources and Director of the Gump Station for his encouragement, assistance and complete support of what we did in Moorea. Without the forethought of the late Richard B. Gump, we would have nowhere to stay. Gordon and Betty Moore have contributed over the years to the support and development of the Station, so that now it is a first-class research facility and ideal place to teach a course like this one.

The faculty are, of course, deeply indebted to Meredith, Norm and James, the GSIs, for their total commitment to the students and the course. Each was a kingpin in the operation both at Berkeley and Moorea. No words can adequately express our thanks!

Without all this help of such various kinds, our students would not have had this fantastic experience that they can remember for the rest of their lives. They have been changed forever!

Jere H. Lipps, Professor, Integrative Biology. Course organizer.  
Jamie Bartolome, Professor, ESPM  
David R. Lindberg, Professor, Integrative Biology  
Brent Mishler, Professor, Integrative  
David Stoddart, Professor, Geography  
Meredith Bauer, Graduate Student Assistant, ESPM  
Norm Hedland, Graduate Student Assistant, Geography  
James Jackson, Graduate Student Assistant, Integrative Biology

# Colonization Habits and Population Dynamics of Coral Reef Fish in *Pocillopora eydouxi* and *Pocillopora meandrina*

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**ABSTRACT.** Colonization habits of reef fish in the lagoon of Moorea Island, French Polynesia, were examined for two species of damselfish, *Dascyllus aruanus* and *Dascyllus reticulatus*, by observing two species of coral that serve as habitat for these fish. The corals utilized for these experiments were *Pocillopora eydouxi* and *Pocillopora meandrina*. These two species are similar in many respects, however, *P. eydouxi* has larger average spacing between branches. *D. aruanus* and *D. reticulatus* demonstrated similarities in habitat preference, settling in *P. eydouxi* when both corals were present and uninhabited, showing that spacing influences colonization patterns. Apart from coral preference, both *D. aruanus* and *D. reticulatus* demonstrated distinct settlement patterns when *Pocillopora* was placed in the lagoon in areas with little coral cover and along the reef. A coral translocation experiment revealed that corals in areas on the perimeter of the lagoon recruit a greater amount of fish than those located in areas with a high percent of coral cover. Another influence of colonization is the presence of juvenile *D. reticulatus*. A second set of experiments discovered that the translocation of juvenile *D. reticulatus* to *Pocillopora eydouxi* affects the settlement behavior of other juveniles. Juvenile *D. reticulatus* attracts fish of the same size and species as well as *D. aruanus*. Reef fish abundance among *P. eydouxi* and *P. meandrina* is shaped in different amounts by coral size and structure, location, and juvenile presence.

## Introduction

*Pocillopora eydouxi* and *Pocillopora meandrina* are two closely related species of coral. They are very similar in structure and color. These branching corals are home to many fish, including *Dascyllus aruanus* and *Dascyllus reticulatus* (Schmitt and Holbrook 1999). Depending on hydrodynamics of the area, coral branches can reach different widths (E-mail). Average distance between each branching arm on a *P. eydouxi* coral is greater than that on a *P. meandrina* when these coral are found in the same area. More shelter is then available for fish and other marine organisms in *P. eydouxi*, making this species of coral a more suitable shelter for reef fish.

Colonization among coral reef fish is highly dependent upon the presence of particular species of coral located in the lagoon areas. The number of coral growth forms designates the amount of fish that can be present (Ormond, Roberts and Jan 1996). There is great spatial variation in the distribution of reef fishes among *Pocillopora eydouxi* and *P. meandrina*. The cause of this can be contributed to location of these smaller branching corals. Location of these coral formations, particularly depth and distance from the barrier reef, plays a major role in colonization. Planktivorous species prefer coral

heads located along the reef slope (Meekan, Steven and Fortin 1995). Fish also exhibit better survivorship and growth in corals located at the perimeter of a lagoon. Colonizing *Dascyllus aruanus* and *D. reticulatus* may not reach central sites because these areas are in a region referred to as a recruitment shadow. Fish settle in corals at the first opportunity when entering a lagoon, leaving central sites less inhabited (Jones 1997).

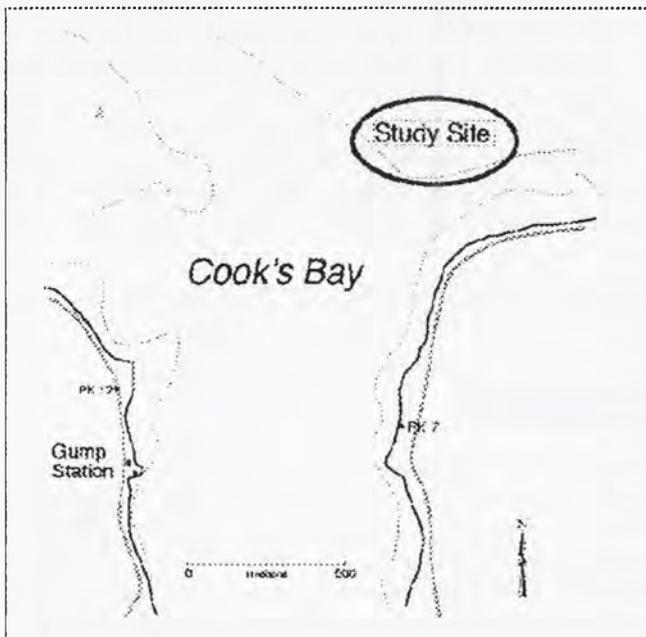
Colonization habits of older fish greatly differ from that of larvae. Adult damselfish disperse their young as pelagic larvae (Gutierrez 1998). Larval recruitment occurs in greater amounts during the first and third quarter moon phases. During these moonless periods, the larvae then enter the lagoon at night (Dufour and Galzin 1993). During a two-month period, 1.8 million settlement-stage fish were recorded entering the lagoon on Moorea in five separate locations (Dufour, Riclet and Lo-Yat 1996). Once larvae enter the lagoon, they must find an area to settle. Juvenile *Dascyllus aruanus* and *D. reticulatus* exhibit preferential patterns of settlement in relation to conspecifics. Selection of a suitable habitat by *Dascyllus aruanus* and *D. reticulatus* is influenced by the presence of juveniles (Jones 1997; Schmitt and Holbrook 1999).

	<i>eydouxi</i> 1	<i>Eydouxi</i> 2	<i>Eydouxi</i> 3	<i>eydouxi</i> 4
Width	3.05	2.95	3.05	2.90
Length	1.20	1.30	1.23	1.20
	<i>meandrina</i> 1	<i>Meandrina</i> 2	<i>Meandrina</i> 3	<i>meandrina</i> 4
Width	1.27	1.02	1.22	1.20
Length	0.61	0.58	0.65	0.60

Table 1. *P. eydouxi* 1, *P. eydouxi* 2, *P. meandrina* 1, and *P. meandrina* 2 were all located in the sandy lagoon area. *P. eydouxi* 3, *P. eydouxi* 4, *P. meandrina* 3, and *P. meandrina* 4 were all located among other coral heads. The width, in meters, is the average length between each arm of the coral heads. The length, in meters, is the circumference of the coral heads minus each base

The area chosen for study was located on the island of Moorea, French Polynesia. The lagoon was on the East side of Avaroa pass entering Cook's Bay (Figure 1). The site was 200 meters offshore and 3.1 to 3.3 meters in depth. There is a large amount of larval recruitment of *Dascyllus aruanus* and *D. reticulatus* in this area.

Figure 1. Map of Study Site



developed coral communities. (At this location, there is a very distinct border running between the two.) Water ranged in depth from 3.1 meters in the coral areas to 3.3 meters in the sandy lagoon areas. The corals received uninhibited sunlight during all hours of the day. Experimentation was carried out through the months of October and November.

The spacing between each individual arm and the length of each *Pocillopora eydouxi* was larger than that of *Pocillopora meandrina* (Table 1).

#### Setup for colonization experiments

Coral heads were removed in this same lagoon using a three-pound sledgehammer and a six-inch chisel. Four specimens of *Pocillopora eydouxi* and four specimens of *Pocillopora meandrina* were successfully removed without damaging the coral. The fish living in these corals were removed and the corals were then attached to six concrete blocks using wire. Two *Pocillopora eydouxi* and two *Pocillopora meandrina* were each attached to four separate blocks. To the two remaining blocks, one of each coral was attached. Three of these blocks were then placed on the sandy lagoon bottom and three were placed among other, larger, coral heads (Figure 2).

## Materials and Methods

### Study Site

The study was conducted in the lagoon on the East side Avaroa pass entering Cook's Bay. This is located on the North side of the island of Moorea. The site was located 260 meters offshore and its borders encompassed both sandy bottoms, with no coral, and very



Figure 2. Position of corals on concrete blocks. E stands for *Pocillopora eydouxi* while M stands for *Pocillopora meandrina*. Three blocks with this set up were located in the lagoon (Corals 1, 2A and B, and 3) and three were located in the reef (corals 4, 5A and B, and 6). The A stands for the *P. meandrina* on the block and the B stands for the *P. eydouxi*.

These vacant corals were then observed everyday between the hours of 1000 and 1700 in two separate fourteen-day phases. I recorded the fish that would colonize each coral head. At the end of each phase, the corals were cleared of all fish. In order to clear the fish out of the corals, the coral heads were detached from the blocks and separately brought to the surface in a 20-gallon bucket. While the bucket was in the boat, the coral was removed very briefly from the bucket and then were brought back down to the lagoon bottom. This would force the fish to remain in the water within the bucket, thus, separating the fish from the coral. The fish were then relocated to the wet laboratory at the Gump Station in order to identify them. After identifying them, they were released off the dock at the station, on the west side of Cook's Bay.

#### Setup for population experiments

The second group of experiments was carried out in three separate five-day phases. The study site was located in the sandy lagoon area and *Pocillopora eydouxi* corals were used because these experimental features attracted a greater number of fish during the colonization experiments. I cleared all of the fish from the two *Pocillopora eydouxi* corals that were located in the lagoon from the previous experiments. I then attached these two corals to separate blocks

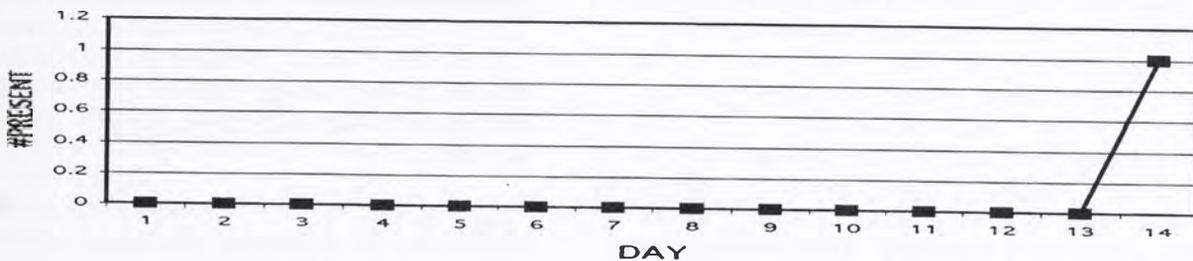
and stocked one with juvenile *Dascyllus reticulatus*. While using the other coral head as a control. I then proceeded to check these two corals everyday as I previously had and I recorded the various fish that would settle in the coral heads.

#### Results

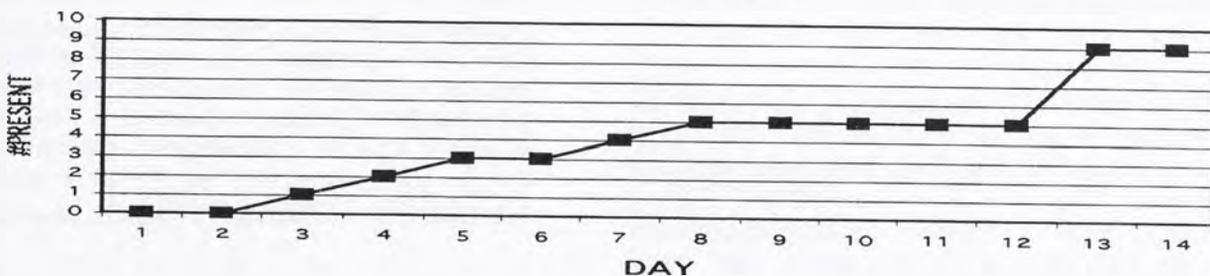
##### *Spatial variation among corals and location dependent colonization habits*

*P. eydouxi* had a greater density of settlers than did *P. meandrina*. Other fish were present in these corals but they were not of the genus *Dascyllus*. The other fish were transients and had no substantial influence on colonization habits of *D. reticulatus* and *D. aruanus*. During the first trial, the corals in the lagoon attracted a total of 10 *D. reticulatus* that settled and remained in these corals for the duration of the trial. *D. reticulatus* settled in Coral 2A (*P. meandrina*), 2B (*P. eydouxi*), and 3 (*P. eydouxi*) located in the lagoon. In the instances in which *D. reticulatus* was recorded colonizing *P. meandrina*, the fish were all juveniles and they were not in high abundance. *D. reticulatus* was very active among the corals located in the lagoon during the first 14-day trial, however, no fish colonized the corals (4, 5A, 5B, and 6) located on the reef (Figure 3).

CORAL 2A: *P. meandrina*  
Juvenile *D. reticulatus*



Coral 2B: *P. eydouxi*  
Adult *D. reticulatus*



**Coral 3: *P. eydouxi*  
Adult *D. reticulatus***

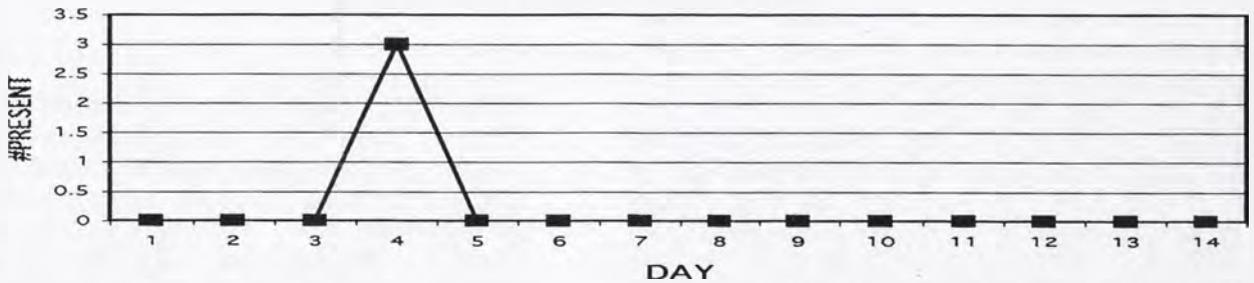


Figure 3. Results from first coral translocation trial

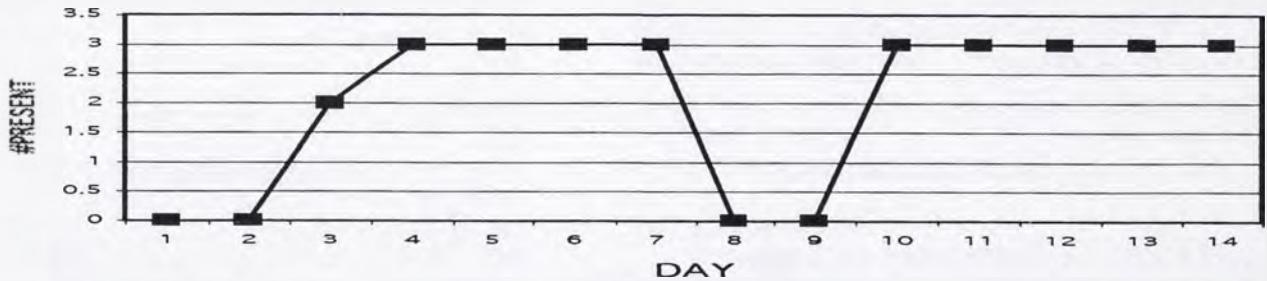
During the second trial, 17 *D. reticulatus* and 5 *D. aruanus* colonized the corals in the lagoon. Few juvenile *D. reticulatus* were once again present in coral 1 (*P. meandrina*) and in coral 2A (*P. meandrina*), but there were no

adults. Both juvenile and adult *D. reticulatus* and *D. aruanus* settled on corals 2B and 3 (both *P. eydouxi*) (Figure 4). Again, no fish colonized the corals located on the reef.

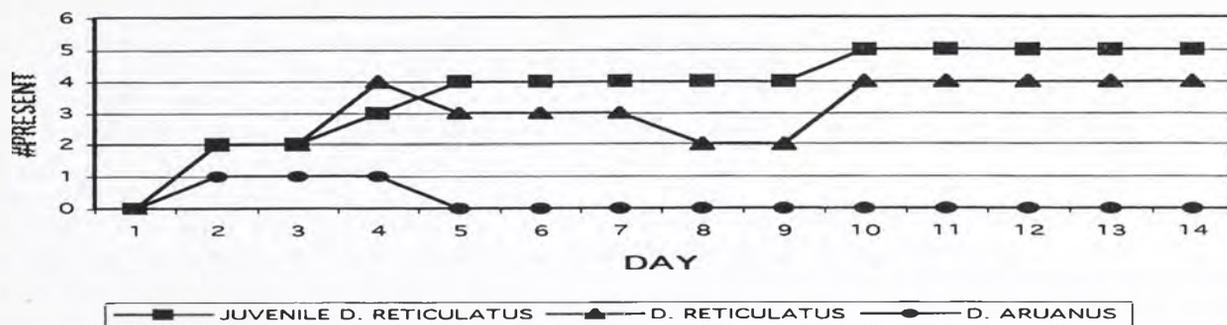
**Coral 1: *P. meandrina*  
Juvenile *D. Reticulatus***



**Coral 2A: *P. meandrina*  
Juvenile *D. reticulatus***



Coral 2B: *P. eydouxi*



Coral 3: *P. eydouxi*

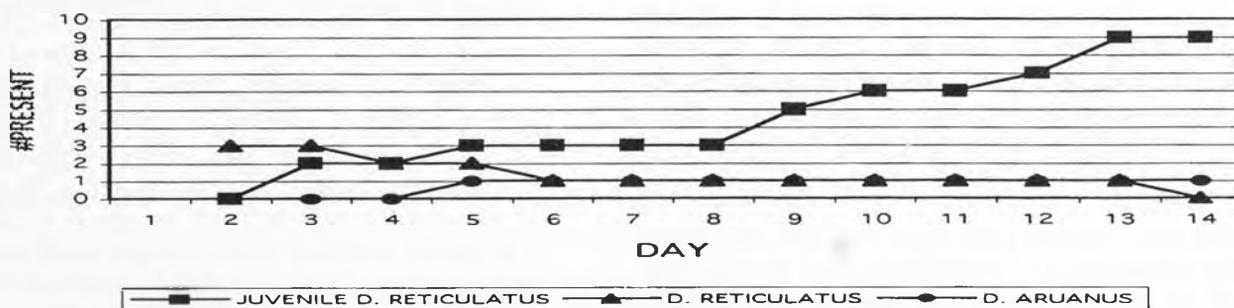


Figure 4. Results from second translocation trial

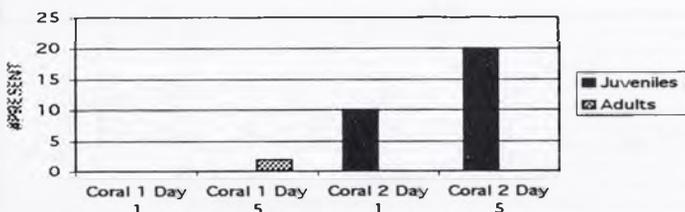
For the two trials, a total of twenty-eight days, the coral habitats located in the lagoon attracted *Dascyllus* while those located on the reef did not attract a single fish of this genus. Simple statistical analysis revealed that the mean amount of fish that colonized the four corals in the lagoon over twenty-eight days was 4.125 (including both *D. aruanus* and *D. reticulatus*) while the corals located on the reef attracted no fish.

Recruitment variables

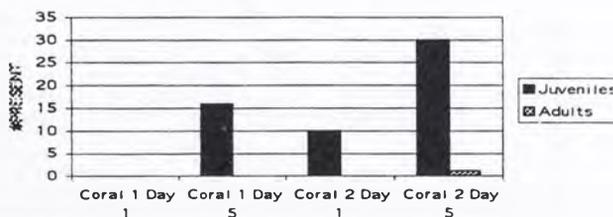
The translocation of juvenile *D. reticulatus* to *P. eydouxi* in the lagoon had a distinct impact on

recruitment of juveniles. For this study, two *P. eydouxi* corals were translocated to the lagoon. Coral 1, which was completely cleared of any fish at the beginning of the trials, recruited only 26 juveniles over the three, five-day periods. Coral 2, which was initially stocked with 10 juvenile *D. reticulatus* at the beginning of the trials, recruited 215 juveniles (Figure 5). I ran Chi squared tests for this last experiment with the null hypothesis that the same amount of fish will settle on each coral. After running these tests and finding  $p < 0.0025$ , the null hypothesis was rejected.

First Translocation Trial



Second Translocation Trial



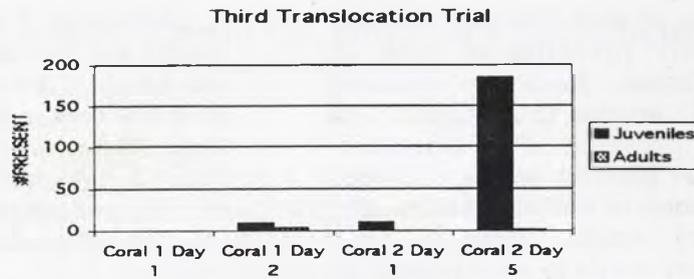


Figure 5. Three five-day trials in which Coral 1 is cleared of all fish and Coral 2 is stocked with 10 juvenile *D. reticulatus* in order to determine whether or not conspecifics influence recruitment

## Discussion

### *Spatial variation among corals and location dependent colonization habits*

The distinct difference in fish preference when settling in coral heads is significant because *P. eydouxi* and *P. meandrina* are commonly located in the same areas of the lagoon and reef. Therefore, it is important to understand why *P. eydouxi* makes a more suitable habitat than *P. meandrina*.

The results from the first set of experiments greatly supported my hypothesis that larger coral branching widths creates more habitat space, leading to greater colonization densities. Larger fish, in greater numbers, settled in *P. eydouxi* rather than *P. meandrina* when these two species of coral were placed in the same areas. Although some fish did occasionally settle in *P. meandrina*, they were only juveniles less than 0.5 centimeters in length. As table 1 showed, the average width between branching for the four *P. eydouxi* corals was 2.99 cm and the average for the *P. meandrina* corals was 1.18 cm. This 3:1 ratio may have been a contributing factor for larger settlement densities in *P. eydouxi*. There may have been other contributing factors as well, but these were the only parameters tested and no previous studies on coral branching widths and their influence on damselfish settlement is available in the literature.

The second part of this experiment dealt with the location dependent colonization habits of reef fish. Both species of corals were placed in the lagoon and along the reef, so *D. reticulatus* and *D. aruanus* had the opportunity to settle these corals in the most suitable area. There is no question that the lagoon does indeed attract more fish as seen in figures 3 and 4. The literature indicates that there are very similar studies and results. Meekan, Steven and Fortin researched colonization habits as well. Their methods included laying transects from the reef crest down the reef slope and identifying and counting species. Although my study involved

placing corals in one area and recording fish abundance on these corals, the two studies had similar results. Planktivorous fish such as *D. reticulatus* and *D. aruanus* are attracted to the deeper, sandy areas along the reef slope. This is because there are greater amounts of food in these waters.

Jones developed similar studies in order to explain something he referred to as a recruitment-shadow. His studies involved the use of transplanted corals. He constructed grids of coral units and placed them in ten areas of the lagoon. These locations encompassed both reef and sandy slope areas and recruits were recorded and collected from these corals. The results revealed that recruitment was 2-3 times higher to corals that were not in the shadow of a large reef. This study also examined the effects that settlement at the perimeter of the lagoon has on *D. aruanus*. When this fish colonizes corals on the perimeter, it increases its chances of surviving to maturity. As a result of this last factor and because central sites are in a recruitment-shadow, the recruitment of *D. aruanus* to the central sites along the reef is low, even when preferred coral substrates are transplanted to the center. Another reason for settlement along the perimeter is that *D. aruanus* would favor windward sides of the lagoon, where the corals from my study were located in the sand, because these areas are expected to have a higher abundance of zooplankton. As a result of this, location of colonization may also be related to food resources. These methods and results of Jones' research were extremely similar to those from my study in the lagoon at Moorea.

### *Recruitment variables*

The second experiment that I developed was to test the hypothesis that fish already present in the coral heads affects recruitment. The results from this study revealed that *D. reticulatus* that are less than 0.5 centimeters in length play a major role in the recruitment of other juveniles. The *P. eydouxi* that contained ten translocated

fish at the beginning of each five-day trial did indeed attract many juveniles of both *D. reticulatus* and *D. aruanus*. Jones also recorded that recruitment of *D. aruanus* to *Pocillopora* was influenced by the presence of conspecifics. Sweatman did further research on the influence of conspecifics on choice of settlement sites. His methods were very similar to mine. He transplanted *Pocillopora* corals to areas located 40 meters from the reef on the sand and to these he translocated *D. aruanus* and *D. reticulatus*, each species on separate corals. His results indicated that *D. aruanus* and *D. reticulatus* do indeed attract conspecifics. Three reasons for this are that fish need refuges, food and opportunities for mating. Conspecifics are necessary for mating and the presence of a conspecific in a coral head shows that food is present at that location, attracting more fish of the same species.

Although I did record very convincing results for this last experiment at an order of magnitude, I did not have enough time for more than just two replications of the original study. More replications would have allowed for more detailed statistical analysis, so future research on the influence that juvenile *D. reticulatus* has on recruitment is necessary.

### Conclusion

Colonization habits and preferences of *D. reticulatus* and *D. aruanus* are very important aspects of marine life because they show the relationships that organisms have with one another. My research has demonstrated how important *P. eydouxi* and *P. meandrina* are to the abundance of these damselfishes and hopefully these corals will be able to thrive and provide a habitat in the lagoon of Moorea for years to come.

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# Sediment Turnover Rate Of The Black Sea Cucumber *Holothuria atra*

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**ABSTRACT.** Sediment turnover rates of a population of *Holothuria atra* (Echinodermata; Holothuria) living on a reef flat near Haapiti, Moorea, French Polynesia were studied. The aim of this study was to determine the potential turnover of sediment by this population. This was accomplished by (1) measuring individual sediment turnover in experimental trials, (2) taking field densities of *H. atra* at the study site, and (3) modeling the annual turnover rates per unit area. Sediment turnover rates of the forty-eight specimens used in aquarium experiments averaged 35 g dry weight of sediment individual<sup>-1</sup> day<sup>-1</sup>. Sediment turnover rate was directly proportional to specimen weight. Field density measurements averaged 708 individuals 100 m<sup>-2</sup>; this is a very high density compared to populations studied by other researchers. A model calculation showed this population has the potential to turn over an estimated 9,046 kg year<sup>-1</sup> 100 m<sup>-2</sup>. This high level of sediment turnover is ecologically important because it contributes to sediment transport, recycling of nutrients, and aeration of the sediment.

## Introduction

Sediment turnover, also known as 'bioturbation,' is a fundamental aspect of coral reef ecology. In this process, animals either ingest or otherwise disturb the layers of sediment on which they live. Bioturbation has profound ecological implications through benefiting the overall health and well-being of reef flat areas. Sea cucumbers are agents of this biological process. The quantity of sediment passing through the gut of *Holothuria* is important because this bioturbation affects the ecology of the coral reef environment (Bonham and Held 1963; Kerr et al. 1993).

Sea cucumbers (Holothuroidea) are among the most common and conspicuous animals living on coral reef flats in the tropical Indo-Pacific (Stoddart 1969; Kerr et al. 1993; Uthicke 1999). Most members in this class of echinoderms are epibenthic deposit feeders. Holothurians use their adhesive buccal tentacles to feed on sediment grains covered by bacteria, microalgae, cyanobacteria, and detritus. This organic matter is digested to provide necessary nutrition for growth and reproduction. This feeding behavior often results in a large amount of sediment turnover, and for this reason, holothurians have been called the 'earthworms of the sea' (Bonham and Held 1963).

*Holothuria atra* is a major contributor to the bioturbation in many tropical reef areas around

the world. Kerr (1994) and Tarvyd (1999) have stated that *H. atra* is the most common holothuroid on shallow reefs in the Western Pacific Ocean. It has been found that the collective feeding activities of *H. atra* turn over large amounts of sediment (Stoddart 1969; Bonham and Held 1963; Uthicke 1999). This is due to high individual rates of sediment turnover and high natural population densities common to this species.

In the present study, the amount of sediment reworked by individuals of *H. atra* was determined. This was used to estimate the annual amount of bioturbation per unit area by a population of *H. atra* living on a reef flat near Haapiti, Moorea, French Polynesia. My goal was to use new techniques, both in the field and in the laboratory, to provide a more complete knowledge and understanding of sediment turnover rates by *H. atra*.

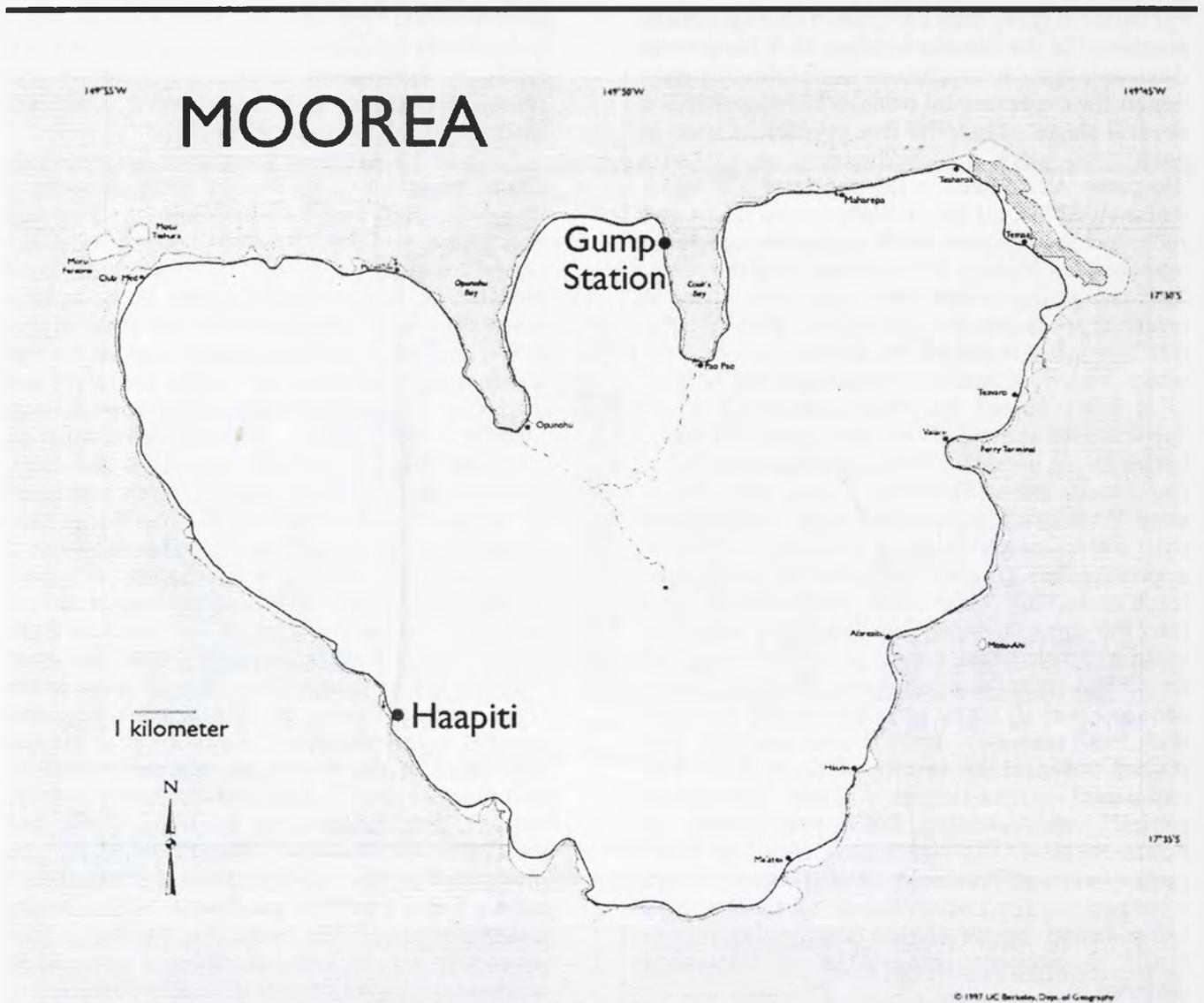
## Materials and Methods

This research was carried out on the island of Moorea (17°30'S, 149°50'W) during October and November 1999. Moorea is part of the Society Islands archipelago, one of several island chains making up French Polynesia (Figures 1 and 2). Moorea is a two-million-year-old volcanic island (125 km<sup>2</sup>) with both fringing and barrier coral reefs. The study site for this research was a reef flat located near Haapiti



(17°30'29"S, 149°52'29"W), on the southwest coast of Moorea (Figure 3). The shoreline adjacent to the reef flat has a dense stand of mangroves, and the reef flat itself consists almost entirely of sandy substrate. I performed

aquarium experiments and most analyses at the Richard Gump South Pacific Biological Research Station (17°29'37"S, 149°49'38"W), located on the west side of Cook's Bay, Moorea (Figure 3).



**Figure 3.** Detailed map of Moorea showing location of Gump research station and Haapiti

I collected 48 representative specimens of *Holothuria atra* from the Haapiti reef flat. I also removed approximately 164,000 cm<sup>3</sup> of surface sediment from the study site using a scoop and a large bucket. I placed this sediment evenly over the bottom of a cement holding tank (244 x 122 x 76 cm) located in the outdoor wet lab facility at the Gump Station. The holding tank had a constant inflow of fresh seawater at a rate of approximately 3.16 L min<sup>-1</sup> supplied by a circulating seawater system. A drainpipe maintained a water depth of 6 cm. The 48

specimens of *H. atra* were transferred from the field site in Haapiti to the Gump station. They were placed into the cement holding tank where they lived and fed on sediment throughout the duration of the experimental trials.

In order to keep records of individual sea cucumber's identities and weights, each specimen was tagged. This was done using small, square plastic tags, labeled with numbers 1-48. Different colored tags were used to aid in the ease of identifying specimens (i.e. specimens 1-10 had orange tags, and specimens 11-20 had

pink tags, etc.). A 5/0 FS3 16 mm suture needle with 60 cm of Ethicrin® polyamide monofil (Johnson and Johnson Intl.) was used to attach a tag to each specimen through the posterior dorsal body wall. The specimens were then returned to the cement holding tank.

After tagging was completed, the specimens remained in the cement holding tank for several days to adjust to aquarium conditions. I then began the experimental trials, which consisted of several stages. First, the five specimens used in each trial were weighed using an OHAUS 'Portable Advanced' scale, model # CT 200-S (capacity: 200 x .01 g). Weights were taken and recorded approximately 60 s after the specimen was removed from the cement holding tank. This weighing procedure measures what is referred to as the sea cucumber 'Dry Weight' (DW) because it allows the animal to expel the water from the cloacal cavity through the anus.

I then placed the five specimens in an "apartment complex" of trays, located on a bench in the wet lab. This complex consisted of five plastic trays (31 x 18 x 8 cm), each with a small hole in one side of the tray. The level of the hole maintained a water depth of approximately 2.5 cm in each tray. I stacked the trays on top of each other so that water flowing into the top tray from the circulating seawater system would flow consecutively through all five trays, from top to bottom. This design ensured that all trays were constantly supplied with fresh seawater. Each *H. atra* specimen was placed individually in one of these trays that contained no sediment. This "starvation period" was executed for approximately 24 hours to allow the specimens to purge their gastrointestinal tracts of all sediment. Feces were periodically removed from all trays using a Mirro-brand baster (nylon shaft with rubber bulb) to prevent reingestion of defecated material.

Upon completion of the purging period, I moved the five tagged *H. atra* specimens back into the cement holding tank to feed on sediment for three hours. After the three-hour feeding period, I placed the five specimens back into the "apartment complex" of trays to collect feces material during the next 24 hours. The defecated sediment sample was collected using a baster and placed into plastic cups which were numbered corresponding to the specimen number. The collection of fecal pellets from the specimens was completed within 24 hours or less following the feeding period.

All sediment samples were rinsed three times with freshwater to remove any saltwater residue prior to final drying and weighing. The

rinse water was decanted, and the samples were dried at 85°C overnight using a Fisher Scientific 'Isotemp Oven.' Dried sediment samples were bagged either in 4 oz. Nasco 'Whirl-Paks' or small, 6.5 cm<sup>2</sup> Zip-loc bags. I repeated the above procedures until all 48 specimens had been used in the trials. At the end of the fieldwork, I brought the 48 sediment samples back to a UC Berkeley laboratory where I measured and recorded their final weights using a Denver Instrument scale (model # XL-6100).

While on Moorea, I returned to my study site at Haapiti to take density measurements of *H. atra* in their natural environment. This was necessary so that I could extrapolate my experimental findings of average individual sediment turnover per unit time to the natural population of *H. atra* living on the Haapiti reef flat. I first set up a 50 m transect across the reef flat that ran perpendicular to the shoreline and started at the low water line. I then used a Texas Instruments TI-85 graphing calculator to generate sets of random four-digit numbers. Each one of these four-digit numbers was used to randomly select plots on the reef flat to take quadrat measurements in the following way: I took the first two digits from each four-digit number and paced out that many steps from the beginning of the transect. If the last two digits of the four-digit number formed an even number, then I paced off that many steps to the right, perpendicular to the transect line and parallel to the shoreline. Conversely, if the last two digits of the four-digit number formed an odd number, then I paced off that many steps to the left, perpendicular to the transect line and parallel to the shoreline. Once I reached the plot prescribed by the random four-digit number, I used a 1 m x 1 m PVC quadrat to take a density measurement at this particular location. This procedure was repeated 50 times to generate 50 randomly-selected density data observations.

Data analyses were executed using MS Excel 5.0 to determine averages of specimen weight, sediment sample weight, population density, and the respective standard deviations. Mean density measurements and mean sediment sample weights were used to extrapolate an estimation of annual sediment turnover rate per unit area by the population of *H. atra* living on the Haapiti reef flat. Statistical analysis of the data was performed using a t-test described by Brower et al. (1998), and a regression analysis using Excel. These tests were used to determine whether a significant relationship existed between the mean specimen weight and the mean sediment sample weight.

## Results

Weights of *Holothuria atra* specimens varied considerably among individuals. The 48 specimens of *H. atra* used in my experimental trials averaged 50.32 g (DW) ( $s=25.16$ , range=94.9). Figure 4 shows the frequency of specimens in each weight class. The 50-60 g weight class had the highest number of specimens with 10 individuals sampled. Fecal (sediment) sample weights from the three-hour

feeding periods averaged 4.38 g ( $s=2.48$ ). Figure 5 graphically depicts the relationship between sediment sample weights and specimen weights. Statistical analysis of this relationship is described below. Field observations of *H. atra* at the reef flat study site showed an average density of 7.08 individuals  $m^{-2}$  ( $s=4.16$ , min=0, max=19). Descriptive statistics of the data are summarized in Table 1.

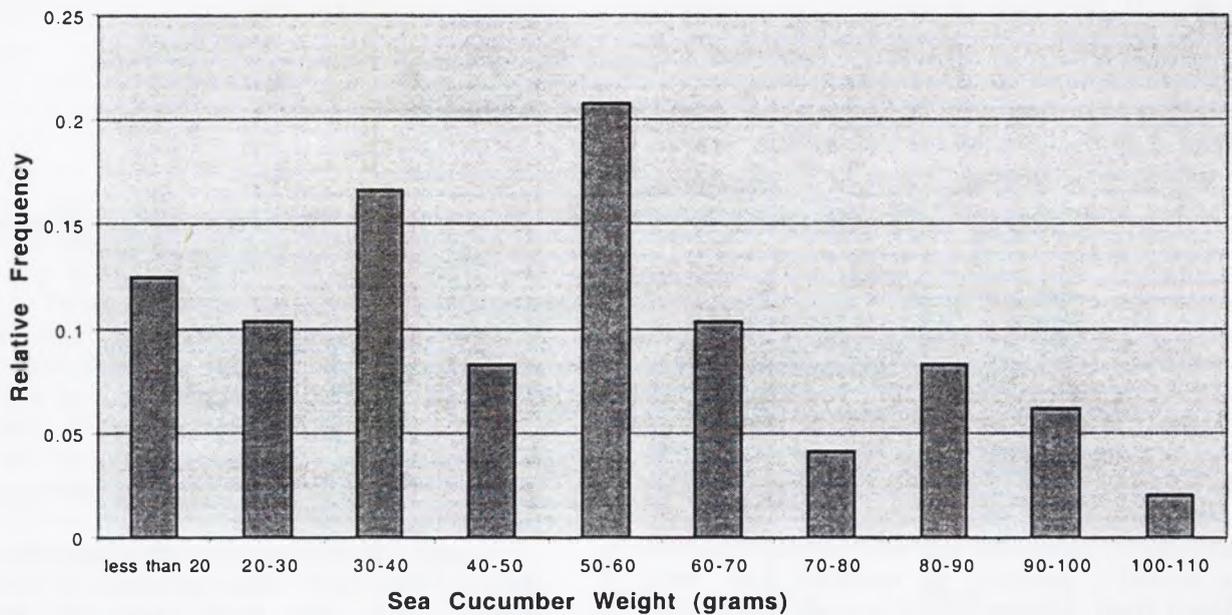


Figure 4. Size Distribution by Body Mass of the Black Sea Cucumber *Holothuria atra*

Statistical tests of the data showed a positive correlation between sediment sample weight and specimen weight. This relationship (Figure 5) was found to be significant ( $t = 7.85$ ,  $P < 0.001$ ) using a t-test.

Data means were mathematically extrapolated to generate a potential sediment turnover rate for the population of *H. atra* living on the Haapiti reef flat. I assumed continuous feeding by *H. atra* which was consistent with my laboratory and field observations. Based on data from the experimental trials, I calculated a

mean sediment turnover rate of 35.00 g individual<sup>-1</sup> d<sup>-1</sup>. This figure was extrapolated to a mean annual sediment turnover rate of 12.78 kg individual<sup>-1</sup>. Computations using average density measurements were used to determine an estimated mean field density of 708 individuals 100 m<sup>-2</sup>. These last two figures were multiplied to calculate a populational sediment turnover rate of 9,046 kg y<sup>-1</sup> 100 m<sup>-2</sup>. A summary of these calculated values can be found in Table 1.

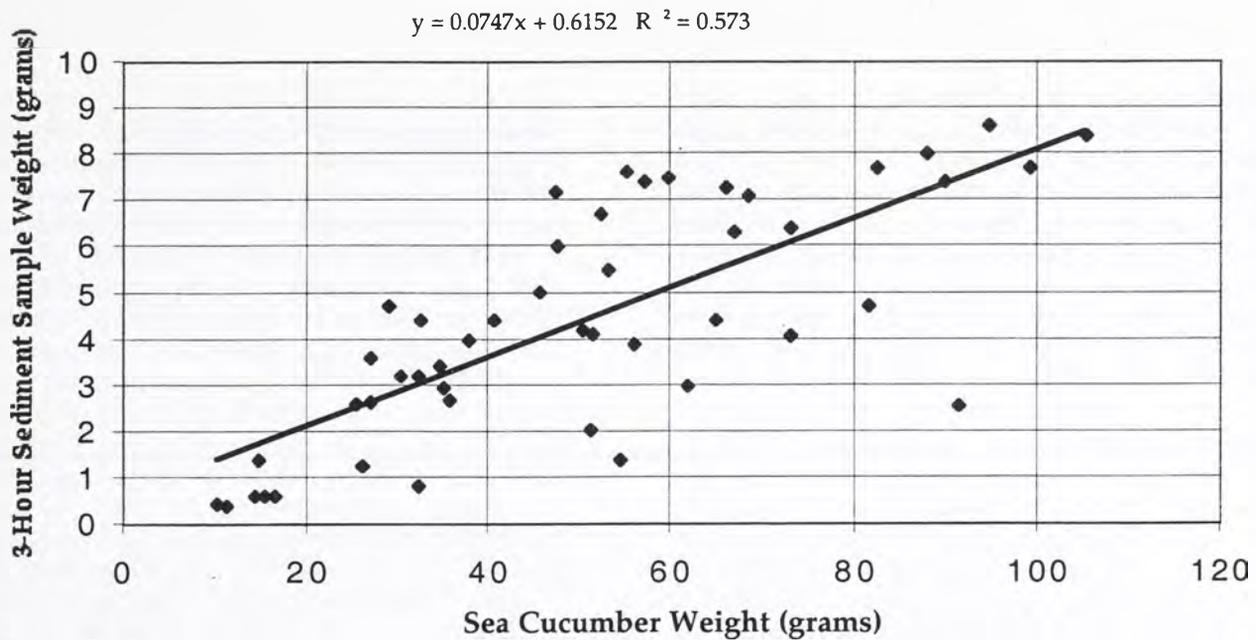


Figure 5. Sediment Sample Weight vs. Specimen Weight

	<i>H. atra</i> Specimen Weights (grams) (n=48)	<i>H. atra</i> Fecal Sample Weights (grams) (n=48)	<i>H. atra</i> Field Density Measurements (per m <sup>2</sup> ) (n=50)
Mean	50.32	4.38	7.08
Standard Error	3.63	0.36	0.59
Median	50.75	4.15	6.50
Standard Deviation	25.16	2.48	4.16
Sample Variance	633.02	6.17	17.34
Minimum	10.24	0.40	0.00
Maximum	105.14	8.60	19.00

Table 1. Summary of Descriptive Statistics

### Discussion

Although many studies of bioturbation by *Holothuria atra* have been conducted (for reviews see Bonham and Held 1963; Stoddart 1969), little is known about the annual turnover rates per unit area for *H. atra*. Still less information is available in the scientific literature on this species' bioturbation activity in French Polynesia. Data from the current study indicate that populations living on reef flats in Moorea, French Polynesia turn over a considerable amount of sediment every year. A

likely explanation for this high level of bioturbation by *H. atra* is that due to the low nutritional content per unit volume of sediment ingested, most sea cucumbers feed continuously on sediment (Uthicke and Karez 1999). Continual feeding and defecating of sediment, together with the high density of *H. atra* living on the reef flat near Haapiti, led to the large sediment turnover rate observed and calculated in this study.

Graphical and statistical analyses of the data indicate that individual amounts of sediment turned over per unit time are directly proportional to the individual's weight (Figure 5). This means that larger, heavier sea cucumbers tend to turn over more sediment than do smaller specimens. One possible reason for this trend is that larger individuals have a greater need for energy, thus requiring more ingestion of sediment to supply the necessary nutrients. Another logical explanation is that larger individuals simply have larger digestive systems that can accommodate and process more sediment per unit time.

Interesting similarities exist between my experimental results of sediment turnover rates and those of other researchers. My results showed an average daily sediment turnover rate of 35 g individual<sup>-1</sup>. Yamanouti (1939) estimated a sediment turnover rate for *H. atra* of 86 g individual<sup>-1</sup> d<sup>-1</sup>; Trefz (1958) projected a value of 200 g individual<sup>-1</sup> d<sup>-1</sup>; and Bonham and Held (1963) showed ingestion of sediment ranging between 144 and 288 g individual<sup>-1</sup> d<sup>-1</sup>. These estimated sediment turnover rates are higher than my findings because the authors studied specimens of *H. atra* that were considerably

larger than those used in my study. This comparison to other studies supports the notion that individual sediment turnover rates are positively correlated to the individual's size and weight. If the sediment turnover rates mentioned above were appropriately scaled down to the specimen sizes used in the current study, the rates would likely be comparable and of the same magnitude.

Uthicke (1999) performed aquarium experiments similar to those used in my procedures. He reported an average sediment turnover rate for *H. atra* of 46.5 g individual<sup>-1</sup> d<sup>-1</sup> (s=28.2). This result is concurrent with my findings considering that Uthicke's specimens averaged 118 g (s=55), and my specimens were of lesser weight, averaging 50.32 g (s=25.16).

Bioturbation rates documented in the scientific literature are similar to my extrapolated annual sediment turnover rate for the population of *H. atra* living on the reef flat near Haapiti. Based on my experimental data and field density observations, I estimated a populational sediment turnover rate of 9,046 kg y<sup>-1</sup> 100 m<sup>-2</sup>. In making this calculation, I assumed that my average from the aquarium experiments accurately estimated the individual sediment turnover rate of the natural populations of *H. atra* studied. In stark contrast to my value, Uthicke (1999) reported a populational consumption value for *H. atra* living on a reef flat near Lizard Island, Great Barrier Reef of 245 kg y<sup>-1</sup> 100 m<sup>-2</sup>. The reason for this apparent discrepancy between our results was a large difference in average density of *H. atra* between the respective field sites. Uthicke recorded an average natural density of 10 individuals 100 m<sup>-2</sup>, whereas I measured an average field density of 708 individuals 100 m<sup>-2</sup>.

Additional documentation exists in the literature regarding natural population densities of *H. atra* in other tropical coral reef environments. Yamanouti (1939) reports up to 53 individuals 100 m<sup>-2</sup> at Palao, Cloud (cited in Stoddart 1969) up to 88 individuals 100 m<sup>-2</sup> in Saipan, Emery (1962) up to 120 individuals 100 m<sup>-2</sup> in Guam, and Taylor (1968) up to 320 individuals 100 m<sup>-2</sup> in Seychelles, though all of these figures are maximum values and the average densities found were much lower. However, as was the case in comparison to Uthicke's observations, these maximum values are much lower than the average density of 708 individuals 100 m<sup>-2</sup> of the *H. atra* population living on the sand flat near Haapiti. This collation supports the conclusion that this population of *H. atra* is extraordinarily dense. One possible explanation for this variance of

densities is that the various populations of *H. atra* studied likely consist of different sized individuals. A population with larger members would likely support lower densities than would a population with smaller individuals. Future studies comparing different populations of *H. atra* would be useful to determine if natural densities are dependent on the average size class.

While most density estimates of natural populations of *H. atra* found in the literature were considerably lower than that demonstrated by the current study, this was not always the case. Kerr et al. (1993) remark that densities of 35 to 52 individuals m<sup>-2</sup> are not uncommon for *H. atra* populations. This observation indicates that some reef flat locations have even higher natural densities of *H. atra* than that found for the Haapiti study site. Christian and Bagnis (1977) state that a high density of *H. atra* near beaches may be indicative of a water pollution problem. Future water quality studies of the Haapiti reef flat habitat are needed to investigate whether or not pollution is a cause of the high density found there.

Although interesting work has been done on the high rate of bioturbation by *H. atra*, little is known about the ecological importance and effects of this sediment turnover on the coral reef environment. Crozier (1918) concluded that the main ecological effect of sea cucumber feeding activity was the transport of sediment from one location to another. While sea cucumbers are not highly mobile, their feeding activity on a populational scale has the potential to rework and transport large amounts of sediment. Other authors assume the main ecological role of deposit-feeding holothurians living on reef flats is the bioturbation of sediment (Bakus 1973; Birkeland 1988). Bioturbation reduces sediment stratification, increases aeration of the sediment, and releases trapped organic material dissolved in the interstitial water. This benefits other organisms living in or on the reef flat and nearby coral reefs because the bioturbation makes available the oxygen and nutrients that would otherwise remain unavailable for metabolic use.

It has also been suggested that holothurians' main role in coral reef ecosystems may be the recycling of nutrients, an important factor in reef ecology (Uthicke 1999; Uthicke and Karez 1999). Uthicke and Karez (1999) further state that bioturbation by sea cucumbers is beneficial to the growth of other reef organisms, especially microalgae. This benefit stems from the large amounts of ammonium excreted by holothurians as a result of metabolic processes

associated with feeding and digestion of sediment. Nutrient regeneration by holothurians and uptake by microalgae is an ecologically important example of the cycling of nutrients within coral reef environments. Additional studies of *H. atra* living on the Haapiti reef flat would be useful to determine the ecological roles of this population's bioturbation activities. If successful studies are developed, we may further explore the relationship between bioturbation by sea cucumbers and coral reef ecology.

### Conclusions

The population of *Holothuria atra* living on the reef flat near Haapiti, Moorea turns over a considerable amount of sediment annually. Average individual sediment turnover rates are comparable to those found by other researchers studying bioturbation rates of *H. atra*. An important factor contributing to the high rate of bioturbation is the extreme populational density of *H. atra* at this study site. Sea cucumbers play

a vital part in the ecology of coral reef environments by contributing to sediment transport, recycling of nutrients, and aeration of the sediment. Thus, the population of *H. atra* studied is a crucial component of the Haapiti coral reef ecosystem.

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# Reproductive ecology of *Freycinetia impavida* (Pandanaceae), a flowering liana of the semi- cloudforest on Moorea, French Polynesia

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**ABSTRACT.** Reproductive ecology is concerned with sexuality, mode of reproduction, and influence of reproductive systems on broader aspects of ecology such as distribution, population structure and both inter- and intraspecific interactions. On Moorea, French Polynesia, the genus *Freycinetia* is represented by both *F. impavida* and *F. moratii*. The latter is restricted to high montane habitat (800+ m elevation) and almost entirely inaccessible for study. Field work was conducted on Moorea during the austral spring, bridging into the beginning of the summer wet season. Germination studies and transects around mature, fruiting vines revealed little to no sexual reproduction. Asexual propagation by stolons is proposed as the primary mode of reproduction for *F. impavida* on Moorea. Asexually derived (and presumably clonal) stolon systems form large stands which dominate the understory. 284 meters of "runners" were followed meter by meter to investigate frequency of branching, leaf distribution, root production and maximum length attained by a single system. Complete stolon systems ranged from 2 m to 27 m, averaging 9.2 m. Frequency of breakage suggests that these stands are composed of a very large number of genetically identical ramets, capable of creating new "individuals" by simply breaking off portions of runners. In many stands, stem density is very high (5 leafy stems/ m<sup>2</sup>) suggesting a great deal of intraspecific competition. However, in a given sampled 1 m<sup>2</sup> quadrat, very few (17%) leafy heads are physically connected to another head in that same quadrat. Competition may therefore occur between stems within a single genet, but rarely between stems within a ramet. Suggestions for further research are discussed, focusing on the use of molecular markers to clarify parentage and conditions of individuality within large stands.

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## Introduction

Reproductive ecology is principally concerned with the sexual condition, reproductive allocation, means of dispersal and resulting population ecology of an organism in question (Willson, 1983). The reproductive ecology of plant populations contributes heavily to the genetic structure of isolated populations (Loveless and Hamrick, 1984), and so may be of interest in issues of plant conservation. Because of their isolation, mid- oceanic islands provide a unique opportunity to study how organisms may cope in the absence of certain reproductive factors, such as coevolved pollinators or a dioecious sexual condition, that may have been present in their place of origin.

The role of sexual reproduction in natural populations has preoccupied biologists since Weismann (Mayr, 1982). More recently, authors (e.g. Harper, 1977; Jenik, 1994) have quibbled over the very use of the term "reproduction." These workers suggest restricting use of "reproduction" to that resulting from a single cell (a zygote), preferring terms such as "vegetative propagation"

or, simply "growth" to describe asexual (or clonal) reproduction in plants. Mishler (1988) points out this distinction is problematic in bryophyte and other plant systems and suggests instead using physiological independence as a criterion for defining reproduction. In the present discussion I follow Williams (1966) in defining sexual reproduction as that resulting in a new combination of parental genes, thus leaving the term "reproduction" to refer to other means of reproduction (e.g. by clones) that Harper would call "growth." The study of clonal growth in plants has received much attention over the last few decades (Herben et al., 1994), especially in angiosperms which are alone in their ability to be facultatively asexual (Mogie, 1992).

*Freycinetia* is a genus of woody climbing and sprawling vines comprised of some 180 species (Wagner et al., 1990), restricted in distribution to the tropical and sub- tropical regions of the Pacific basin. The genus occurs in nearly every island group of the Pacific Ocean from Hawaii in the northeast to New Zealand in the southwest, with

its center of diversity and hence presumed center of origin in the central western Pacific. *Freycinetia* has been studied heavily in the western Pacific, focusing primarily on floral biology and *Freycinetia*'s ability to be facultatively monoecious (Cox, 1982; Cox et al., 1984; Huynh and Cox, 1992), in the otherwise obligately dioecious Pandanaceae. Other studies have dealt with the role of vertebrate pollination, especially by bats, and the role of different pollinators in determining sexual condition (Cox, 1982; Cox, 1984; Cox, 1990; Lord, 1991). Elsewhere (e.g. Hawaii), *Freycinetia* has been studied as it relates to endemic and introduced bird species (Cox, 1983). None of the vertebrate pollinators that visit *Freycinetia* in the plant's western range are known to occur in the Society Islands of French Polynesia, and the depauperate avian fauna of the island chain has uncertain relationships with most of the native flowering plants.

The present study aims to clarify the identity and distribution of *Freycinetia* populations on Moorea, to establish the current means and nature of reproduction, and to determine what effect, if any, this reproductive system has on the population structure of *Freycinetia impavida* on Moorea, French Polynesia.

### Methods

Field studies were conducted on Moorea, French Polynesia, during October and November, 1999. A pilot study surveying the major drainages of the island was undertaken to identify the location, taxonomic identity and extent of living populations of *Freycinetia*. *Freycinetia* populations seem to be highly localized and discrete assemblages of apparently similar individuals. For logistical reasons, only those large populations (area greater than ca. 100m<sup>2</sup>) occurring on the northern portion of the island were included in the study. The six study sites were located on the

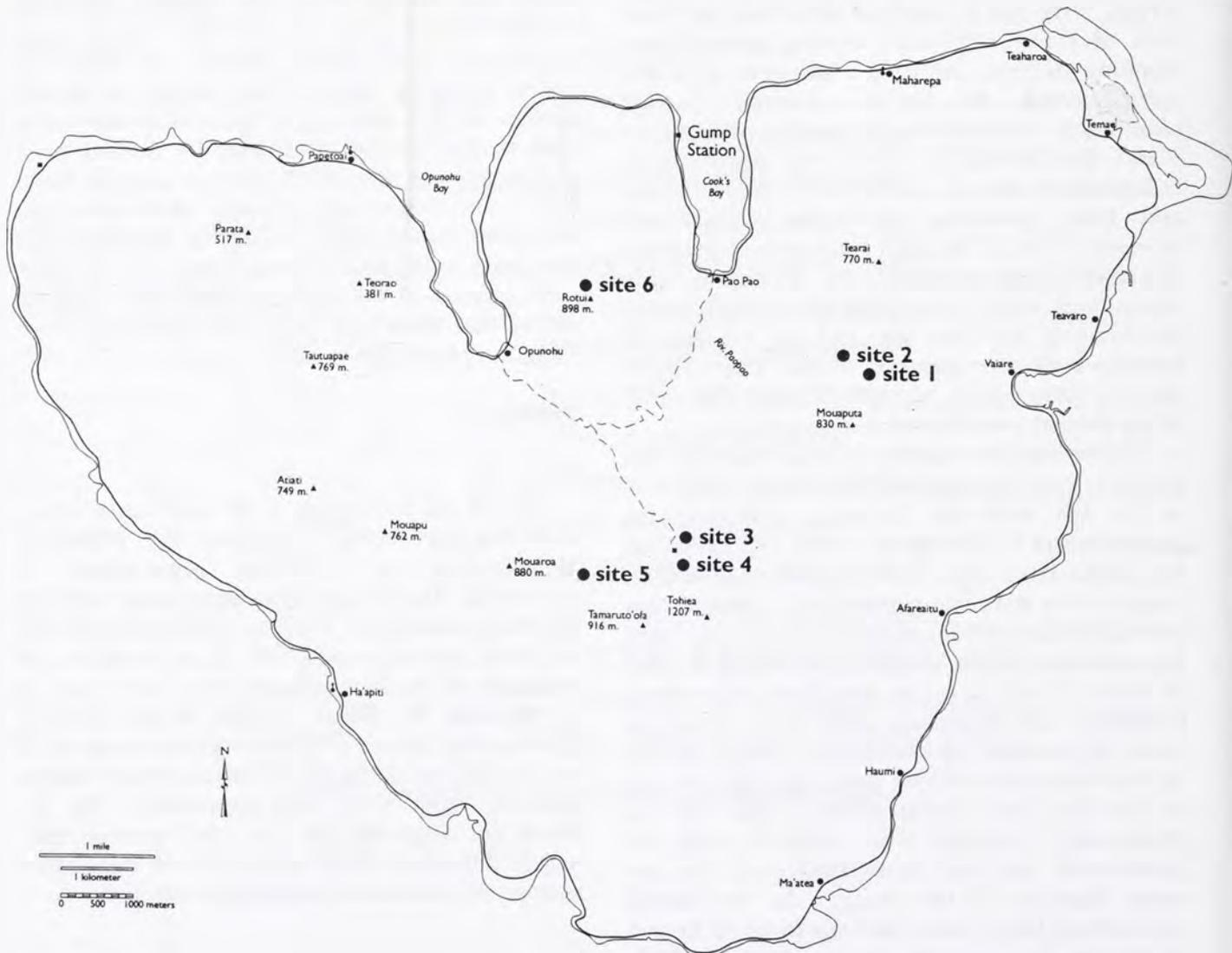


Figure 1. Locations of study and collection sites on Moorea, French Polynesia.

north and west-facing slopes of what remains of the old caldera. Locations of the study sites are shown in Figure 1, and characteristics of the study sites are included in Table 1. With the exception of the Mount Rotui population (elev. 870 meters), all sites were between 200 and 500 meters in elevation and in semi-cloud forest, with annual rainfall in the range of 300-500 centimeters.

To determine the identity of *Freycinetia* populations, field collections of fruit and leaves were compared with those deposited in the Jepson Herbarium at UC Berkeley. Huynh (1995) provided characters for this identification. Four collections of *F. impavida* and five of *F. arborea* were compared with six field collections, focusing on characters of fruit and leaf morphology.

Pilot field studies indicated that all fruiting individuals grow up the trunks of mature canopy trees. To establish the presence or absence of seedlings, four 30 meter belt transects, 2 meters across, were run in cardinal directions out from each of three such large, fruiting plants found climbing in trees. Along the transects, all plants were scored as runner-derived (having identifiable connections to nearby runners or plants and having no below-soil structures) or independent (that is, presumably seed-derived and thus unattached to nearby plants and runners). Due to the high frequency of breakage of *Freycinetia* stems, making the distinction as to origin was often quite difficult; in such cases, surrounding soil was searched for evidence of recently broken or decaying stems. Plant height, distance from parent, number of leaves and width of the stem at ground level were recorded.

To estimate the viability of field-collected fruit samples, two germination experiments were run in the lab while on Moorea. Following the suggestion of P. Cox (pers. comm, Oct 1999) that *Freycinetia* seeds may require partial digestion by mammals to stimulate germination, I treated ripe (orange, fleshy) field-collected fruits in 5% acetic acid solution (white vinegar) for varying lengths of time (Table 2). In the first experiment, following acid treatment, seeds were placed on moist tissue paper in closed petri dishes and left on a windowsill receiving direct sunlight for part of the day, and bright indirect light for the remainder. Samples were checked daily for germination and kept moist throughout the six-week duration of the study. In the second experiment, longer time intervals (6 hr, 12 hr and 24 hr) of acid treatment were used, and a shade

growing condition was added to more accurately mimic the light levels of the soil where *Freycinetia* was found growing.

In an effort to understand the population dynamics of the expansive runner systems, thirty runners were randomly chosen from two populations and followed until endpoints (either physical breaks or terminal leafy stems) were reached at both ends of the stem system. For each runner, ten meters were mapped in detail, recording number of leafy stems, number of leaves per stem, breaks, branches, fate of each branch and root innovations per meter. In those cases where the total runner section length exceeded 10 meters, nature and fate of branches beyond 10 meters were qualitatively described and sketched.

To estimate population density and structure of the large stands of *Freycinetia*, nine 50 meter transects were randomly chosen from four populations. One m<sup>2</sup> quadrats were sampled every five meters along the transect, counting number of runners crossing the transect line, number of leafy stems, number of branching points along the runners, and number of breaks (ends). Because stem width has a minimum value (due to the method of growth, see below), non-parametric statistics were used to analyze these data. The 'relatedness' of leafy stems was also estimated within each quadrat by following the stem back to the nearest branching point. If a new stem located in the same quadrat came directly out of that branching point, the two stems were scored as physically related.

## Results

### *Taxonomy*

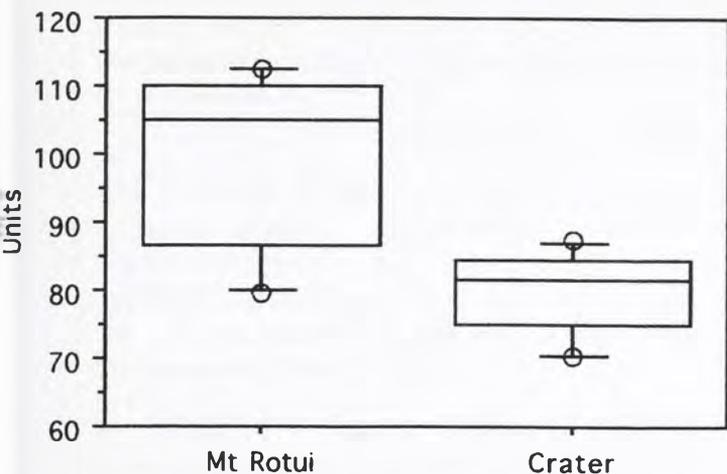
Based on herbarium work and comparison with Huynh (1995) I propose the following identification for Moorean populations of *Freycinetia*: The Mount Rotui population is likely the newly described *Freycinetia moratii* Huynh, and the lower elevation congener found in all major drainages at moderate elevation in deep shade is *F. impavida* BC Stone. Fruit length differed significantly between the two species (student t-test:  $t=4.87$ ,  $p=0.028$ ,  $df=6$ ) between fruit lengths collected from these two populations (Fig 2). While not diagnostic by itself, the reported fruit length difference lends weight to the qualitative assessment made from herbarium collections.

Site number	Name	Elevation	Conditions	Study
Site 1	Vaiare ridge	460 meters	Fairly dry ridge with short canopy	Parent transect, fruit difference
Site 2	Pao Pao slope	300 m	Fairly wet mesa on steep slope	50 meter transect, runner- following
Site 3	Belvedere area	240 m	Rainforest slopes dominated by <i>Inocarpus</i>	50 meter transect, runner- following, germination expt.
Site 4	3 Cocos trail	290 m	Rainforest slopes dominated by <i>Inocarpus</i>	Parent transect, fruit difference
Site 5	3 Cocos junction	250 m	Rainforest flatland at base of steep slope	Parent transect
Site 6	Mount Rotui	870 m	Dry, steep ridge and slopes, dominated by <i>Dicranopteris</i>	Relict <i>F. moratii</i> population

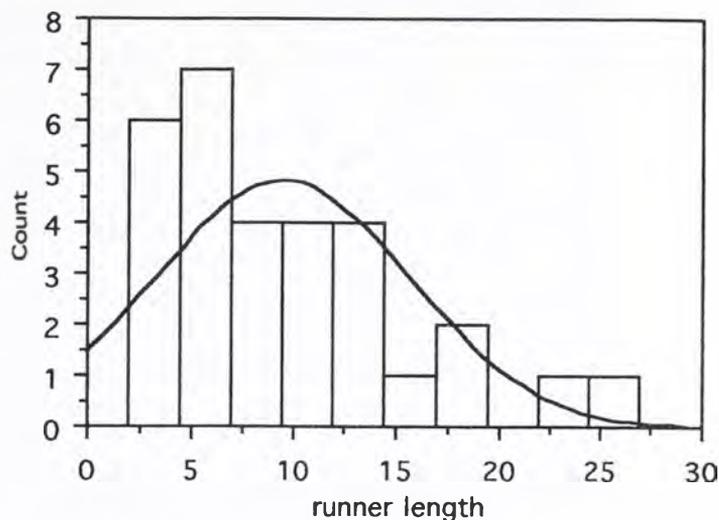
**Table 1.** Characteristics and use of study sites.

Experiment	Acid treatment (5% Acetic Acid)	Growing conditions
1.1	dipped	Indirect sunlight on moist paper
1.2	1 minute	Indirect sunlight on moist paper
1.3	5 minutes	Indirect sunlight on moist paper
1.4	30 minutes	Indirect sunlight on moist paper
1.5	1 hour	Indirect sunlight on moist paper
1.6	24 hours	Indirect sunlight on moist paper
2.1	6 hours	Indirect sunlight on moist paper
2.2	6 hours	Deep shade on moist paper
2.3	15 hours	Indirect sunlight on moist paper
2.4	15 hours	Deep shade on moist paper
2.5	24 hours	Indirect sunlight on moist paper
2.6	24 hours	Deep shade on moist paper
2.7	6 hours	Deep shade in moist soil (collected at site 3)
2.8	15 hours	Deep shade in moist soil (collected at site 3)
2.9	24 hours	Deep shade in moist soil (collected at site 3)

**Table 2.** Treatments and growing condition for germination study.



**Figure 2.** Distribution of fruit lengths between two sampled populations. Mt. Rotui population is *F. moratii* and Crater population is *F. impavida*. Units are millimeters, horizontal lines indicate population means and vertical bars are 95% confidence intervals. Circles are significant outliers.



**Figure 3.** Distribution of maximum length reached by runner systems (in meters)

#### Reproductive condition

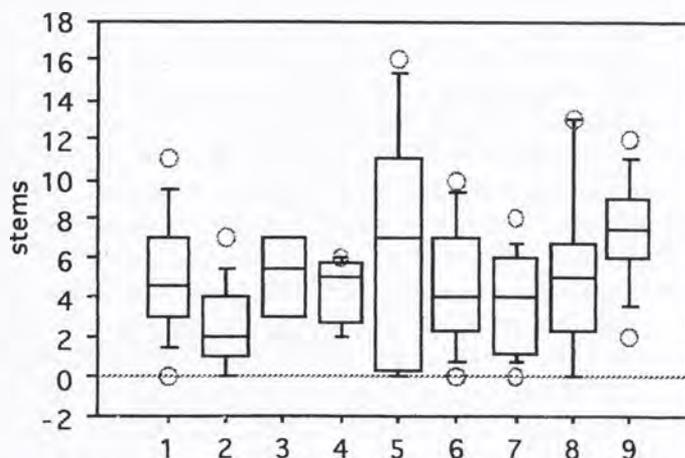
In the 30 meter transects radiating out from fruiting individuals, two plants were scored as independent compared with 73 scored runner-derived. Plant height did not vary significantly with distance from parent (1-way ANOVA  $F=3.35$ ,  $p=.071$ ), nor did plant width vary significantly with distance (Kruskal-Wallis test  $H=7.2$ ,  $p=0.21$ ). Plant density per meter along these transects was 0.1 stems/  $m^2$ .

No seedlings were observed during the germination study, although one non-*Freycinetia* seedling, an unidentifiable dicotyledon, was observed, indicating that the soil could support life.

#### Asexual reproduction

In the runner-following study, 186 meters of runners were measured meter by meter, and an additional 98 meters were qualitatively described. Mean runner length was 9.47 m (Standard Error= 1.13 m,  $N=30$ ). With the exception of two outliers, all sampled runners remained below 20 meters in total system length (Figure 3). Along the runners, leafy stems averaged 38 leaves/head (SE= 1.17,  $N=41$ ) with a maximum of 56 leaves in one head. Runner systems produced a mean of 11.36 leaves/ meter of stem (SE= 0.81,  $N=30$ ) and a mean of 1.15 roots/ meter of stem (SE= 0.77,  $N=30$ ). In general, roots were produced more frequently in lengths of stem without leaves. Roots were found to grow from horizontally-propagating runners and to enter

the ground, but were also abundant on vertically-growing runners, providing support by anchoring the runner to the substrate. There was a strong correlation between system length and mean runner width (1-way ANOVA,  $F=30.42$ ,  $p<0.0001$ ,  $df=28$ ), but no significant correlation between the number of roots produced per meter and total system length or mean runner width. Leafy heads or physical breaks always marked the ends of runner systems. On only one occasion was a runner found to enter into the soil for more than a few centimeters.



**Figure 4.** Number of leafy stems per quadrat along each of the nine transects. Horizontal lines indicate population means and vertical bars are 95% confidence intervals. Circles are significant outliers.

### Population structure

Along the 50 meter transects, the density of leafy stems was five per m<sup>2</sup> (SE= 0.4, N= 85). Despite this high density, 16.9% of sampled stems were physically connected to another stem in the same quadrat. Runner density varied more within populations than between them (1- way ANOVA F= 1.16, p= 0.33) as did stems per quadrat (1- way ANOVA F= 1.65, p= 0.12, see figure 4). Strong correlation was found between number of runners and number of stems in a quadrat (1- way ANOVA F= 116.9, p<0.0001) and between number of "ends" (or breaks) and number of branches (1- way ANOVA F= 24.07, p< 0.0001).

### Discussion

#### Possible causes for lack of sexual reproduction

The lack of effective germination in the laboratory study and the small number (two) of putative seedlings in the field suggest that sexual reproduction is infrequent- if occurring at all- on Moorea at the present. The apparent sterile condition of what appear to be mature, ripe fruits may be indicative of several barriers to sexual reproduction. First, the pollinator that *Freycinetia* is adapted to elsewhere may be absent on Moorea. In Samoa and mainland areas further west, *Freycinetia* is fertilized exclusively by large fruit-eating bats (Cox, 1984). In these areas, floral morphology is such that only these bats may efficiently pollinate *Freycinetia*. No such bats occur on Moorea. On Hawaii *F. arborea* was historically pollinated by the native Drepanid birds, but after the extinction of several of these species an introduced bird, the Japanese white-eye (*Zosterops japonica*), proved an effective substitute for the Drepanids and now frequents *F. arborea* (Cox, 1983). Introduced pollinators may have arrived so recently that they have not started habitually visiting *Freycinetia*, or the plant may have been fertilized by one of Moorea's now- extinct native birds.

A second factor causing sterility may be the lack of male plants. In some parts of its range, *Freycinetia* has been known to become monoecious in the absence of co-evolved pollinators and thus increase the chance of self- fertilization (Cox et al., 1984). Moorean populations may be incapable of doing this, or the necessary mutation may simply not yet have arisen by chance. Under any of these scenarios, fruit observed on Moorea may have developed from unfertilized female flowers. The

lack of sexual reproduction may have important implications for *Freycinetia*'s ecology and genetic structure on Moorea.

#### Implications of asexual reproduction

The traditional assumption that asexual reproduction reduces genetic diversity within populations has been questioned in recent years (see review in Widen et al., 1994). Loveless and Hamrick (1984) reported high levels of within-population genetic diversity (based on  $H_s$ , expected heterozygosity) in both sexually and vegetatively propagating species. Interpopulation genetic diversity ( $G_{ST}$ ) was found to be high in hermaphroditic and autogamous species, a feature that promotes inter- population divergence. *Freycinetia*'s asexual reproduction might lead to differentiation between populations on Moorea, and even greater between- island differentiation. If *Freycinetia* is able to maintain high  $H_s$  despite its asexual condition, it may avoid problems such as susceptibility to disease and inability to colonize new habitat which often plague low- diversity populations.

Mishler (1988) reviewed a prevailing consensus among ecologists that asexual reproduction is favored in spatially unpredictable environments "where colonizing and rapid clonal growth are important," whereas sexual reproduction is better suited to so- called K- selecting environments. The clonally reproducing *Freycinetia* populations examined in the present study represent an important departure from this general statement. If these large stands do indeed represent a single genotype- a genotype which, considering the expansive and dominating nature of the stands it forms, is very successful- then asexual reproduction is favored because it allows the genotype to persist in an environment for which it is clearly well suited. By reproducing asexually, only the youngest and healthiest physical manifestations of the same successful genotype carry the genetic information forward, unaltered by the disrupting forces of meiosis. Such a strategy for the 'good of the genotype' is analogous in some ways to the notion of the 'selfish gene' (Dawkins, 1989). I argue that asexual populations such as the ones investigated here are perhaps more effective in stable, spatially predictable, environments than is the sexually reproducing alternative.

#### Asexual propagation

*Freycinetia* is known to be a vigorous asexual reproducer (Talley et al., 1996). However, little if any work has been done on the mechanism of

asexual propagation in the genus. I propose that *Freycinetia's* ability to dominate the forest understory on Moorea is made possible by a rapidly growing and flexible system of stolons, allowing for frequent breakage of stems and thus "reproduction" in the asexual, vegetative, non-Harperian sense. What appear to be "runners" the brown structures that form an extensive net across the forest floor- are actually stems lying flat (see Figure 5). Following one of these stems will invariably lead to a leafy head which is always actively growing, with a finite number of leaves as described above. Once shaded by newer leaves at the top, leaves at the base of the head drop off, revealing the stem. As these leafy heads continue to grow upwards, the weight drags the stem down, making it appear as though the stems propagate horizontally. Thus in the absence of a climbing substrate, there is a maximum height these heads may reach above the forest floor. The horizontal stems (stolons) may sprout adventitious buds, which appear initially to be a different growth form from the heads just described, but over time they will become indistinguishable from any other leafy head in the system. Upon breaking off, these new stems will become independent (though genetically identical to the "parent") systems (ramets). Over time, an overhead view of a stand of *Freycinetia* may reveal that the heads migrate about in a somewhat chaotic fashion, with their lengthening stolons trailing behind.

#### *Population structure*

The product of the mechanism of propagation just described is a very dense, apparently random assemblage of genetically related ramets. Greater within- transect than between- transect variation in density suggests that spatial clumping on a microscale is not present. There does appear to be a large amount of clumping on an island- wide scale, however. The low physical relation of ramets (17%) within a given space indicates that while there may be little competition for light, soil nutrients, and climbing substrate within physically- connected and physiologically- dependent stem systems, there is likely to be a good deal of competition between ramets (within a genet). Such competition shows the utility of Mishler's (1988) concept of physiological independence for delineation of individuals. A genetic consideration of individuality would likely produce a very complicated and self-contradicting picture of competition in asexual populations such as those described here. De

Kroon (1993) notes that the past assumption that the ability of clonal plants to control shoot dynamics- especially self- thinning by an individual- through physiological integration is perhaps overstated. This observation is supported by the finding in the current study that stolon systems remain fairly short, and that physically related stems rarely grow close together.

Several interesting insights can be gained from the study of population density. No flowering or fruiting plants were found in the large stands (e.g. those in which the 50 meter transects reported 5 stems/ m<sup>2</sup>). The five fruiting plants I observed were in comparably non- dense stands of *F. impavida*, averaging just 0.1 stems/ m<sup>2</sup>. This marked difference between population densities of plants investing in sexual versus asexual reproduction echoes Weiner's (1988) assertion that low- density environments tend to stimulate sexual effort, whereas more biomass is invested in vegetative reproduction (Harper's "growth") in high- density situations.

According to the model of Janzen and Connell (Janzen, 1970), there should be a marked decrease in numbers of young, presumably offspring, plants near mature adults. (Janzen and Connell assumed sexual reproduction in their model, but the model should hold for asexual propagation as well, if not more so, because of the role pathogens play in restricting genetically similar offspring.) No significant correlation between distance and plant size was observed in the transects taken around fruiting plants, supporting the findings of Condit et al. (1992) that the Janzen- Connell hypothesis is not widely supported among tree species. However, this observation may instead reflect a bias of scale in the present study (in which only 30 meters were sampled), or those other considerations of population density and reproductive strategy discussed above.

Some of the more descriptive findings of this study should come as no surprise. The tight positive correlation between runner length and runner width likely reflects the age of these larger individuals, and might be useful for dating such systems. The greater thickness of older stems may prove interesting in its effect on structural stability, as there could be a positive feedback that permits large stems to get even larger by reducing the chance of breakage. Leafy stem density should correlate positively with the number of stolons running beneath such stands, a prediction well supported by the present study. The high number of leaves per meter of stolon (11.36) relative to

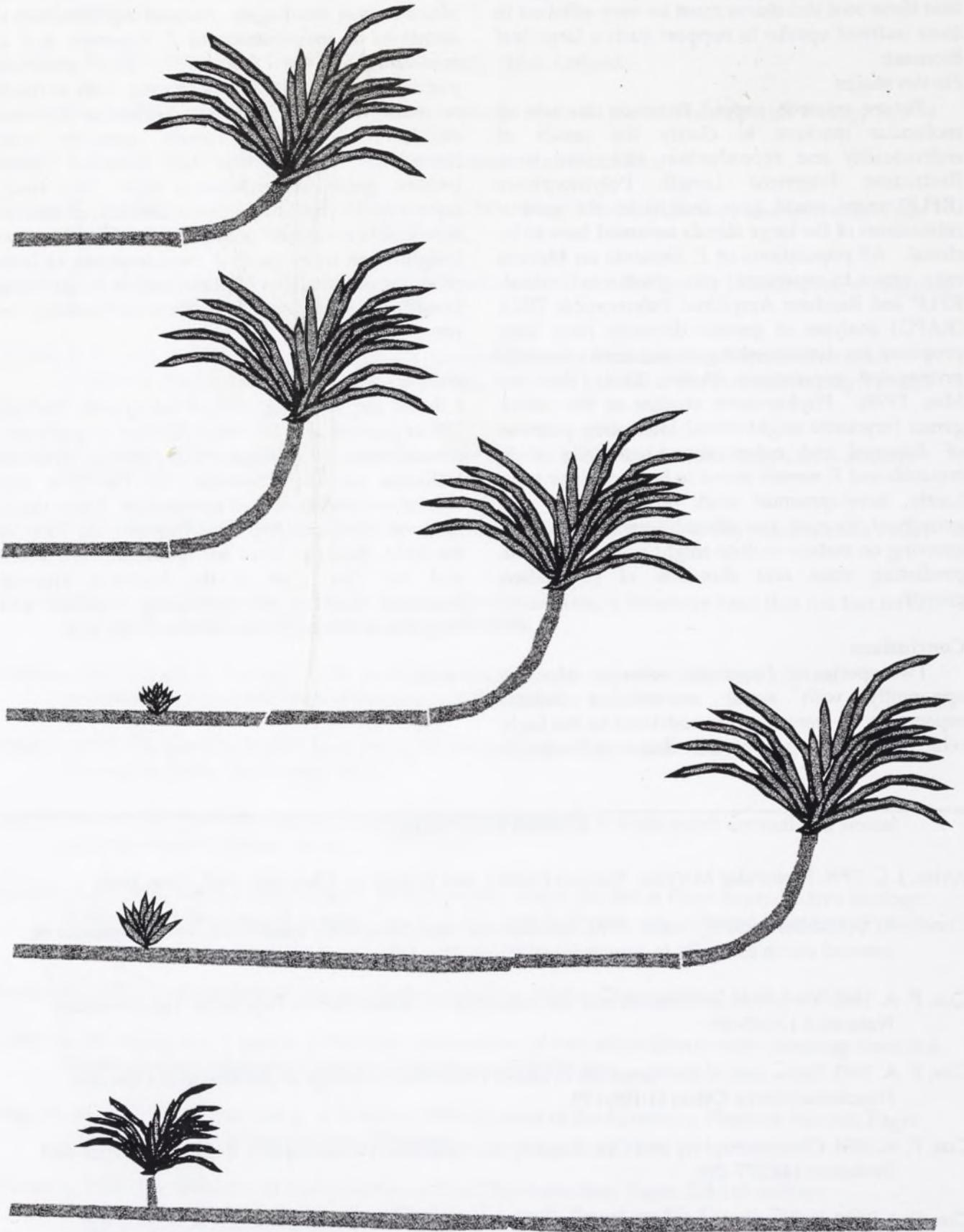


Figure 5. Proposed mechanism of asexual reproduction. See text for discussion.

number of roots per meter of stem (1.15) suggests that these root structures must be very efficient in their nutrient uptake to support such a large leaf biomass.

#### Further studies

Future research should focus on the use of molecular markers to clarify the issues of individuality and reproduction addressed here. Restriction Fragment Length Polymorphism (RFLP) maps could give insight to the genetic relatedness of the large stands assumed here to be clonal. All populations of *F. impavida* on Moorea may prove to represent one genetic individual. RFLP and Random Amplified Polymorphic DNA (RAPD) analyses of genetic diversity have been proposed for distinguishing sexual from asexually propagated populations (Avise, 1994; but see Mes, 1998). Phylogenetic studies of the entire genus *Freycinetia* might reveal interesting patterns of dispersal and colonization, especially if *F. impavida* and *F. moratii* prove to be non-sister taxa. Lastly, developmental work on the origin and growth of the root and adventitious stems found growing on mature stolons might prove helpful in predicting rates and direction of population growth.

#### Conclusions

Two species of *Freycinetia* occur on Moorea, apparently with some amount of habitat separation. *F. moratii* seems restricted to the high, relatively dry slopes of Mt. Rotui, whereas *F.*

*impavida* occupies the wetter, shadier forests of the island's river drainages. Asexual reproduction is dominant in populations of *F. impavida*, and is accomplished by stolons. The resulting population structure is very chaotic, with as much or more variation in density within as between stands. Individual ramets compete with themselves infrequently, but between ramet (within-genet) competition is high. This study represents the first careful consideration of asexual reproduction in the genus, and should prove insightful in more general considerations of both modular construction of plants and in the growing literature considering the effects of clonality on competition.

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# Distribution, Abundance, and Habitat Relationships of Terrestrial Land Birds of Moorea, French Polynesia

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**ABSTRACT.** I assessed the abundance, distribution, and habitat preferences of thirteen of the nineteen resident species of landbirds that survive in Moorea, French Polynesia. Five terrestrial habitats were sampled, of which are previously unmentioned in ornithological literature. These habitats vary in species composition, structural complexity, and level of disturbance. I conducted circular plots along transects, and placed each count location into one of the five habitat categories: 1) native *Hibiscus* forests 2) native *Inocarpus* forests 3) coconut plantations 4) pine plantations and 5) home gardens. Of the thirteen species of landbirds that were encountered, eleven are introduced and widespread, ten of which are omnivores that have become fully established. The remaining two species are endemic. The Tahitian Kingfisher (*Halycon venerata youngi*), a native insectivore, and the Gray-green Fruit Dove (*Ptilinopus purpuratus frater*), a native frugivore, rely on fewer sources for nutrition than omnivores and may be more sensitive to constraints of insularity. This may account for why five of the six species of landbirds that were not encountered, were native insectivores; their current status remains unknown. Due to the high proportion of introduced species, species richness and abundance are greater in highly disturbed structurally complex habitats than in native forests. There were more introduced species in more disturbed, introduced habitats. Native species, however, were found more abundantly in less-disturbed native habitats. Overall, structural complexity of the habitat plays a greater role than the level of disturbance in determining abundance, distribution, and habitat relationships of landbirds on Moorea.

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## Introduction

One important characteristic of island bird populations is that they have a high number of endemic species (Thibault and Rives 1988). However, due to islands' restricted geographical area, where the arrival of new immigrants is rare, many factors threaten the extinction of island birds. The islands of French Polynesia, far from any continental landmass, are often cited as an example of an isolated ecosystem, with a small number of birds species, relatively many of which are unique to a particular island (Thibault and Rives 1988).

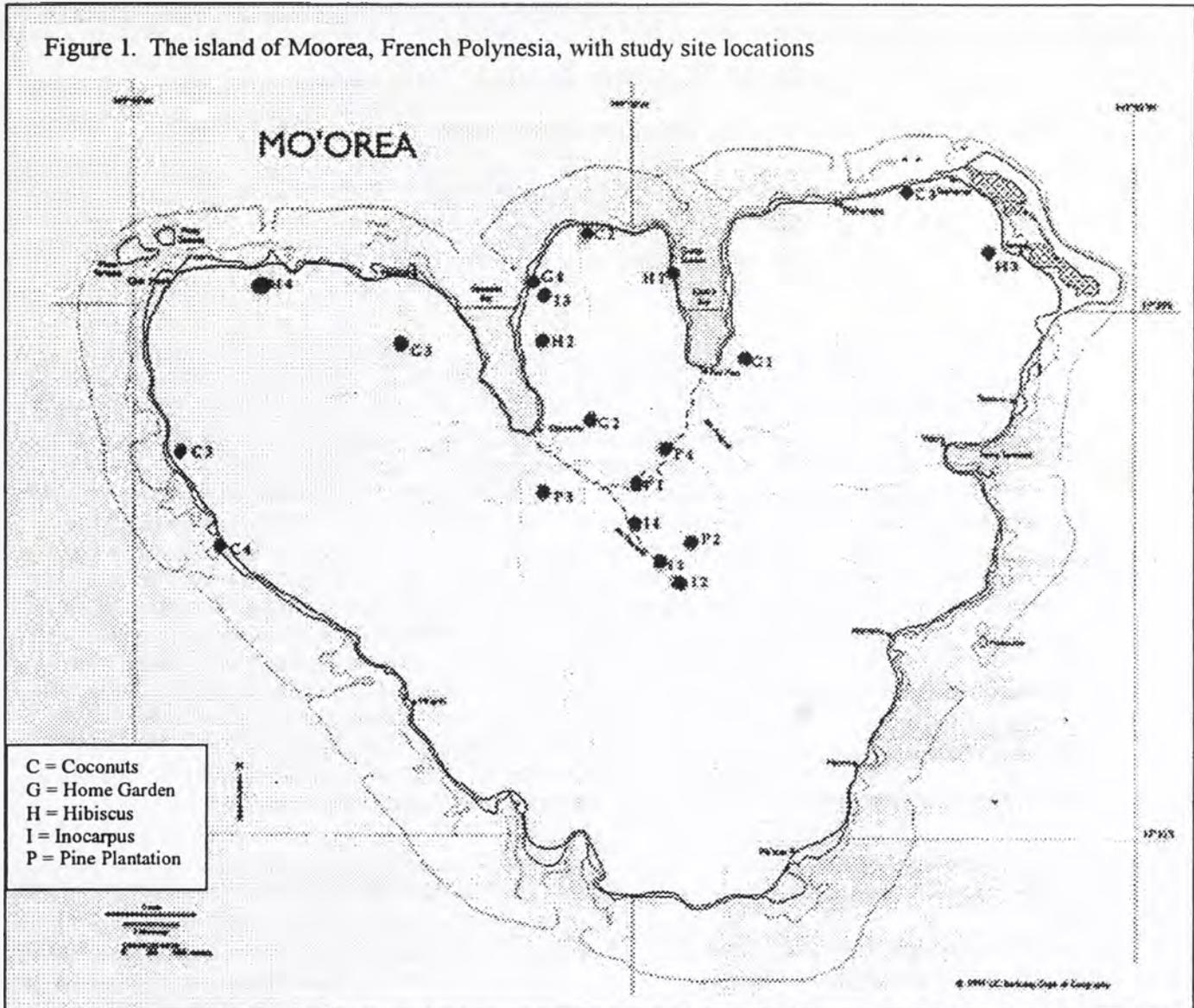
The island of Moorea, French Polynesia currently has a low diversity of land birds, consisting mainly of introduced species. There are nineteen different species of nesting landbirds found on Moorea, eleven of which are recent introductions that have become well established (Thibault and Rives 1988).

Archeological sites on Moorea indicate continuous human occupation for the past 1,500-2000 years. One consequence of this human occupation has been the loss of most indigenous species of birds (Steadman 1997). At least six nesting land birds have become extinct over the past 200 years (Thibault and Rives 1988).

Another result of human occupation is disturbance to native vegetation. The vegetation on Moorea is a mosaic of dense and open undisturbed native forests (native *Inocarpus* and *Hibiscus* stands), successional or disturbed forests (e.g. forestry plantations), active agricultural plantations (e.g. coconuts), and home gardens.

This study reports the species that were encountered and how abundantly they occur on Moorea, within five habitats: 1) native *Hibiscus* forests 2) *Inocarpus* forests 3) coconut plantations 4) pine plantations, and 5) home gardens. These habitats vary in structural complexity and level of

Figure 1. The island of Moorea, French Polynesia, with study site locations



disturbance. Based primarily upon transect surveys, I assessed the distribution, abundance, and habitat relationships of native land birds in Moorea, French Polynesia.

Studies of birds in Polynesia have been based primarily on sight/sound records (Steadman and Freifeld 1998). The birds of Moorea are treated in a general manner in regional books such as Pratt et al. (1987). Despite of accounts of selected species on Tahiti (Thibault and Rives 1988), descriptions of ecology and behavior of any land bird species on Moorea is unknown or poorly documented. Surveys such as this, provide a first look at the incidence and abundance of land birds in various habitats on Moorea. Using similar methods on a regular basis and ideally throughout the

year, these surveys can be an efficient way to monitor bird populations (Steadman and Freifeld 1998).

I hypothesized that 1) bird species richness and abundance increase as structural complexity increases; 2) due to the high proportion of introduced species, the structural complexity of the habitat plays a greater role than the level of disturbance in determining bird species distribution, abundance, and habitat preference; and 3) native birds are more abundant in native less disturbed habitats.

## Methods

### *Habitat Categories*

I selected five terrestrial habitats of Moorea: home garden, open canopy coconut

Habitat type	Habitat characteristics	Level of Disturbance	Structural Complexity
1. Home garden	Active cultivation of a large diversity of non-native crops comprising five vertical strata; ground cover grass, bare soil, or roads	5	5
2. Open Coconut Plantation	Open canopy; upper canopy comprised only of Coconut trees; understory controlled with fire; no regeneration by native tree species	4	2
3. Wooded Plantation/ Early successional forest	Semi-open canopy; dominant trees non-native pine, codominant trees comprise second vertical strata, and dense understory of both native and non-native species	3	4
4. Mature <i>Inocarpus</i> Forest	Nearly closed canopy of predominantly native species; rather open understory of primarily native fern species	2	3
5. Mature <i>Hibiscus</i> Forest	Closed extremely dense canopy of native <i>Hibiscus</i> ; Little to no understory plants, ground cover primarily bare soil	1	1

Table 1. Characteristics of habitat types in Moorea (5=high 1=low).

plantation, forestry plantation, and native *Hibiscus* and *Inocarpus* forests (Table 1).

Four sites at each of the five habitats were sampled totaling twenty sites (Figure 1). A random number table determined the sampling order of these sites. Sites were chosen on the basis of their plant community composition, level of disturbance, and structural complexity. Level of disturbance was determined by the amount of human intervention over time. Structural complexity was determined by observing vertical stratification within the foliage height diversity comprising each habitat. The five habitat sites are described as follows:

#### 1. Native *Hibiscus* Forest

This forest type was comprised of one dominant plant genus, *Hibiscus*. The first site was located on the northwest side of Cook's Bay approximately 15m west of Black Rock (17°29'37"S, 149°49'59"W). The second site was located at the head of Opunohu Bay directly west of Opunohu River by 25m (17°31'17S, 149°50'56W). The third site was located in a small valley on the northwest side of the island (17°29'44S, 149°54'05W). The fourth site was located on the northeast side of the island approximately 150m from Temae public beach (17°29'53S, 149°45'28W). Structural complexity at each site ranked a 1 (on a 1-5 low-high scale) due to the single vertical

strata comprised of *Hibiscus* averaging a foliage height of 9.2 m. Level of disturbance at each site ranked a 5 (on a 1-5 low-high scale) because it is a relatively dense forest with few signs of recent human intervention.

#### 2. Coconut Plantation

The coconut plantations were comprised of coconuts (*Cocos nucifera*) in the upper canopy, and *Mimosa pudica* and *Poacea* species in the understory ground cover. The first site was located on the northeast side of Moorea (17°31'23S, 149°52'16W); the second site on the northeast side of Opunohu Bay (17°29'46S, 149°51'02W); the third site on the southwest side of the island (17°29'47S, 149°53'35W); and the fourth site also on the southwest side of the island (17°32'16W, 149°54'07W). Structural complexity at each site ranked a 2 due to the two vertical strata layers in which *Cocos nucifera* existed in the upper canopy at an average height of 19.4m and *Mimosa pudica* and *Poacea* species existed in the lower strata ground cover at an average height of .1m. The level of disturbance was ranked a 4 because of the heavy use of fire for understory removal.

#### 3. Native *Inocarpus* Forest

The native *Inocarpus* forest was comprised of an upper canopy dominated by *Inocarpus fagifer*, a mid canopy

comprised of mainly *Pandanus tectorius*, *Hibiscus*, and *Acacia* species, and a lower canopy comprised of *Miconia calvensis*, *Freycinetia impavida*, *Angiopteris*, and other fern species. The first, second, and third sites were located approximately 4.4km (first site), 5.2km (second site), and 3.5km (third site) from the head of Opunohu Bay up the single paved road that runs through the valley. The fourth site was located approximately 1km inland from the southwest edge of Opunohu Bay. Structural complexity at each site ranked a 3 due to the three vertical strata layers. *Inocarpus fagifer* existed in the upper canopy at an average height of 24.5m, *Pandanus tectorius*, *Acacia* and *Hibiscus* species existed in the mid strata at an average height of 7.7m, and *Angiopteris*, *Miconia calvensis*, *Freycinetia impavida*, and other fern species exist in the lower strata at an average height of 1.5m. The level of disturbance was ranked a 2. This forest type is considered mature and relatively undisturbed except for a few hiking trails.

#### 4. Pine Plantation

The pine plantations were comprised of Caribbean pine (*Pinus caribaea* var. *hondurensis*) in the upper canopy, with a mid canopy comprised of mainly *Inocarpus fagifer* and *Acacia* species, and a lower canopy comprised of mainly *Lantana camara*, *Stachys decemdentata*, *Dichranopterus linearis*, and *Mimosa pudica*. The first and second sites were located in Pao Pao Valley on the north side of the island, approximately 3.7km (first site) and 3.0km (second site) from the head of Cook's Bay. The third and fourth sites were located in Opunohu Valley on the northwest side of the island, approximately 5.0km (third site) and 1.2km (fourth site) from the head of Cook's Bay. Structural complexity at each site ranked a 4 because the strata layers were seen more frequently in the pine plantations than in the *Inocarpus* forest. In the three vertical strata layers, *Pinus caribaea* var. *hondurensis* dominated the upper canopy at an average height of 25.2m. *Inocarpus fagifer* and *Acacia* species exist in the mid strata at an average height

of 4.2m. *Lantana camara*, *Stachys decemdentata*, *Dichranopterus linearis*, and *Mimosa pudica* comprised the lower strata at an average height of 0.8m. This habitat was categorized as wooded plantation/early successional forest because native woody species begin to reoccupy plantations in the understory. The level of disturbance was ranked a 3. In active plantations the land is usually cleared again before or just as the native species begin to develop a canopied secondary forest.

#### 5. Home Gardens

The home gardens comprised a number of different agricultural crops, resulting in the greatest number of foliage species and height diversity within these five different habitats. The coconut (*Cocos nucifera*), avocado (*Persea* species), and mango (*Mangifera indica*) represented the uppermost strata, with an average height of 17.9m. The second strata layer included sour sop (*Annona muricata*), breadfruit (*Artocarpus communis*), pomelo (*Citrus grandis*), and pacay (*Inga feuillei*) with an average height of 10.2m. The third strata layer was comprised of banana (*Musa* species), papaya (*Carica papaya*), Indian mulberry (*Morinda citrifolia*), and guava (*Psidium guayava*), with an average height of 4.5m. The fourth strata layer comprised mostly ornamental plants, primarily *Hibiscus* species, *Delinonia* species, Ti (*Cordyline fruticosa*), Tiare (*Gardenia tahitensis*), Fragipani (*Plumeria* species), *Bougainvillea* species, and *Ficus* species, with an average height of 2.7m. The fifth strata layer comprised Taro (*Colocasia esculenta*), Tarua (*Xanthosoma sagittifolium*), pineapple (*Ananas comosus*), and watermelon (*Citrullus vulgaris*), with an average height of 0.9m. The structural complexity at each home garden site ranked a 5 due to these five vertical strata layers. The first site was located on the east side of Cook's Bay (17°30'25S, 149°48'55W); the second site 200m inland from the head of Opunohu Bay (17°31'02S, 149°50'45W); the third site approximately 5.0km from the west side of Opunohu Bay (17°30'19S, 149°52'21W); and the fourth site on the east

Species	English Name	Tahitian Name	Native/Introduced	Diet
<i>Zosterops lateralis</i>	Silver Eye	Vini Lunette	Introduced	Omnivore
<i>Acridotheres tristis</i>	Indian Mynah	no vernacular name	Introduced	Omnivore
<i>Pycnonotus cafer</i>	Red-bellied Bulbul	no vernacular name	Introduced	Omnivore
<i>Gallus gallus</i>	Jungle Fowl	Mo'a Oviri	Introduced	Omnivore
<i>Geopelia striata</i>	Zebra Dove	no vernacular name	Introduced	Omnivore
<i>Estrilda astrild</i>	Common Waxbill	Vini	Introduced	Omnivore
<i>Emblema temporalis</i>	Fire-tailed Waxbill	Vini	Introduced	Omnivore
<i>Circus approximans</i>	Swamp Harrier	Manu'Amu Mo'a	Introduced	Carnivore
<i>Columba livia</i>	Rock Dove	no vernacular name	Introduced	Omnivore
<i>Lonchura castaneothorax</i>	Chestnut-breasted Mannikin	Vini	Introduced	Omnivore
<i>Ramphocelus dimidiatus</i>	Crimson-backed Tanager	Vini	Introduced	Omnivore
<i>Ptilinopus purpuratos frater</i>	Grey-green Fruit Dove	U' Upa	Native	Herbivore
<i>Halycon venerata youngi</i>	Tahitian Kingfisher	Ruro Otatare	Native	Insectivore

Table 2. Land Bird Species Encountered in Moorea, French Polynesia.

Species	Common Name	Tahitian Name	Native/Introduced	Diet
<i>Acrocephalus caffer</i>	Tahiti Reed Warbler	Otatara	Native	Insectivore
<i>Pomerea nigra</i>	Tahiti Monarch	Omama'O	Native	Insectivore
<i>Pterodroma rostrata</i>	Tahitian Petrel	Noha	Native	Omnivore
<i>Urodynamis taitensis</i>	Long-tailed Cuckoo	Arevareva O'Ovea	Native	Insectivore
<i>Aerodramus leucophaeus</i>	Polynesian Swiftlet	Ope'A	Native	Insectivore
<i>Hirundo tahitica</i>	Pacific Swallow	Ope'A	Native	Insectivore

Table 3. Landbird species known to occur in Moorea but not encountered. side of Opunohu Bay (17°31'32S, 149°49'55W).

### Bird Surveys

The scientific, English, and Tahitian names for each species along with their native or introduced status and feeding preferences are given in the Species Account in Table 2 and 3 (Thibault and Rives 1988). I surveyed birds during September-November 1999.

Pilot censuses at 06:00, 12:00, and 15:00 were conducted in September 1999 at each habitat, to determine the most effective time of day required to count all bird species as well as become familiar with bird calls and songs. Bird censuses at 12:00 and 15:00 detected fewer individuals and species present when compared with the 06:00 census. Initial observations established count periods of 20 minutes along the 100m transect to keep the time interval short enough to minimize the probability of counting the same bird more than once in the area being sampled.

To estimate abundance and distribution of birds among different habitat types, I conducted 20-minute, fixed-radius counts along transects (Hutto et al. 1986).

Morning observations were conducted between 06:00 and 09:00 using a variable circular-plot method, where stations are established at equal intervals along a 100m transect so as to minimize the probability of observing the same bird from more than one station (Reynolds et al. 1980). The transect took two hours to walk, stopping at stations at 0, 20, 40, 60, 80 and 100m for twenty minutes each to observe all birds roosting, foraging, and/or nesting within a circle of 10m radius.

At each station I recorded each bird detected within the 10m radius during the 20-minute period. Each bird was recorded as being heard and/or seen. Individual birds recorded at the previous station were monitored during travel between stations to avoid recounting the same bird at two stations. This was most easily done for species that vocalize consistently, such as the Tahitian Kingfisher (*Halycon venerata youngi*). Aquatic species, such as herons, ducks, and migrant shorebirds, as well as seabirds flying overhead, were excluded from the analyses. Observations were not made during days of poor lighting or weather conditions.

Species	Hibiscus	Coconut	Inocarpus	Pine	Garden	Totals
<i>Acridotheres tristis</i>	0.17	4.17	0.75	1.67	3.21	9.96
<i>Zosterops lateralis</i>	1.17	1.21	2.04	2.08	2.71	9.21
<i>Estrilda astrild</i>	0.21	1.88	1.96	2.17	2.29	8.50
<i>Pycnonotus cafer</i>	0.17	0.33	1.71	1.75	1.83	5.79
<i>Gallus gallus</i>	0.08	0.21	0.63	-	1.58	2.50
<i>Emblema temporalis</i>	-	-	0.71	0.83	1.17	2.71
<i>Lonchura castaneothorax</i>	-	-	-	0.50	0.92	1.42
<i>Geopelia striata</i>	-	0.17	-	0.29	0.33	0.79
Pigeon	-	0.08	-	-	0.08	0.17
<i>Ramphocelus dimidiatus</i>	-	-	-	-	0.13	0.13
<i>Circus approximans</i>	-	-	-	0.04	-	0.04
<i>Ptilinopus purpuratus frater</i>	0.25	-	0.25	0.08	0.04	0.63
<i>Halycon venerata youngi</i>	-	-	0.50	-	-	0.50
TOTALS	2.04	8.04	8.54	9.42	14.29	

Table 4. Distribution (mean number of landbirds per station) for each habitat.

To estimate mean abundance among the different habitat types, calculations were based on "birds per station" within each habitat category, which is simply the mean number of birds seen or heard per station, regardless of age, sex, behavior, or vocalization (Steadman and Freifeld 1998).

Total abundance estimated from a number of fixed plots in habitats that differ structurally for a designated time may not be comparable. Although station distance may depend on how far away the birds can be detected, how fast they move, their behavior and vegetation, it remained uniform in all five habitats. The time counted at each station must also match the structural characteristics of the vegetation and the number of bird species in the plant community being sampled. Smaller quieter birds living in closed canopy forests (e.g. *Inocarpus* forests) are less likely to be seen than larger birds living in open habitats (e.g. coconut plantations). One way of adjusting for varying detectability among species is to use small plots in dense vegetation and large plots in open habitats (Steadman and Freifeld 1998).

Species richness was determined by summing the total number of bird species seen within the four plots of that particular habitat type. The number of bird species present was correlated with the structural diversity and level of disturbance found at each habitat using a One-Way Anova Bonferroni test.

## Results

### Species Accounts

There are nineteen species of nesting land birds that occur on Moorea; consisting of one medium-sized predator, the Swamp Harrier (*Circus approximans*); ten omnivores, the Zebra Dove (*Geopelia striata*), Indian Mynah (*Acridotheres tristis*), Fire-tailed Waxbill (*Emblema temporalis*), Common Waxbill (*Estrilda astrild*) Jungle Fowl (*Gallus gallus*), Red-bellied Bulbul (*Pycnonotus cafer*), Silver Eye (*Zosterops lateralis*), Chestnut-breasted Mannikin (*Lonchura castaneothorax*), Rock Dove (*Columba livia*), Tahitian Petrel (*Pterodroma rostrata*), and Crimson-backed Tanager (*Ramphocelus dimidiatus*); five insectivores, the Long-tailed Cuckoo (*Urodynamis taitensis*), Polynesian Swiftlet (*Aerodramus leucophaeus*), Tahitian Kingfisher (*Halycon venerata youngi*), Tahiti Monarch (*Pomarea nigra*), Tahiti Reed Warbler (*Acrocephalus caffra*) and Pacific Swallow (*Hirundo tahitica*); and one frugivore, the Gray-green Fruit Dove (*Ptilinopus purpuratus frater*) (Pratt et. al 1987).

The species encountered within the five habitats are summarized in Table 2. The species not encountered but presumed still to occur on Moorea are summarized in Table 3. Throughout the Species Accounts, refer to Table 1 and Table 4 for details of the distribution and relative abundance of individual species.

Results prove there is a general trend in abundance and species richness consistently

increasing in all habitats as structural complexity increases. The lowest values for the single strata *Hibiscus* forests and a stepwise increase in more structurally complex habitat categories (Figure 2).

The transect data between abundance

disturbance with species richness resulted in 4° Freedom, F Ratio = 6.6 and P = .002.

The transect data reveal differences in the total abundance of birds and the presence and/or abundance of individual species in all habitats sampled (Table 4).

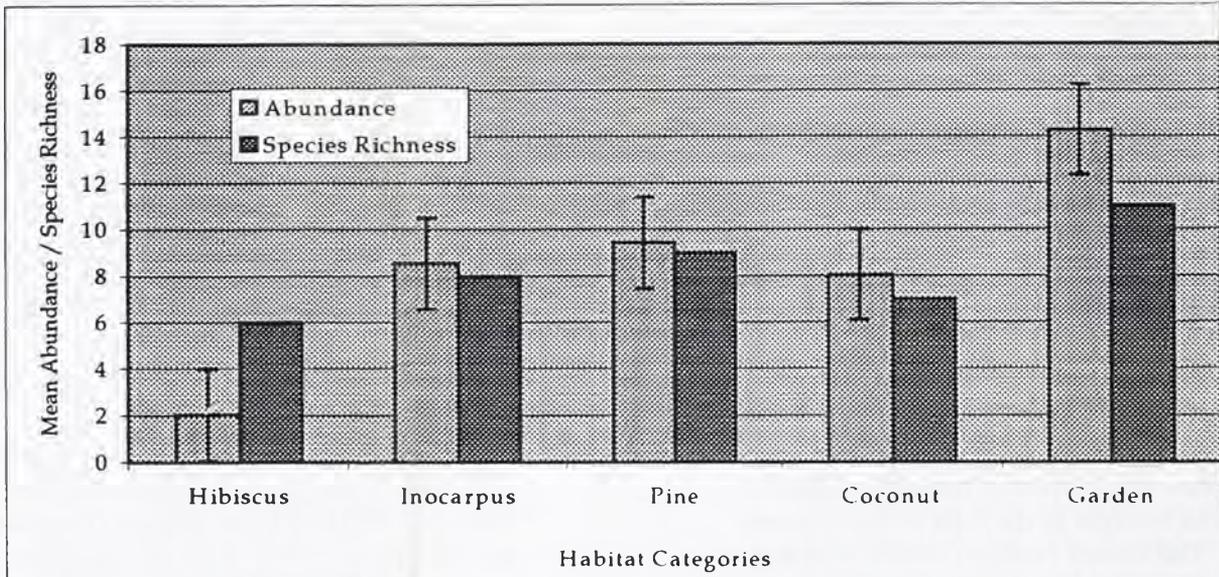


Figure 2. Total abundance (mean +/- SE) and species richness in relation to increasing levels of disturbance in the five categories

and species richness in relation to increasing levels of disturbance do not prove as clear a relationship as structural complexity (Figure 2, Table 4). The two extremes in levels of disturbance, the *Hibiscus* forest and the home garden, do show significant differences which suggest a relationship. But these results might likely be related to structural complexity. Abundance and species richness are scarcest in native *Hibiscus* forests (the least structurally complex and the least disturbed habitat) and are highest in home gardens (the most structurally complex and the most disturbed habitat).

The One-Way Anova Bonferroni Test demonstrates a significant difference between species richness and abundance as habitat categories increase in structural complexity and level of disturbance. Significance between structural complexity and level of disturbance with mean abundance resulted in 4° Freedom, F Ratio = 96.26, and P < .001. Significance between structural complexity and level of

Introduced omnivores appear in more habitat types with greater abundance and species richness, than native insectivores and frugivores (Figure 4). Seven omnivores showed a trend of increasing abundance with more structural complexity. Of the species encountered, only the Gray-green Fruit Dove (*Ptilinopus purpuratus frater*), a native frugivore, showed a trend of decreasing abundance with increasing levels of disturbance and increasing abundance with increasing structural complexity. Of the ten omnivores encountered, seven showed a trend of increasing abundance with increasing structural complexity, and two showed a trend of increasing abundance with increasing levels of disturbance. Of the one frugivore and one insectivore encountered both were more abundant in the less disturbed native forests (Table 4).

Among the two endemic species of resident landbirds that were surveyed on Moorea, neither was widespread in any of the habitats sampled. However, both

endemic birds were more abundantly found in native *Inocarpus* and *Hibiscus* forests. The Gray-green Fruit Dove (*Ptilinopus purpuratus frater*) preferred either forest. The Tahitian Kingfisher (*Halcyon venerata youngi*) appeared to be a habitat specialist and was found only in the *Inocarpus* forest.

#### *Additional Observations*

The patterns of abundance among habitats for individual species are highly variable (Table 4). The Indian Mynah (*Acridotheres tristis*) was found most abundantly in the coconut plantations (4.17 birds/station). I recorded breeding and nesting behavior of the Indian Mynah (*Acridotheres tristis*) at each plot within the coconut plantation habitat. Birds were seen in pairs and were observed establishing territories and gathering nesting material that was brought to the tops of the coconut trees. The Brown Noddy (*Anous stolidus*), a common seabird in Moorea, as well as most of the other islands of Polynesia, has been observed nesting in the tops of coconut trees. However, this species was not present in coconut plantations where the Indian Mynah (*Acridotheres tristis*) clearly had established territories and nesting sites. I also recorded breeding and nesting behavior of the Silver Eye (*Zosterops lateralis*), Fire-tailed Waxbill (*Emblema temporalis*), and the Common Waxbill (*Estrilda astrild*) in the home gardens and pine plantations.

#### *Discussion*

##### *Factors Influencing Community Composition*

Knowledge of the landbird communities in Moorea lacks direct prehistoric perspective. Based upon data from Tonga, however, a typical island avifauna there included at least 25-30 native species of landbirds when humans first arrived (Steadman 1989, 1993, 1995). Thus it can be assumed that many species of landbirds have become extinct in Moorea during the past three millennia of human occupation. The forest habitat specialists in Moorea, the

Tahitian Kingfisher (*Halcyon venerata youngi*), Tahiti Reed Warbler (*Acrocephalus caffer*), Tahiti Monarch (*Pomerea nigra*), Long-tailed Cuckoo (*Urodynamis taitensis*), Polynesian Swiftlet (*Aeodramus leucophaeus*), and the Pacific Swallow (*Hirundo tahitica*) are remnants of a much larger set of native species that probably required forested conditions (Thibault and Rives 1988). The present-day variation of landbird communities among habitats in French Polynesia is the product of long-term anthropogenic influences on the landscapes and on individual species. Interpretation of this data rests on understanding how these processes have operated.

The mean abundance of native landbirds was greater in mature forest than in any other habitat. This has been documented as well in Samoa (Bellingham and Davis 1988), Tonga (Steadman and Freifeld 1998) and Cook Islands (Franklin and Steadman 1991). Lack of information about Polynesian landbirds constrains me to speculative discussion of the requirements underlying the apparent habitat preferences of particular species. Nevertheless, I explore four factors that may help to explain the patterns of habitat preference, abundance, and distribution that were observed.

1. Seasonally variable associations between bird and plant taxa. Landbirds may occupy certain forest types seasonally in continental environments to exploit particular food resources (Levey 1988). If this is the case, the data determining that the Gray-green Fruit Dove (*Ptilinopus purpuratus frater*) was more abundant in native *Hibiscus* forests than in other categories may only be part of an annual cycle of intra-island movement that cannot be represented in my seasonally limited data.
2. Vegetation structure. The overall abundance and richness of landbirds consistently increases with structural complexity. For understory birds such as the Common Waxbill (*Estrilda astrild*), the presence of a well-developed shrub layer may be a critical

habitat component. The understory plants in the less-disturbed *Inocarpus* forest may sustain a richer prey base for insectivores such as the Tahitian Kingfisher (*Halycon venerata youngi*).

Human disturbance (e.g. deforestation, cultivation) do not restrict the extent of structurally complex forests on Moorea. Most introduced birds have adapted well to the spread of agricultural and disturbed forests. The Chestnut-breasted Mannikin (*Lonchura castaneothorax*) and the Zebra Dove (*Geopelia striata*) are more abundant in more disturbed introduced habitats than in native forests.

- Intensity of predation by humans and other mammals (rats, cats, dogs, and pigs). Polynesians have hunted birds for several thousand years (Steadman 1995). Current hunting, however, is not intense and may have little effect on distribution or population size. Mortality of birds from toxic chemicals is a form of indirect human predation that has not been studied in Moorea. Pesticides are used on crops regularly in Moorea, with an unknown influence on food webs involving birds.

Various species of non-native

mammals occur on Moorea. These include the black rat (*Rattus rattus*), house cat (*Felis catus*), dog (*Canis familiaris*), horse (*Equus caballus*), goat (*Capra hircus*), and cow (*Bos taurus*). Understory birds such as the Common Waxbill (*Estrilda astrild*), Fire-tailed Waxbill (*Emblema temporalis*), and the Zebra Dove (*Geopelia striata*) probably were subjected to more predation by non-native mammals than canopy species.

- Interactions (disease, competition, predation) with non-native birds. The Jungle Fowl (*Gallus gallus*), Silver Eye (*Zosterops lateralis*), Indian Mynah (*Acridotheres tristis*), Common Waxbill (*Estrilda astrild*), and the Red-bellied Bulbul (*Pycnonotus cafer*), are the most common species of birds observed on Moorea and were abundant in all habitats sampled. The spread of non-native species has not been contained, and the interactions of these species with native birds are unknown.
- Feeding requirements. Considering feeding requirements of arboreal species, omnivores appear in more habitat types while frugivores and

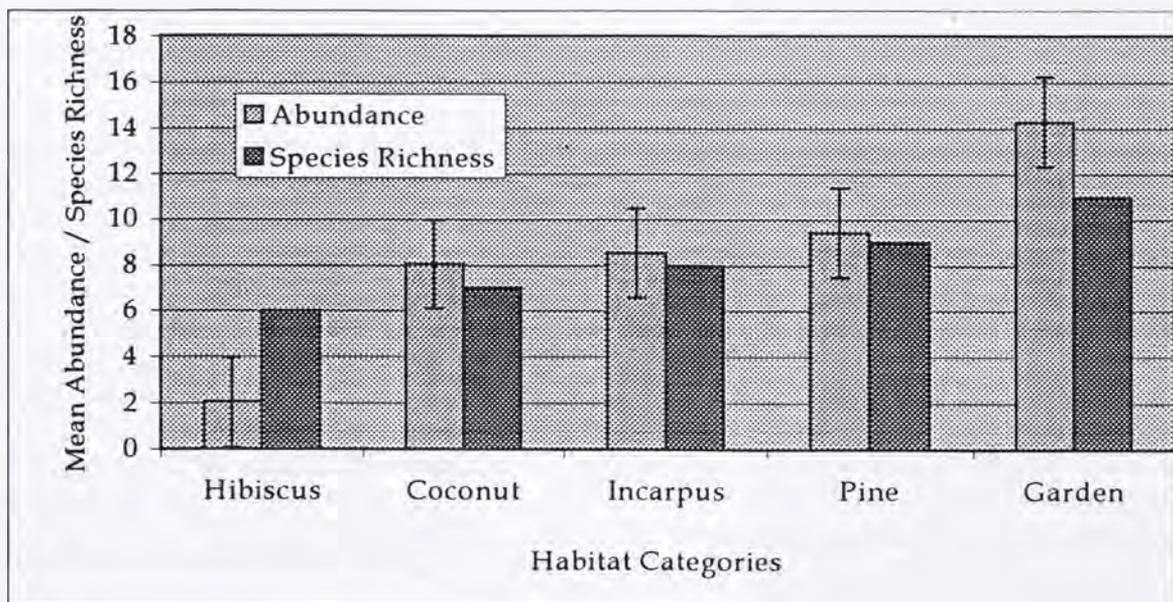


Figure 3. Total abundance (mean +/- SE) and species richness in relation to increasing structural complexity in the five habitat categories

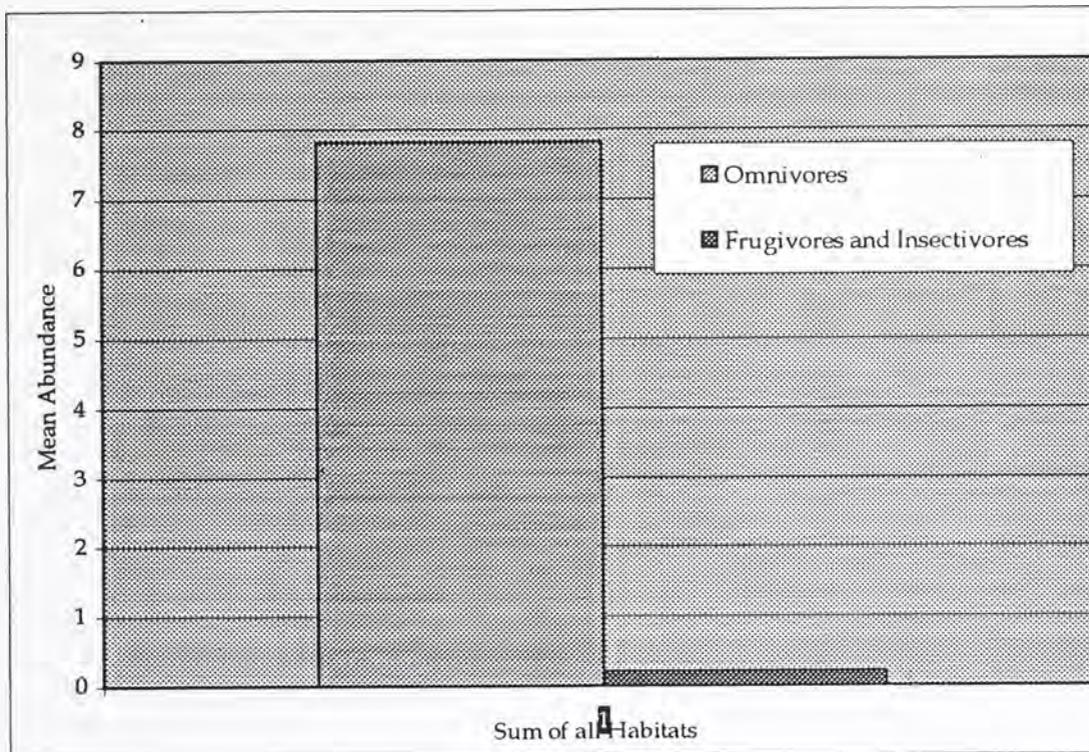


Figure 4. Mean Abundance of Omnivores v. Frugivores and Insectivores in the five habitat categories

insectivores show a general trend of habitat preferences (Steadman 1997). Introduced omnivores appear in more habitat types, with abundance and distribution consistently greater than native insectivores and frugivores. Omnivores have a more diverse diet. It is more risky for island birds to depend on a single source of nourishment, which could one day fail them, than to survive on a more diverse diet. The more land birds show their responses to the constraints of insularity, the greater chance they have at survival (Thibault and Rives 1988). In Moorea, this theory holds and omnivores occur in greater abundance and distribution than island insectivores or frugivores (Figure 4). The Silver Eye (*Zosterops lateralis*), Common Waxbill (*Estrilda astrild*), Indian Mynah (*Acridotheres tristis*), Red-bellied Bulbul (*Pycnonotus cafer*), Jungle Fowl (*Gallus gallus*), Zebra Dove (*Geopelia striata*), Fire-tailed Waxbill (*Emblema temporalis*),

Pigeon (*Columba livia*), and the Chestnut-breasted Mannikin (*Lonchura castaneothorax*) are omnivores and appear to be habitat generalists of similar relative abundance regardless of habitat type. On the other hand, of the four insectivores residing in Moorea, only the Tahitian Kingfisher (*Halycon venerata youngi*) was encountered and only in one habitat type, appearing to be more of a habitat specialist.

#### Conclusions and Conservation Implications

The overall species richness and relative abundance of land birds in Moorea today are greater in disturbed introduced habitats that are more structurally complex than in native forests. However, of the native land birds known to occur in Moorea but not encountered during my survey, their habitat preferences are confined to a few areas of native forests (Thibault and Rives 1988). Although my census encountered only the Tahitian Kingfisher (*Halycon venerata youngi*) and the Gray-green Fruit Dove (*Ptilinopus purpuratos frater*), the remnant patches of mature forests may well sustain

the remaining populations of native species. Further investigation is called for.

The most vulnerable species of birds already have been lost throughout Moorea (and all of Polynesia) to anthropogenic predation, habitat loss, and competition or predation of non-native mammals (Steadman 1989, 1993, 1995). Coastal and valley-floor land-use by humans is intense on most islands of French Polynesia today. Given the evident importance of mature forests for some species and the large number of extinctions that already have occurred in Moorea, protection of the native forests of Moorea may be essential to preserve what little remains of Moorea's indigenous birds.

Finally, the fundamental aspects of avian behavior and ecology are unknown or poorly documented for most species of landbirds in Moorea. Detailed nesting and feeding studies of individual species are needed to understand their role in terrestrial ecosystems and their responses to disturbance and alteration of these systems.

#### Acknowledgments

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# A Report on the Symbiotic Relationship Between the Cushion Star (*Culcita novaguineae*) and its Commensal Shrimp (*Periclimenes soror*)

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**ABSTRACT.** Adult and juvenile *Periclimenes soror* exhibit a wide variety of colors from red to orange to purple that often correlate to the color of their cushion star host, *Culcita novaguineae*. The number of shrimp associates is not correlated to the size of their original host. Experiments to test *Periclimenes*' affinity for its original host suggest that these sea star associates exhibit no host preference. *Periclimenes* was observed to have the ability to adapt to its background. The shrimp's ability to color match offers one explanation for the absence of host preference. The implications of *Periclimenes*' ability to camouflage itself include the increased chance of predator evasion.

The rapid color change, involving the dispersion or concentration of pigment granules in chromatophores, experienced by *Periclimenes*, is known as a physiological color change. Physiological color changes of *Periclimenes* were affected by external stimuli. The responses of adult and juvenile shrimp to white, purple, red and blue light are reported.

Key words: symbiosis, commensalism, echinoderm, *Culcita novaguineae*, crustacea, *Periclimenes soror*, host preference, chromatophore, color change

## Introduction

Symbiotic associations are adaptations that enable pairs of organisms to live in, on, or with each other. These associations attract a large amount of curiosity and scientific interest. Crustacea have more symbiotic relationships with members of other phyla and with one another than perhaps any other major group of invertebrates (Ross 1983).

Symbiotic associations involving crustaceans are common throughout the tropics. Crustacea are frequently found in special relationships with sponges, cnidarians, annelids, mollusks, ascidians, fishes and echinoderms, including the sea urchins and sea stars (Gosliner et al. 1996; Ross 1983; Green 1961). Although known and observed to be an associate of *Linckia laevigata* and the crown-of-thorns, *Acanthaster planci*, the sea star shrimp, *Periclimenes soror*, is commonly found in French Polynesia, as an associate of *Culcita novaguineae* (Bruce 1978).

*Culcita*, extremely variable in its coloration, is the most widespread and common species of cushion star in the Indo-Pacific, a common inhabitant of shallow patch, barrier and fringing reefs (Gosliner et al. 1996). According to Alexander Bruce (1993, 1989, 1978), the relationship between *Culcita* and *Periclimenes* is not a random or occasional association, but a true symbiotic relationship.

It has been noted in the literature that, very often, crustacea and their echinoderm host are similarly colored. Copepods of the genus

Ascomyzon often exactly match the color of the sea star on whose surface they live (Green 1961).

In order to investigate the possibility that *Periclimenes soror* exhibits host preference, an experiment was designed and conducted to test shrimp affinity for its host cushion star. A shrimp, isolated from its original host, was placed in a plexi-glass Y maze and given an opportunity to choose between its original host and a host of similar size and color.

Just like their hosts, *Periclimenes* is known to exhibit a wide variety of colors (Gosliner et al. 1996; Bruce 1993, 1989). During this study, red, red orange, orange, maroon, purple, clear and white shrimp were observed. Although the majority of the shrimp observed were a solid color, it was common to collect shrimp with a white or cream colored median dorsal stripe.

In crustaceans with a thin, translucent exoskeleton, the color of the organism is due to pigments occurring inside the body or in a special kind of cell known as a chromatophore. Chromatophores are found primarily in the integument underlying the exoskeleton, or more deeply, around organs (Ghidalia 1985; Waterman 1961).

The color of a shrimp depends on the number of chromatophores, the nature of the pigment each chromatophore contains, and the degree of pigment dispersion (Fingerman 1963). In order to allow accurate observation of individual chromatophores and provide quantitative study and graphic representation of changes, a method for dividing the degree of pigment dispersion was

established by Hogben and Slome (1931). According to their definition, stage 1 (punctate) represents the most concentrated state of the pigment, stages 2 (punctate-stellate), 3 (stellate), and 4 (stellate-reticulate) are intermediate, and in stage 5 (reticulate), pigment is the most dispersed.

Many species of crustacea experience two general modes of integumental color change. Morphological color change is dependent upon the number and nature of the integumental pigment cells, also known as chromatophores, and often requires several days or months to manifest itself. Physiological color changes result from the dispersion or concentration of cytoplasmic pigment granules within chromatophores and occurs in a matter of minutes or hours (Thurman 1988).

The role of cellular processes in color change have been known for over a century. Color change was first described by Kroyer (1842) in the prawn *Hippolyte*. It was later shown that the color change in crustacea was due to the movement of pigment within special integumentary cells (Sars 1967). The movement of pigment granules within chromatophores contributes to rapidly reversible, adaptive color changes in crustacea (Carlson 1935).

To better understand the relationship between *Culcita* and its associate shrimp, *Periclimenes*, this study has the following goals: (A) to document color characters of 70 cushion stars, (B) to document the chromatophore colors of *Periclimenes*, (C) to examine the effect of star size on the number of shrimp associates (D) to experimentally examine the possibility of host preference among *Periclimenes soror*, and finally, (E) to experimentally examine of the presence of polychromatism in *Periclimenes*.

## Materials and Methods

### *Species Collection and Characteristic Identification*

Observations and collections of *Culcita* and *Periclimenes* were conducted on the shallow reef flat adjacent to and just north of UC Berkeley's Gump Research Station in Moorea, French Polynesia (Figure 1). Collections and the identification of color characters of *Culcita* occurred from 28 September through 9 November, 1999. Individual cushion stars, with their shrimp associates, were gently collected by hand while snorkeling and free diving on the reef flat. Stars and shrimp were isolated in one gallon Ziplock plastic bags and carefully transported from the reef flat to a large circular tank. A seawater system pumped water directly from Cook's Bay into the tank and throughout the study, the large circular tank functioned as an artificial

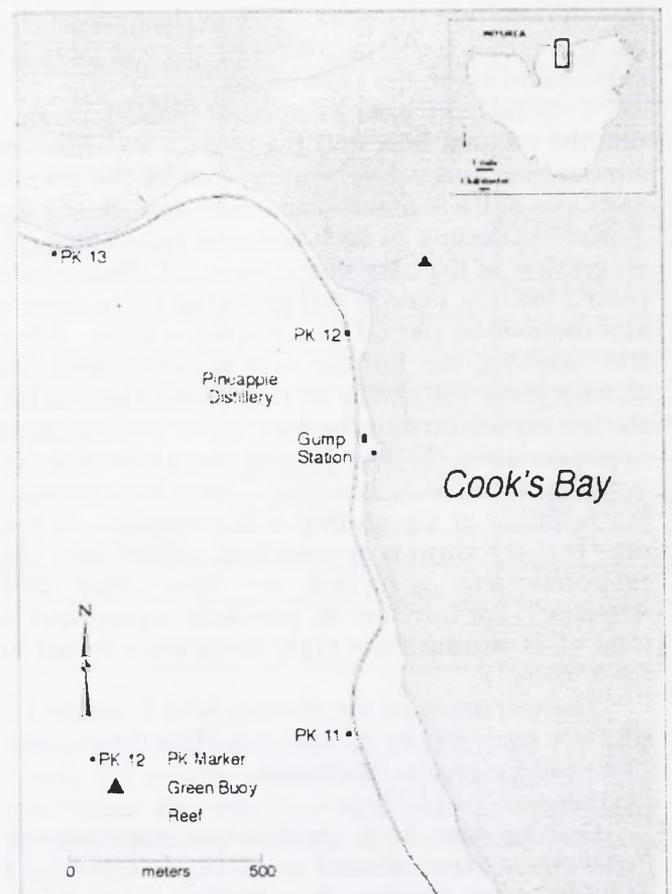
environment in which to hold, observe and record information about the sea star and its associate.

*Culcita* is extremely variable in its coloration. In order to distinguish individuals and establish a record of the incredible variation amongst the species, aboral background color, aboral tiny dot color, aboral dot color, oral background color, oral dot color and star color are reported. Colors were matched to a waterproof set of color mixing recipe cards (Powell 1994). The colors of the star characteristics were later identified using the Methuen Handbook of Colour (Kornerup and Wanscher 1961). The full list of character colors is reported (Appendix 1).

### *Chromatophore Color of Periclimenes*

Twenty shrimp were isolated from their original hosts and their observed color recorded. In order to elucidate the components that make up the color observed with the naked eye, the color and shape of the shrimp's chromatophore(s) were recorded. Chromatophore colors were matched to the waterproof set of color mixing recipe cards (Powell 1994), and later identified using the Methuen Handbook of Colour (Kornerup and Wanscher 1961). In Moorea,

Figure 1. Map of Observation and Collection Site, Moorea



unaware of the Hogben and Slome (1931) method for identifying chromatophore stages, I defined chromatophore shapes as either a dot (punctate) or a burst (stellate). A hue was assigned when the chromatophores appeared to be on top of a solid colored background.

#### *The Affect of Star Size on Shrimp Number*

In addition to identifying star and shrimp colors, the diameter (sum of radii A and the radii of interambulacrum CD) of each cushion star and the original number of shrimp associates is recorded.

To examine the possibility that host size has a direct effect on the number of associates carried, a correlation coefficient for the relationship was calculated. The size and number of associates is recorded for 62 stars.

#### *Host Preference:*

The Y maze had two arms, 50 cm long and 25 cm wide, with walls 12.5 cm high. In order to conduct the experiment, shrimp were first removed from the host star and isolated in opaque, 30 centiliter cups. In order to isolate shrimp from their sea star host, the star was placed in a plastic dissecting tray. The star was briefly removed from the water and if the shrimp did not voluntarily jump off the star and into the plastic tray, the shrimp was gently washed off the host by a stream of water. Shrimp were transferred from the plastic tray to the opaque cup using a turkey baster and kept on the wet table for subsequent use in the experiment.

Two cushion stars stripped of their associates, one the original host and the other a non-host, of similar size and color, were placed at the end of each arm of the Y maze. Salt water flowed into the Y maze at the end of each arm and exited through an outflow at the base of the maze. A shrimp was placed into the Y maze and provided a five minute acclimatization period in an opaque tube. After five minutes, the blinder was removed and the shrimp given the choice of two stars. The shrimp started equidistant to the two stars, a distance of approximately 50 cm (slight variation due to minor differences in star size). After five minutes, the response of the shrimp was recorded. In the case that the shrimp approached neither star, the response was recorded as "free after five minutes." For the host vs. non-host experiment, a total of 24 shrimp from eight hosts were tested in the Y maze.

The responses of the shrimp, which reached a star, are analyzed by  $X^2$  statistics (Freedman et al. 1998) and the results illustrated.

#### *Physiological Color Change:*

During the host preference experiment, *Periclimenes* demonstrated an ability to undergo a dramatic color change. In a matter of two days,

dark colored shrimp, isolated from their original host and placed out of direct sunlight, became colorless. These same shrimp, when exposed to direct sunlight, almost immediately developed pigment. It is believed that *Periclimenes*' ability to undergo a rapid physiological color change has never before been described. In order to look more closely at the shrimp's ability to change color, an experiment was designed to test chromatophore response to external stimuli, light.

Originally, 24 shrimp, 12 blind and 12 with the ability to see, were to be placed under the light and their response to different colored lights recorded. Blinding half of the shrimp would test whether the response to light was a primary or secondary response.

A reaction is known as a primary response when isolated chromatophores respond to the external stimuli (Brown and Sandeen 1948; Weber 1983). On the other hand, when the color change is a result of the ocular sinus-gland system, the shift is known as a secondary response. Hormonal factors released from the sinus gland coordinate chromatophore responses (Brown 1933; Welsh 1938).

I felt that lancing or removing the ocular sinus-gland was out of question due to the fact that I did not know how to correctly perform the procedure. Unsure of how the consequences of damaging the ocular sinus-gland and disrupting hormonal control of the chromatophore would confound my observations and eventual comparisons with the un-blinded shrimp, I decided to pursue another approach to blinding 12 shrimp.

A mixture of whiteout and soot was mixed to make a dark liquid. Once a shrimp had been removed from the water and its eyes dried with a tissue, a small amount of the dark liquid was dotted onto the shrimp's eyes. Although the mask had an opportunity to dry and remained attached to the shrimp's face, after the blinded shrimp was returned to the water, it took only minutes for the shrimp to remove the blindfold using its first set of chelipeds.

Rather than continue my attempts to compare primary and secondary responses, I chose to expose 12 shrimp to a light schedule and subject 12 shrimp to perpetual darkness. Not only would it be possible to compare the light exposed shrimp color with a dark control, it was also an opportunity to explore the possibility of diurnal color change.

24 shrimp were isolated in 30 centiliter cups, in the dark room at the research station. The color of the shrimp exposed to the light schedule and perpetual darkness was recorded at six hour intervals beginning at 12 p.m. on 11 November,

1999. The actual color of the shrimp was later ranked on a scale from one to five for analysis. A one indicates that the shrimp is clear, a two indicates a clear shrimp with a light pink tail or faint median dorsal stripe, a three indicates that the coloration is a very light color, four indicates a solid coloration and a five indicates that the shrimp is very dark in color.

A cardboard enclosure, with a thrice folded black cloth cover, housed twelve shrimp, six adults and six juveniles, in perpetual darkness for the duration of the study.

The light schedule exposed six adults and six juvenile *Periclimenes* to white, purple, red and blue light. A green light schedule was performed. However, two thirds of the shrimp died during the two day trial and as a result, the average responses to green light are not reported. Shrimp were exposed to white light for two and a half

days at six hour intervals; the light was on for six hours and off for six hours, during the day and night. For the purple, red and blue light schedules, shrimp were exposed to one day of six hours of light followed by six hour of darkness, for a complete 24 hour period. On the second day, the shrimp were exposed to 12 hours of light during the day, followed by 12 hours of darkness at night.

## Results

### *Chromatophore Color of Periclimenes:*

Red, orange, yellow and white chromatophores, in punctate and stellate forms, are reported. The chromatophores that make up the median dorsal stripes were white or yellow. The observed shrimp color and chromatophore color and shape are recorded (Table 1).

**Table 1.** Shrimp Color & Chromatophore Color and Shape

Shrimp	color observed w/ the naked eye	hue: at x	1: punctate	3: stellate	chromatophores on median dorsal stripe
1	purple	purple 18C6	white 1A1	red 10B8	
2	maroon	purple maroon 15E7	white 1A1	red 10B8	
3	clear		red 10B8		
4	salmon			orange 6A8	
5	purple	purple 18C6	white 1A1	red 10B8	
6	clear		red 10B8		
7	purple	purple 18C6		red 10B8 & white 1A1	
8	clear		red 10B8		
9	purple	purple 18C6		red 10B8 & white 1A1	
10	clear w/ stripe		red 10B8 & yellow 3A5		stellate: white 1A1
11	light purple	purple 18C6	red 10B8 & yellow 3A5		
12	light maroon w/ stripe			red 10B8, white 1A1	solid white 1A1
13	light purple w/ stripe	purple 18C6			solid white 1A1
14	light pink	orange 6A8	red 10B8 & white 1A1		
15	bright purple	dark purple 18D7	red 10B8 & white 1A1		
16	light orange		orange 6A8		
17	dark pink			red 10B8 & white 1A1	
18	purple w/ stripe	purple 18C6	red 10B8	white 1A1	stellate: yellow 3A5
19	dark purple	dark purple 18D7	red 10B8 & white 1A1		
20	light purple	light purple 18A5	red 10B8 & white 1A1		

### *The Affect of Star Size on Shrimp Number*

The diameter (sum of radii A and the radii of interambulacrum CD) of cushion stars and the original number of shrimp associates is recorded (Table 2). The number of original shrimp

associates was not recorded for stars 63-70; as a result, the equation examining the possibility of a correlation between host size and the number of shrimp associates uses the data collected for stars 1-62.

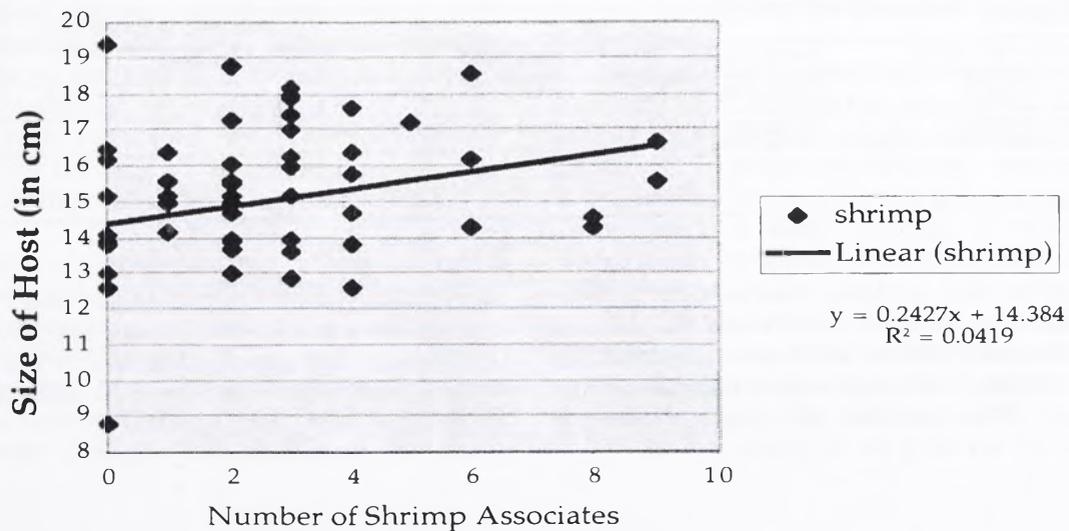
**Table 2.** Cushion Star Diameter and Original Number of Shrimp Associates

star number	star diameter (in cm)	original # of associates	star number	star diameter (in cm)	original # of associates	star number	star diameter (in cm)	original # of associates
1	14.3	6	25	14.7	2	48	18.8	2
2	15.6	9	26	14	3	49	15.2	2
3	12.6	4	27	13.9	0	50	17.9	3
4	15.6	2	28	13.9	2	51	15.2	3
5	13.7	2	29	17.3	2	52	18.2	3
6	14.7	4	30	15	2	53	16.4	4
7	15.6	1	31	15.2	1	54	17	3
8	14.3	8	32	13.9	0	55	15.8	4
9	12.9	3	33	19.4	0	56	16.4	1
10	16.2	6	34	13.6	3	57	14.6	8
11	8.8	0	35	-	1	58	15	1
12	16.2	0	36	14.2	1	59	15.5	2
13	16	3	37	12.6	0	60	17.6	4
14	15	2	38	13	0	61	18.6	6
15	17.2	5	39	15.2	0	62	17.4	3
16	14	2	40	14.1	0	63	18.7	-
17	15	2	41	16.5	0	64	15.4	-
18	13.9	2	42	14.1	0	65	17.2	-
19	18	3	43	16.5	0	66	14.7	-
20	16.7	9	44	13.8	4	67	11.8	-
21	16.1	2	45	15.2	3	68	15.1	-
22	14.7	2	46	13.8	0	69	16.5	-
23	13	2	47	16.3	3	70	16	-
24	14	2						

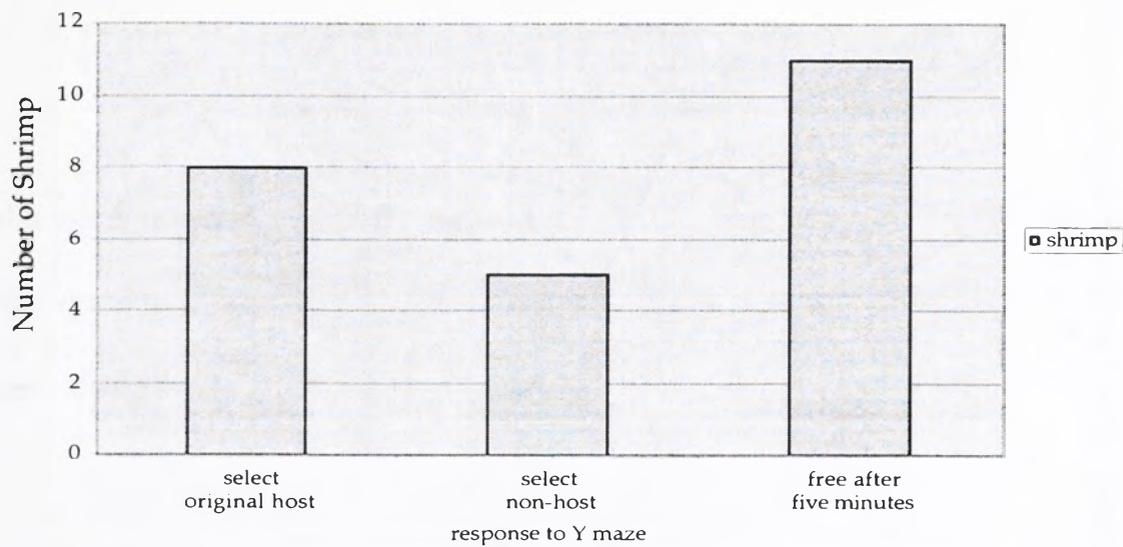
The relationship between the size of the star and the original number of shrimp associates is graphically illustrated (Figure 2); the equation of

the best fit line and the correlation coefficient are depicted with the graph.

**Figure 2:** Star Size vs. Original Number of Shrimp Associates



**Figure 3: Shrimp Responses to Host Preference Experiment**



*Host Preference*

No evidence to support the presence of a host preference was found. The response of the 24 shrimp, after five minutes in the Y maze, is illustrated in Figure 3. A  $X^2$  analysis of the shrimp

that found a host, within five minutes, provides a p-value ( $>.995$ ) which suggests that the deviation from the expected value is most likely due to chance.  $X^2$  calculations are included in Table 3.

**Table 3:  $X^2$  Calculations for Host Preference Experiment**

location:	observed	expected	deviation from	deviation			
after 5 minutes	frequency	frequency	expected	squared			
	(fo)	(fe)	(fo-fe)	(fo-fe) <sup>2</sup>	(fo-fe) <sup>2</sup> / fe	X <sup>2</sup> :	0.692
to original host	8	6.5	1.5	2.25	0.346153846	degrees of freedom:	12
to non-host	5	6.5	-1.5	2.25	0.346153846	p-value:	p > .995

*Physiological Color Change:*

Average responses of the adult and juvenile shrimp, held in perpetual darkness during the light schedules, are graphically illustrated in figures 4-7. The effect of 60 watt colored bulbs, run

on 220 volts, on both adult and juvenile shrimp is graphically illustrated in figures 8-11.

The comparison of adults exposed to a light schedule and adults exposed to perpetual darkness, during the same time period, are illustrated (Figures 12-15).

Figure 4: Average Response to White Light

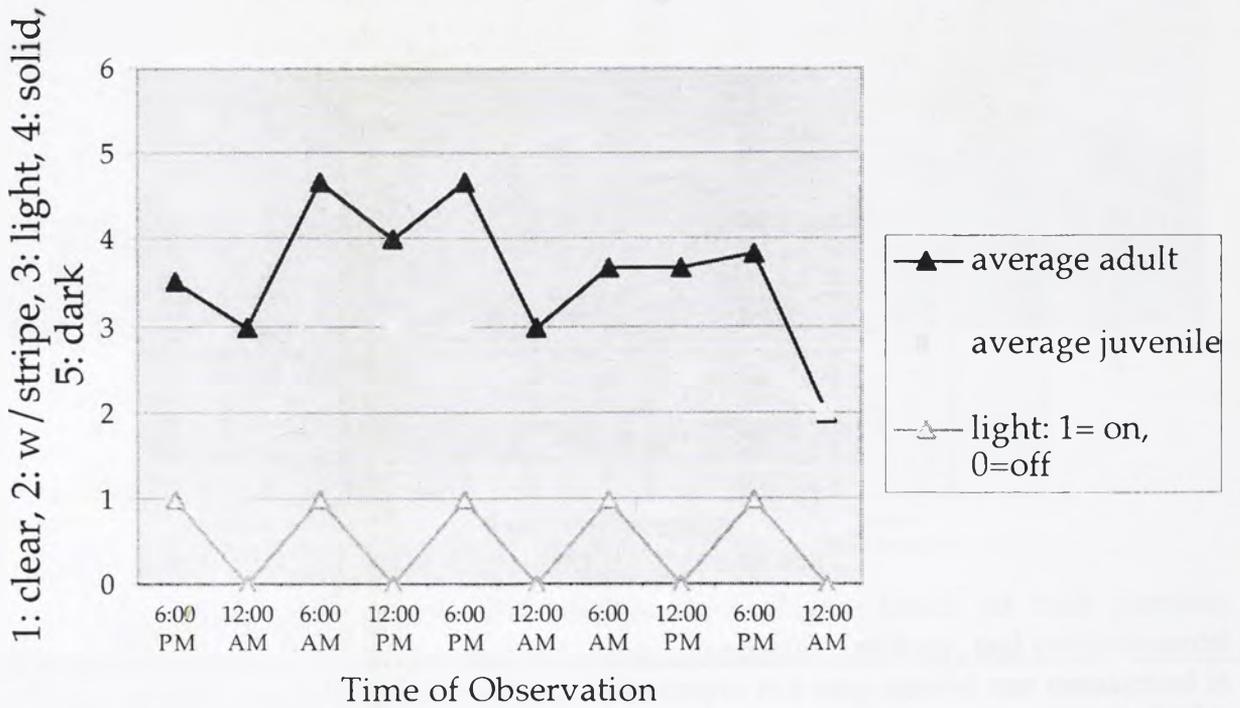


Figure 5: Average Response to Purple Light

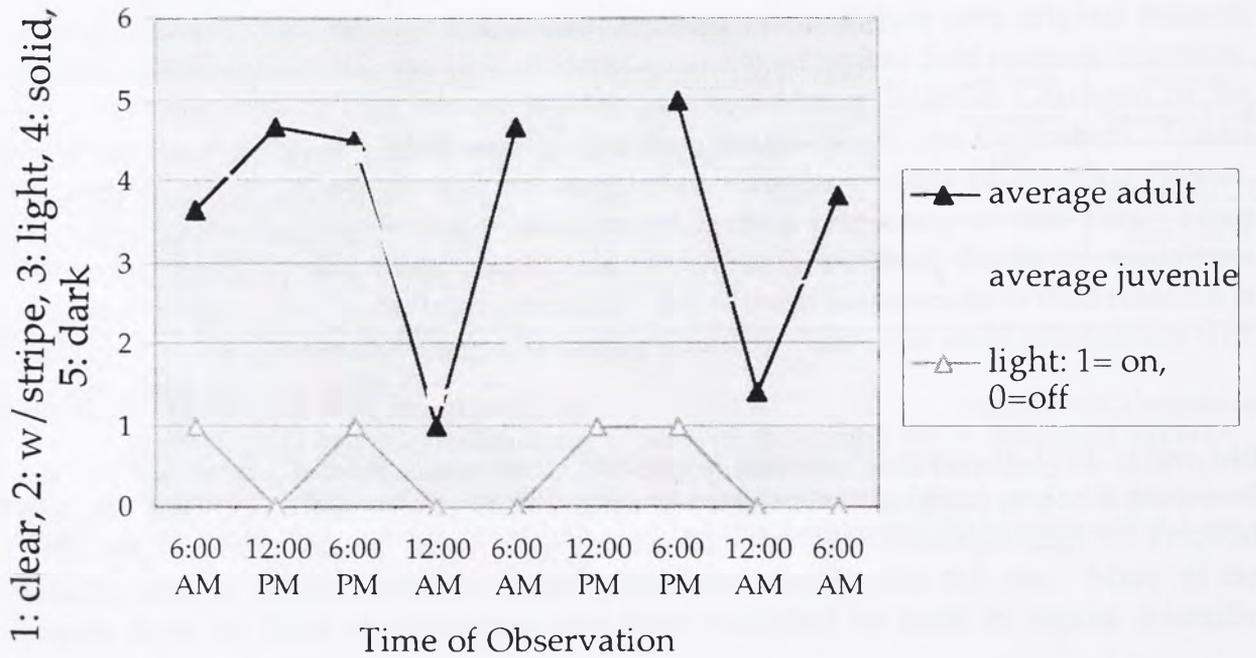


Figure 6: Average Response to Red Light

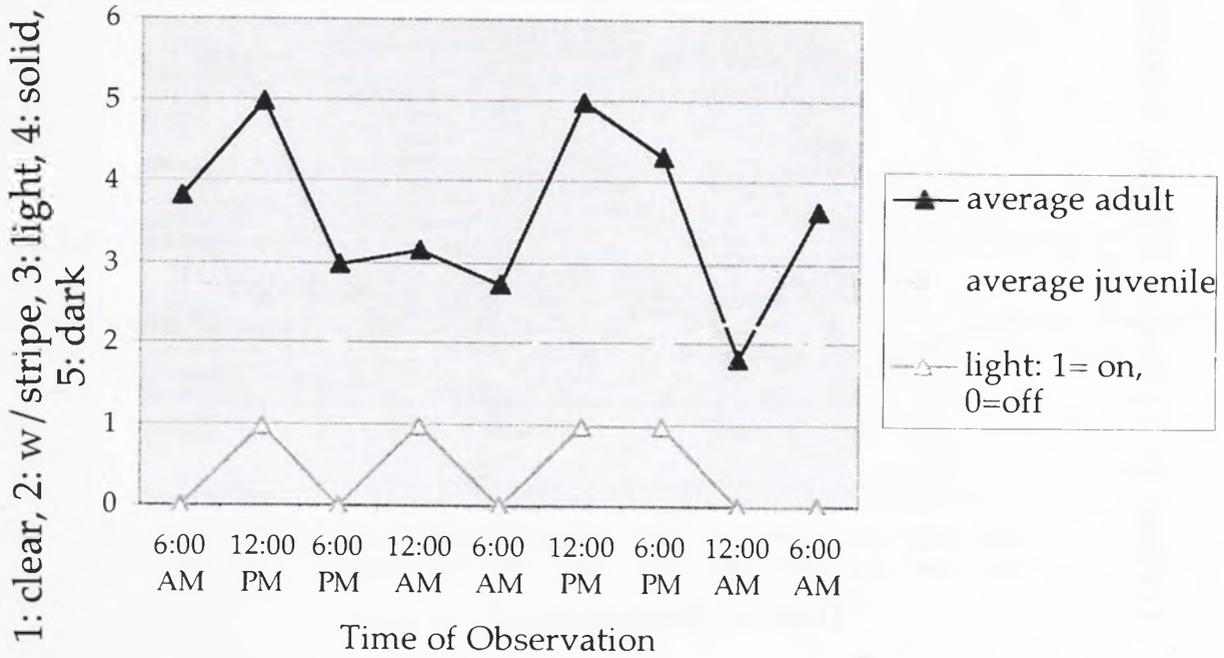
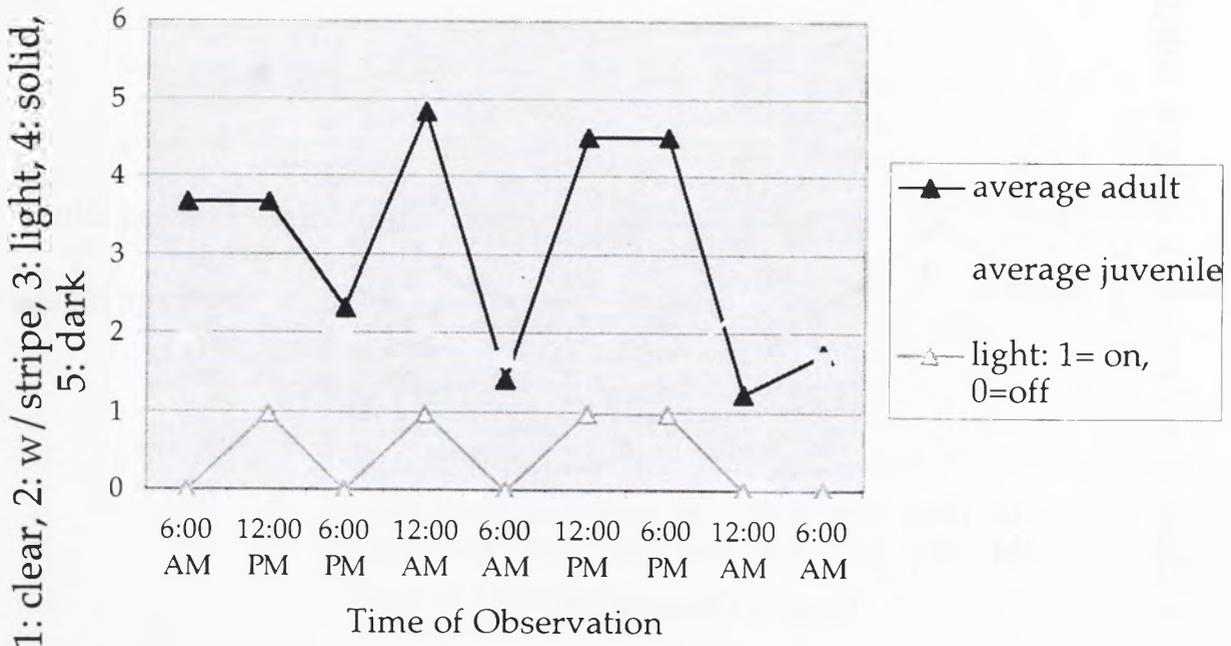
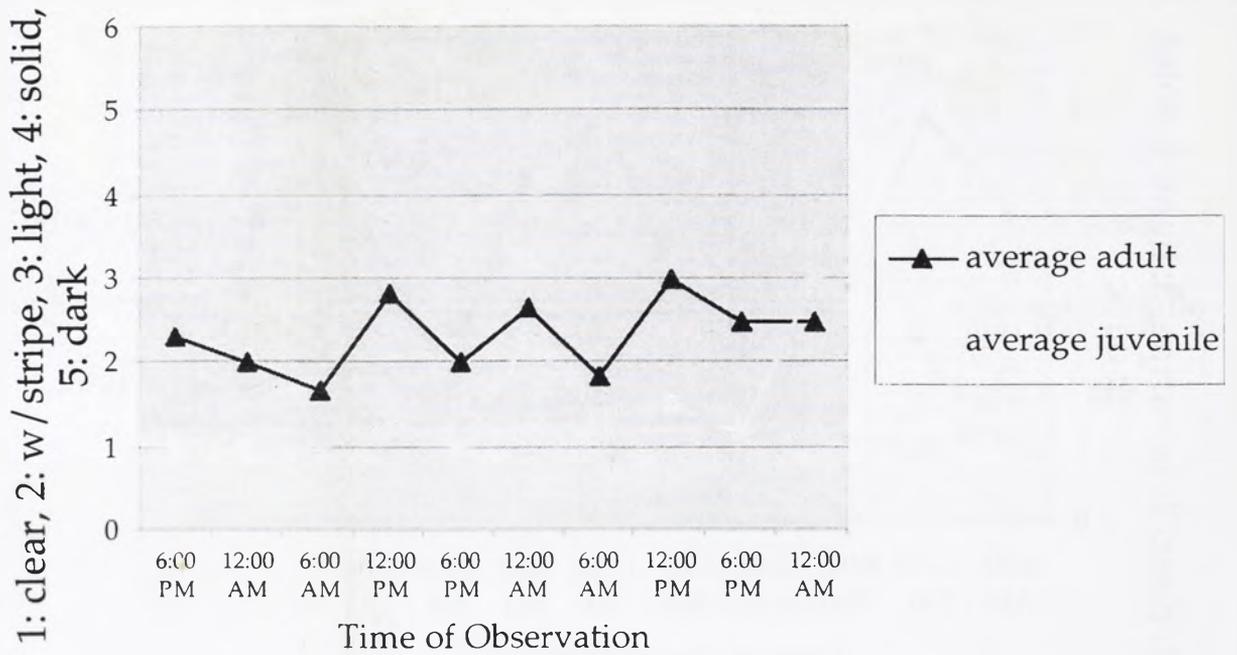


Figure 7: Average Response to Blue Light



**Figure 8:** Average Response to Perpetual Darkness During White Schedule



**Figure 9:** Average Response to Perpetual Darkness During Purple Schedule

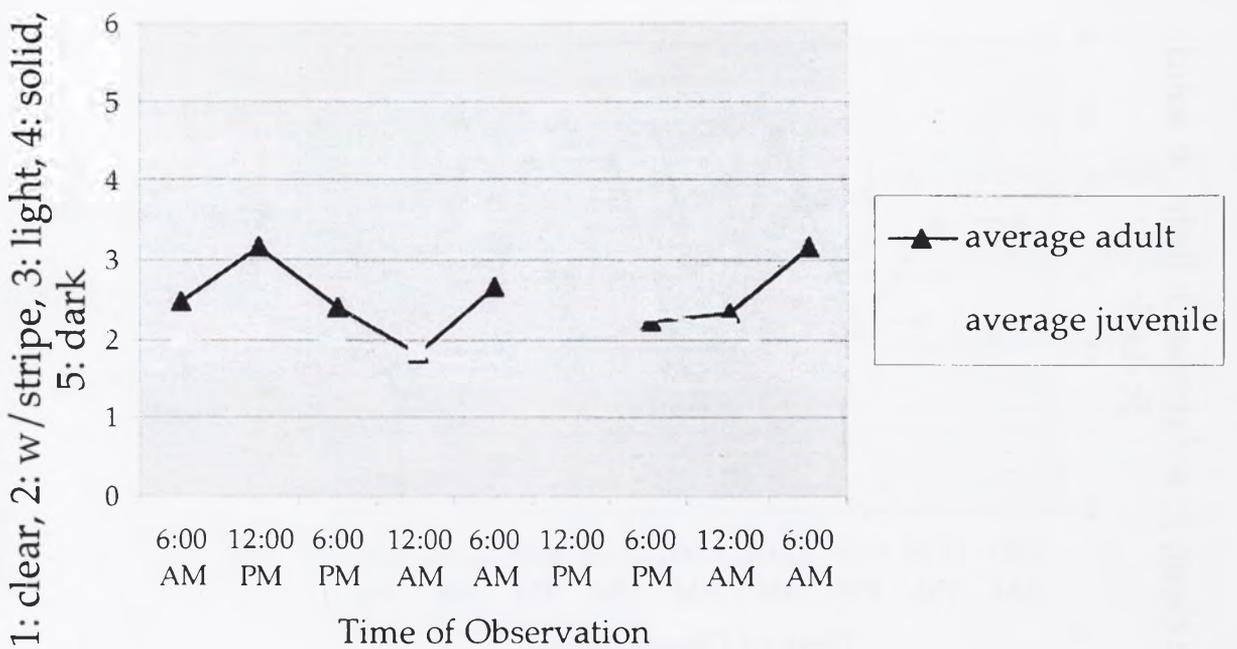


Figure 10: Average Response to Perpetual Darkness During Red Schedule

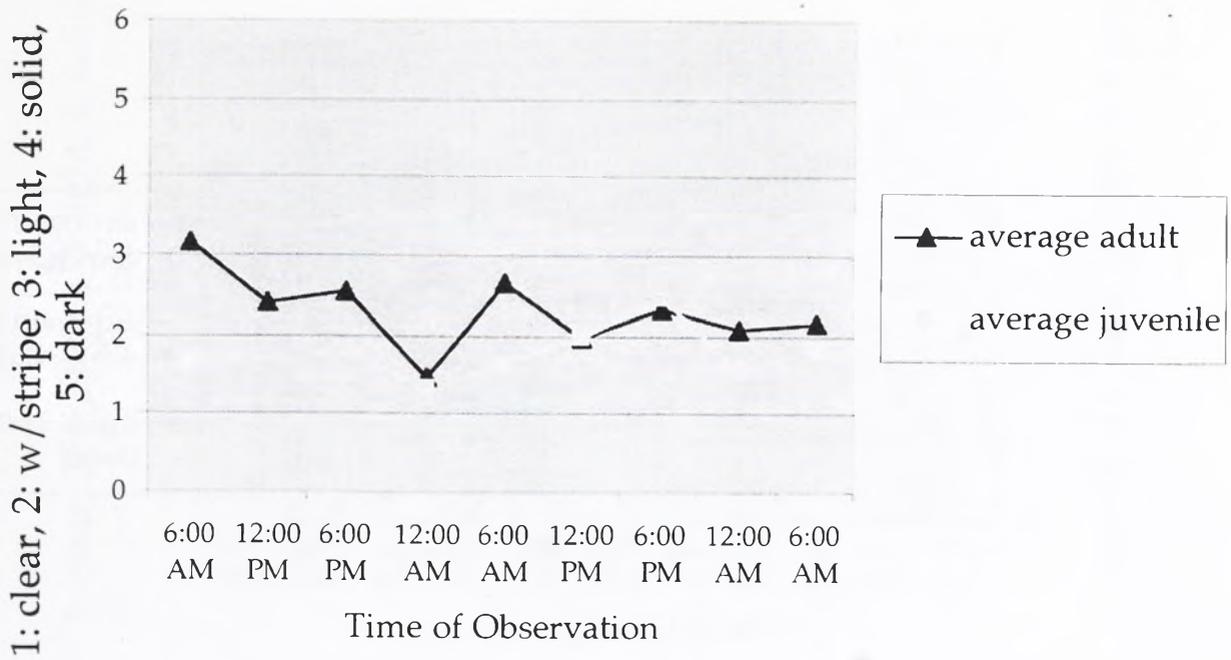


Figure 11: Average Response to Perpetual Darkness During Blue Schedule

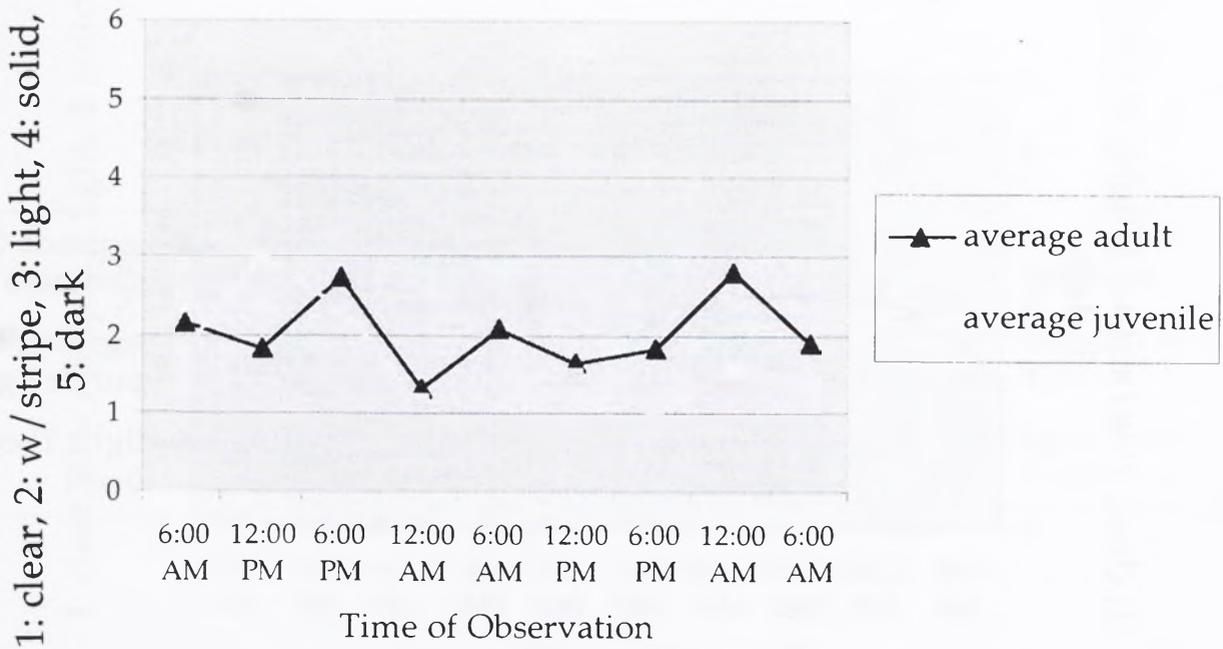


Figure 12: Average Adult Response During White Schedule

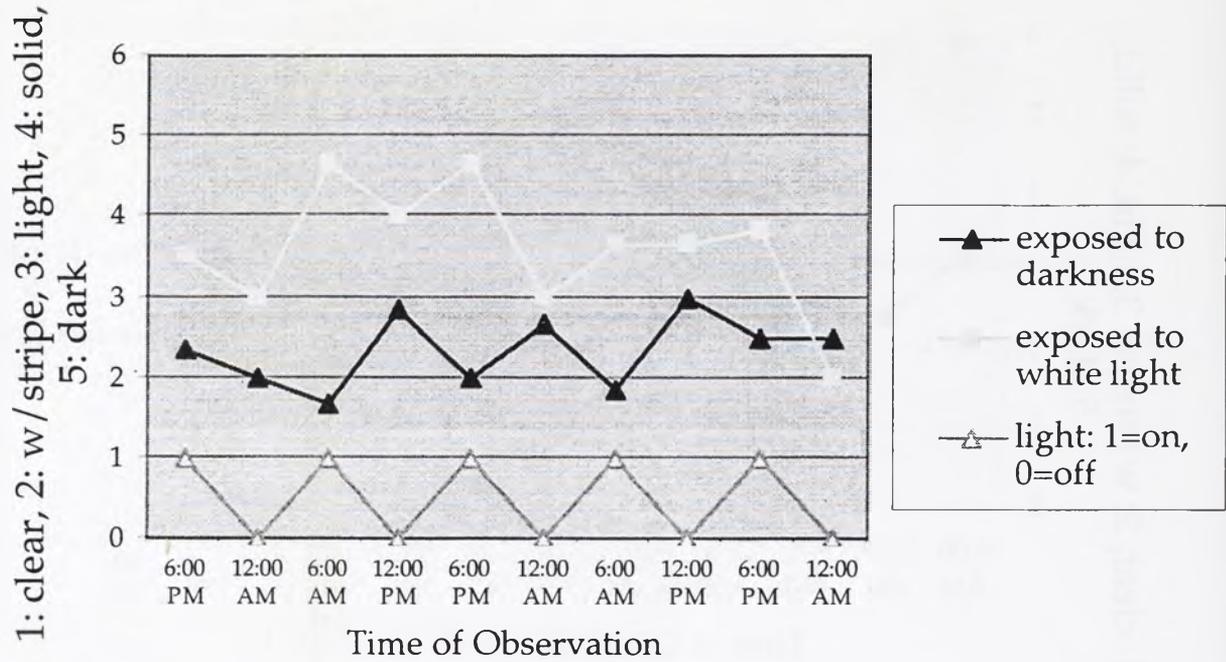
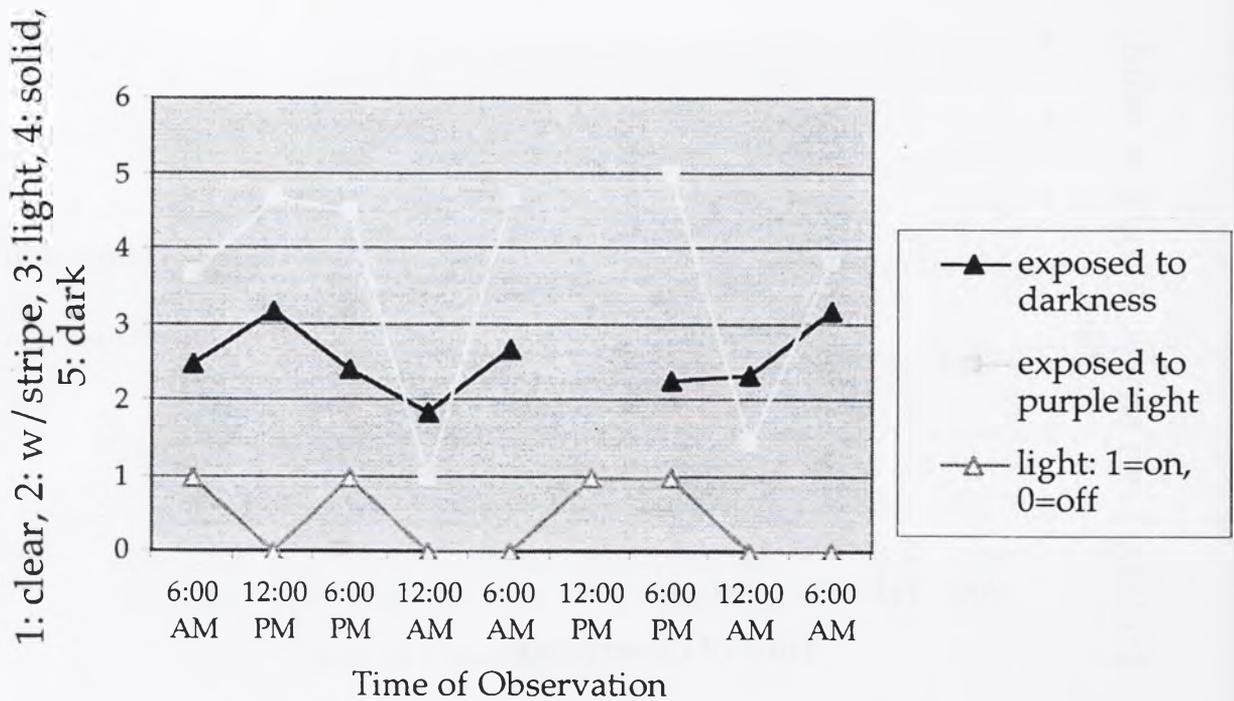
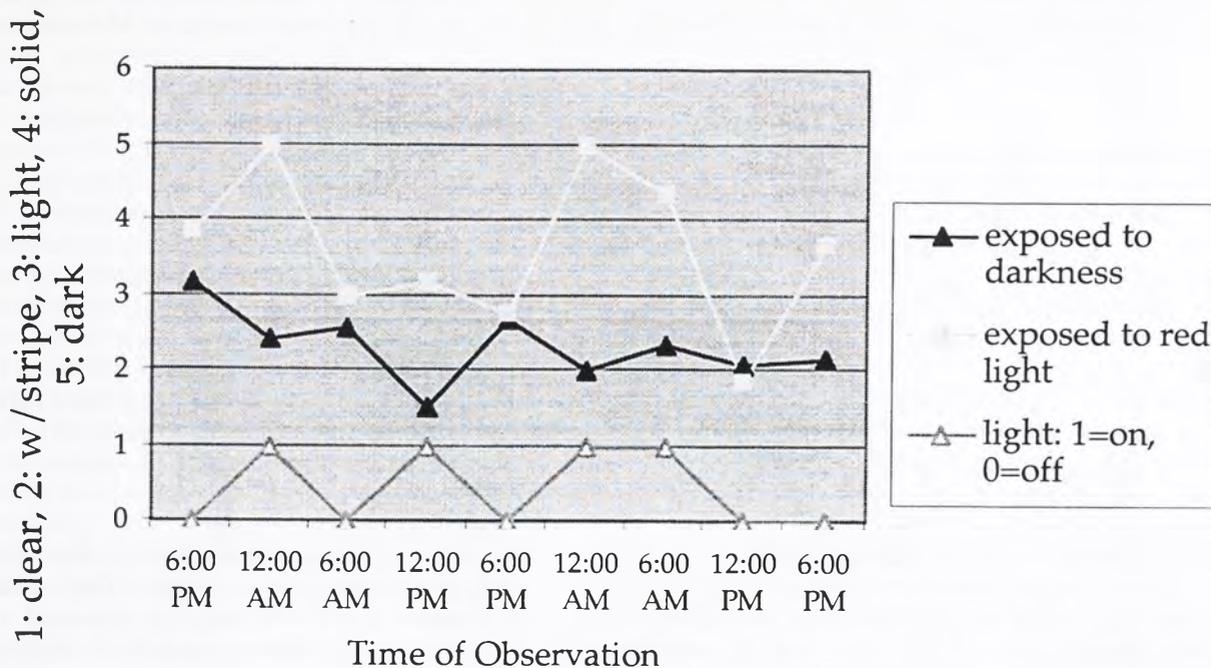


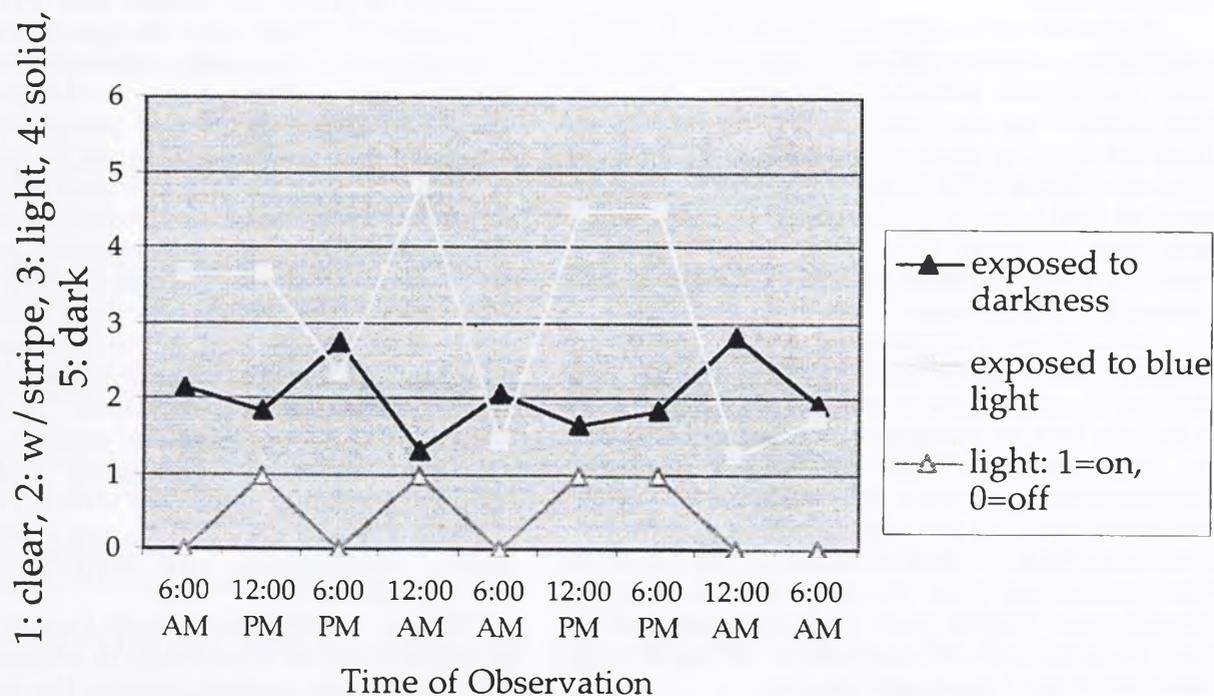
Figure 13: Average Adult Response During Purple Schedule



**Figure 14:** Average Adult Response During Red Schedule



**Figure 15:** Average Adult Response During Blue Schedule



## Discussion

### *Species Collection and Characteristic Identification:*

*Culcita* displays a wide variety of colors. The color identity of the seven characters, from 70 stars, illustrates the incredible phenotypic variation among the species. Each individual has a unique appearance and although not described here, the presence of a wide range of designs and patterns on the aboral surface of each star, lends support the possibility that no two cushion stars are alike.

### *Chromatophore Color of Periclimenes:*

*Periclimenes* is also capable of displaying a wide variety of colors. The range of colors is made possible by chromatophores. The reaction of chromatophores to external stimuli is dramatic and future research might identify the size and color(s) displayed by chromatophores under a variety of different conditions.

### *The Affect of Star Size on Shrimp Number:*

The small correlation coefficient (0.0419) strongly suggests that there is no relationship between the size of the star and the number of shrimp associates. How stars acquire associates is unknown; future research could look at shrimp recruitment onto the cushion star. The fact that shrimp were frequently observed, in the lab and in the field, moving between hosts, adds additional evidence to the argument that *Periclimenes* does not exhibit host preference.

### *Host Preference:*

Experimental evidence, from the Y maze experiment, lends additional support to the fact that *Periclimenes* lacks host preference. The fact that *Periclimenes* does not exhibit host preference does not come as much of a surprise. There is no apparent reason why *Periclimenes* would prefer an original host when it has an ability to color match any host. Whether *Periclimenes* is able to color match a background of non-living origin is one avenue for future research.

*Periclimenes* demonstrates an ability to undergo physiological color changes. The fact that the tiny shrimp is able to adjust its color to match a sea star host or an opaque cup, led to a decision to end further host preference studies. Experiments to examine the possibility of a color preference and/ or star color preference appeared to be unnecessary. After completing one round of host preference tests (original host v. host of similar size/ shape), pursuit of an experiment to test chromatophore responses to light was determined to be more appropriate.

More than 240 species of pontonine shrimp have been reported from the waters of the Indo-Pacific and many of these shallow water tropical

shrimp are generally described as participants in commensal relationships (Gosliner et al. 1996). Field and laboratory observations made over the course of my two months in Moorea, support the notion that *Periclimenes* exhibits no apparent negative or positive effect on its host and sometimes, gains obvious benefits from the association.

Observations made during the host preference experiment, support the commensal title. The eleven shrimp, free after five minutes, were found to move directly toward the shelter of a star when approached for removal from the Y maze. As soon as the shrimp saw or sensed an unidentifiable object or movement in the water, the potential threat caused it to take refuge on the nearest cushion star. When and why *Periclimenes* adopts a sea star host would make an excellent future investigation.

### *Physiological Color Change:*

The chromatophores of *Periclimenes* are extremely sensitive to light. The color intensity achieved by *Periclimenes* exposed to a light schedule indicates a marked ability by the chromatophores to expand. It was observed that there is a difference between the abundance and responsiveness of chromatophores in adult and juvenile *Periclimenes*. The difference lends itself to the belief that shrimp undergo morphological color changes as they mature. Although the experimental results do not lend themselves to strongly support the notion that *Periclimenes* experience rhythmic color changes according to a diurnal cycle, it is rapidly apparent that external stimuli have a direct effect on the presence or absence of color. These rapid changes in color are suggested to have several adaptive functions.

Rapid chromatophore-mediated color changes are important in background matching where they act to camouflage and subsequently protect the shrimp from predators (Thurman 1988). Another proposal for the purpose of rapid color change comes from Coohill et al. (1969); the change could possibly function as a protective mechanism against excessive u.v. radiation. It would be interesting to expose adult and juvenile shrimp to u.v. light and record the response. The range of adaptive functions associated with a pigmentary system depends on the shrimp's abundance, types, distribution, and responsiveness of chromatophores

Future investigations might look at the effect of temperature on coloration. In addition, should it be possible to carefully remove the sinus gland and observe the chromatophores of both blind and un-blind shrimp, the difference between the primary and secondary responses of *Periclimenes*

could possibly be determined. Following this line of research, observations of the second, somewhat less conspicuous, pigmentary effector would be interesting. The ommatidial cells of the compound eye are comparable to chromatophores in many respects and participate in photomechanical adaptations that influence visual acuity. Movements of retinal pigments are often rapidly reversible and often rhythmic (Welsh 1930, 1938).

### Conclusion

Although the association between *Culcita* and *Periclimenes* is defined as commensal, the definition offers little information regarding the details of their relationship. A closer look at *Periclimenes'* relationship with *Culcita*, reveals a complex set of behaviors which allows for a tight association with the host. How *Periclimenes* arrives at its association and how long it maintains its relationship with *Culcita*, remains unknown. The variety of approaches one can take to look at the sea star shrimp's relationship with its host are far more numerous than the variety of colors exhibited by both animals combined.

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Appendix 1 star number	aboral		color	aboral		color	aboral		color	aboral		color	aboral		color
	primary color	primary color		dot color (in)	dot color (out)		dot color (in)	dot color (out)		dot color (in)	dot color (out)		primary color	primary color	
1	green		27D6	blue	20E8	blue	20E8	bright orange	black	20E8	black	light orange	6A6		
2	maroon		12F6	purple	18A5	bright orange	7B8	dark brown	red	7B8	red	beige	4A2		
3	yellow & purple		3A8 & 18C8	grey	1C1	dark brown	7F5	grey	purple	7F5	purple	beige	4A2		
4	yellow		3A8	blue grey	23C3	dark maroon	1C1	grey	purple maroon	1C1	purple maroon	peach	6A3		
5	yellow		3A8	blue grey	23C3	dark maroon	12F4	dark maroon		12F4		light yellow	3A4		
6	yellow		3A8	blue grey	23C3	bright orange	7B8	bright orange	dark red	7B8	dark red	light yellow	3A4		
7	yellow		3A8	purple grey	18D3	yellow	3A8	yellow	dark purple	3A8	dark purple	beige & purple	4A2 & 18C8		
8	yellow		3A8	grey	1C1	dark red	10D8	dark red	black	10D8	black	beige	4A2		
9	orange brown		7C8	brown	6E8	maroon	12F6	maroon		12F6		beige & ivory	4A2 & 3A2		
10	dark purple		18E8	purple	18A5	yellow	3A8	yellow		3A8		purple	18C8		
11	light yellow		3A4	blue	20E8	light yellow	3A4	light yellow	tan	3A4	tan	light yellow	3A4		
12	yellow		3A8	black	20E8	dark purple	18E8	dark purple		18E8		ivory	3A2		
13	yellow		3A8	grey	1C1	black & orange	1E1	dark grey	black	1E1	black	peach	6A3		
14	light orange		6A6	blue grey	23C3	black & orange	10D8	black & orange	black	10D8	black	peach	6A3		
15	maize		4B8	black	black	dark red	10D8	dark red	black	10D8	black	peach	6A3		
16	black		black	black	black	yellow	3A8	yellow	black	3A8	black	light yellow	3A4		
17	purple		18C8			olive	3E8	olive		3E8		maroon	12F6		
18	yellow & maroon		3A8 & 12F6	grey	1C1	yellow	3A8	yellow	dark maroon	3A8	dark maroon	light yellow	3A4		
19	light orange		6A6	blue grey	23C3	maroon	12F6	maroon		12F6		light red	10C6		
20	yellow		3A8	purple	18A5	blue	20E8	blue	black	20E8	black	peach	6A3		
21	light yellow		3A4	brown	6E8	dark purple	18E8	dark purple	black	18E8	black	maroon	12F6		
22	maize		4B8	black	black	blue grey	23C3	blue grey	black	23C3	black	beige	4A2		
23	black		black	blue	20E3	maroon	3A8	yellow	black	3A8	black	light yellow	3A4		
24	maize		4B8	blue grey	23C3	maroon	12F6	maroon	black	12F6	black	beige	4A2		
25	maize		4B8	light purple	18A5	blue grey	23C3	blue grey	black	23C3	black	beige	4A2		
26	light purple		3A4	dark maroon	12F4	maroon	20E8	blue	maroon	20E8	maroon	beige & maroon	4A2 & 12F6		
27	light yellow		3A8	blue grey	23C3	purple	12F6	maroon	dark maroon	12F6	dark maroon	beige	4A2		
28	yellow		3A8	blue grey	23C3	purple	18C8	purple	brown	18C8	brown	beige	4A2		
29	yellow		3A8	brown	6E8	yellow	3A8	yellow	brown	3A8	brown	light yellow	3A4		
30	yellow		3A8	blue grey	23C3	maroon	12F6	maroon	brown	12F6	brown	dark peach	6A4		
31	light yellow		3A4	blue grey	23C3	orange	7A8	orange	maroon	7A8	maroon	ivory	3A2		
32	yellow		3A8	dark grey	1E1	fuscia	15B8	fuscia	maroon	15B8	maroon	beige	4A2		
33	yellow		3A8	blue	20E3	maroon	12F6	maroon	brown	3A2	brown	beige & purple	4A2 & 18C8		
34	yellow		3A8	grey	1C1	yellow orange	4A6	yellow orange	purple	12F6	purple	beige	4A2		
35	maize		4B8	grey	1C1	maroon	12F6	maroon		12F6		black	black		
36	maroon		12F6	grey	1C1	maroon	12F6	maroon		12F6		peach	6A3		
37	yellow		3A8	brown	6E8	maroon	12F6	maroon		12F6		brown	6E8		
38	dark yellow		4A8	blue grey	23C3	seafoam	1A1	white	brown	1A1	brown	brown & beige	6E8 & 4A2		
39	brown		6E8	brown	6E8	brown	26A3	seafoam	lime	26A3	lime	ivory	3A2		
40	maize		4B8	brown	6E8	brown	4A8	bright yellow		4A8		light yellow	3A4		
41	brown		6E8	brown	6E8	brown	4A8	bright yellow	brown	4A8	brown	beige	4A2		
42	maize		4B4	brown	6E8	brown	7B8	bright orange	brown	6E8	brown	dark maroon	12F4		
43	maize		4B4	blue grey	23C3	yellow	3A8	yellow	forest green	3A8	forest green	tan	5C5		
44	maize		4B4	grey	1C1	maroon	12F6	maroon	black	12F6	black	beige	4A2		
45	dark yellow		4A8												

star number	oral	color	oral	color	oral	color
1	dot blue		star blue			
2	light blue	21A3	light blue			21A3
3	red & orange	10C8 & 7A8	bright orange			7B8
4	maroon purple	13F4	maroon purple			13F4
5	light blue	21A3	light blue			21A3
6	maroon purple	13F4	maroon purple			13F4
7	light yellow	3A4	yellow & red			3A8 & 10C8
8	sunshine yellow	3A6	sunshine yellow			3A6
9	purple & lt blue	18C8 & 21A3	purple & lt blue			18C8 & 21A3
10	reddish brown	10F5	dark purple			18E8
11	purple	18C8	purple & bt orange			18C8 & 7B8
12	yellow	3A8	yellow			3A8
13	purple	18C8	purple			18C8
14	maroon	12F6	maroon & grey			12F6 & 1C1
15	dark blue	20F6	dark blue & yellow			20F6 & 3A8
16	reddish brown	10F5	purple & blue			18C8 & 10E8
17	light yellow	3A4	light yellow			3A4
18	light blue	21A3	light blue			21A3
19	light yellow	3A4	light orange			3A4
20	wine red	11D8	wine red			11D8
21	dark maroon	12F4	dark maroon			12F4
22	maroon & purple	12F6 & 18C8	light purple			18A5
23	maroon purple	13F4	dark maroon			12F4
24	light yellow	3A4	light yellow			3A4
25	red & maroon	10C8 & 12F6	maroon & red			10C8 & 12F6
26	blue	20E8	dark blue			20F6
27	maroon	12F6	dark & light blue			20F6 & 21A3
28	reddish brown	10F5	maroon			12F6
29	reddish brown	10F5	purple			18C8
30	light yellow	3A4	yellow			3A8
31	maroon brown	10F5	brown			6E8
32	ivory	3A2	ivory			3A2
33	maroon	12F6	maroon			12F6
34	light blue & grey	21A3 & 1C1	light blue purple			19A3
35	maroon	12F6	maroon			12F6
36	white	1A1	yellow			3A8
37	maroon	12F6	maroon			12F6
38	red brown	10F5	red brown			10F5
39	light blue	21A3	light blue			21A3
40	ivory	3A2	ivory			3A2
41	wedgewood	22B3	wedgewood			22B3
42	bright yellow	4A8	bright yellow			4A8
43	lt fluorescent org	5A6	lt fluorescent org			5A6
44	dark maroon	12F4	dk fluorescent org			5A8
45	orange & maroon	7A8 & 12F6	orange & maroon			7A8 & 12F6
46	maroon	12F6	maroon			12F6

Appendix 1 star number	aboral primary color	color	aboral tiny spot color	color	aboral dot color (in)	color	aboral dot color (out)	color	aboral primary color	color
46	light orange	6A6	blue	20E8	light maroon	12D4	dark maroon	12F4	beige	4A2
47	yellow	3A8	blue grey	23C3	yellow	3A8	black	black	beige	4A2
48	yellow	3A8	blue grey	23C3	yellow	3A8	black	black	beige	4A2
49	orange brown	7C8	blue grey	23C3	grey	1C1	black	black	peach	6A3
50	yellow	3A8	grey	1C1	dark maroon	12F4			beige	4A2
51	orange brown	7C8	grey	1C1	purple	18C8	maroon	12F6	beige	4A2
52	yellow	3A8	grey	1C1	maroon	12F6			peach	6A3
53	brown	6E8	grey	1C1	ice blue	23A3	light green	27A4	beige	4A2
54	light yellow	3A4	grey	1C1	maize	4B8	dark brown	7F5	beige	4A2
55	black	black	grey		ivory	3A2			beige	4A2
56	maroon	12F6			light green	27A4	lime green	29A4	ivory & brown	3A2 & 6E8
57	yellow & maize	3A8 & 4B8	blue grey	23C3	bright yellow	4A8	brown	6E8	maize	4B8
58	yellow	3A8	dark grey	1E1	light yellow	3A4	brown	6E8	dark brown	7F5
59	light green	27A4	grey	1C1	grey	1C1	maroon	12F6	beige	4A2
60	maize	4B8	dark brown	7F4	tan	5C5	dark brown	7F5	beige	4A2
61	orange	7A8	blue grey	23C3	grey	1C1	brown	6E8	peach	6A3
62	yellow	3A8	blue	20E8	purple	18C8	dark maroon	12F4	peach	6A3
63	brown	6E8	grey	1C1	lt grey & purple	1B1 & 18C8			beige	4A2
64	yellow orange	4A6	black	black	light grey	1B1	dark maroon	12F	beige & red	4A2 & 10C8
65	brown maroon	10F5	grey	1C1	grey	1C1	maroon	12F6	beige	4A2
66	yellow	3A8	dark grey	1E1	purple	18C8	grey	1C1	ivory	3A2
67	bright yellow	4A8	maroon	12F6	white	1A1	maroon	12F6	beige & red	4A2 & 10C8
68	maize	4B8	grey	1C1	dark purple	18E8	black	black	peach	6A3
69	yellow & maize	3A8 & 4B8	blue grey	23C3	purple	18C8	black	black	peach	6A3
70	bright yellow	4A8			grey	1C1	dark purple	18E8	beige & maroon	4A2 & 12F6

star number	oral	color	oral	color
1	dot color		star color	
47	dark lavender	18A4	dark lavender	18A4
48	brick red	9D8	brick red	9D8
49	orange	7A8	orange	7A8
50	maroon & grey	12F6 & 1C1	maroon & grey	12F6 & 1C1
51	maroon	12F6	maroon	12F6
52	maroon	12F6	purple	18C8
53	lavender	18A3	lavender	18A3
54	light blue	21A3	light lavender	18A2
55	dark brown	7F5	dark maroon	12F4
56	purple	18C8	purple	18C8
57	ivory	3A2	lightest blue	23A2
58	yellow & maroon	3A8 & 12F6	yellow & maroon	3A8 & 12F6
59	ice blue	23A3	ice blue	23A3
60	wine red	11D8	wine red	11D8
61	lavender	18A3	lavender	18A3
62	turquoise	24A6	wedgewood	22B3
63	wine red	11D8	purple	18C8
64	lightest purple	18A2	lavender	18A3
65	grey blue	23C3	grey blue	23C3
66	brown	6E8	grey & blue	1C1 & 20E3
67	brick red	3A2	wine red	11D8
68	grey	1C1	purple grey	18D3
69	purple	18C8	lavender	18A3
70	brown red	10F5	blue grey	23C3
	beige & blue grey	4A2 & 23C3	off white & red	1A1 & 10C8

# Fauna of Natural and Resort Beaches on Moorea, French Polynesia

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**ABSTRACT.** The high island of Moorea located in French Polynesia is a prime tourist destination. Species richness and abundance was measured for three natural and three resort beaches in order to assess anthropogenic disturbance. Opunohu natural beach had the highest species richness while Club Med resort had the lowest. Species richness was concentrated above the intertidal zone on beaches with high amounts of organic matter and within the intertidal zone on beaches with low amounts of organic matter. Natural beaches mostly contained amphipods, polychaetes, and oligochaetes, while resort beaches contained mostly polychaetes and anomurans. Similarity between beaches was low according to Jaccard's coefficients. A complete absence of amphipods and isopods on resort beaches may make these animals good bio-indicators of disturbance brought on by the construction of resort hotels.

## Introduction

Sandy beaches were once thought of as ecological deserts. It was not until 1953, when Dahl published a paper on crustaceans living on European and South American beaches, that this view began to change. Today, sandy beaches are widely regarded as diverse and dynamic systems worthy of study.

The spatial and temporal variation of species on sandy beaches is well documented (Brazeiro and Defeo 1996; Dexter 1984; Baron and Calvier 1994; McLachlan *et al.* 1981). While natural processes on sandy beaches have been extensively studied, anthropogenic disturbance has not received the same attention. Some notable exceptions include the studies by Moffett (1998) and Jaramillo and Conterns 1996. Moffett studied the effect of human trampling on sandy beach fauna and observed that the isopod *Eurydice longicorus* was particularly vulnerable. It is ironic that tropical beaches are some of the most threatened and least studied in regards to human disturbance.

Tourism in tropical locales is increasing at an exponential rate. Nowhere is this more evident than in the Society Islands of French Polynesia. Tourism has quadrupled in these regions in the last three decades, with 180,000 people visiting in 1997 (Stanley 1999). The island of Moorea, lying 16 km west of Papeete, is the third most visited island in the Societies. Moorea's north coast includes many beautiful beaches, and it is here that the majority of its bungalow style resorts have been built.

In October and November of 1999, I conducted a study on Moorea designed to look at the effects resort tourism has on the fauna of sandy beaches. Six beaches, three natural and three resort, were studied to answer the following questions: 1) how does species richness differ between natural and resort beaches; 2) do natural and resort beaches have different kinds of faunas and in

different proportions; and 3) what specifically causes these differences? The information and ideas presented in this paper are intended to help conserve tropical beaches, and to catalyze further studies in the area of beach conservation, specifically on Moorea.

## Methods

Along the northern end of Moorea (17°30' S, 149°50' W), six beaches, three resort and three natural, were sampled (Figure 1, natural beaches marked with a star). The Club Med resort, Beachcomber resort, Temae natural, and Temae Sofitel resort were white sand beaches of coralline origin. The Beachcomber resort was an artificial white sand beach with sand imported from Bora-Bora (interview). Opunohu natural beach was a basaltic black sand beach, and Beachcomber natural was a gray sand beach. Both of these beaches had high amounts of organic matter. In general, natural beaches tended to have more organic debris, a larger range of sand grain sizes including small rocks, and less human disturbance. Resort beaches appeared to consist of homogenous white sand with little or no organic debris, and were highly disturbed through trampling and combing of the sand.

The field protocol for each site consisted of two six meter transects placed perpendicular to the shore at a random distance from each other. At Club Med resort, Beachcomber resort, and at Opunohu, the two transects were laid down at the same time on the same day. At Beachcomber natural, Temae natural, and at Temae Sofitel resort beach, the two transects were laid down ten to fifteen days apart. Sampling for all sites took place between 7:30 and 11:00 A.M., with sampling within sites taking place at the same time. One end of the transect was placed at the water line, and if the beach had a substantial swash zone, the middle of this zone was chosen. Six samples were taken on each transect every meter starting at

the water line, making a total of 12 samples per site. Each sample consisted of approximately five scoops of sand to a depth of about 30 centimeters. Sand was washed through a 1 mm sieve, recording species types and abundance. Data from samples taken equal distances from the water line within each site were pooled together.

Species diversity was not calculated for any sites because of the tendency of natural beaches to fluctuate widely in species density, but not in richness over time (Baron and Clavier 1994). This was seen within sites where transects were taken on different days. Abundance of certain species varied widely, but overall species richness stayed relatively constant. In this paper, species richness specifically refers to the different morphological forms I saw. Each form was labeled a different species. Amphipods and isopods were each labeled one kind of species because of the difficulty in identifying novel morphological attributes.

Two sample one-tailed t-tests and cluster analysis using Jaccard's coefficients were used to analyze the data.

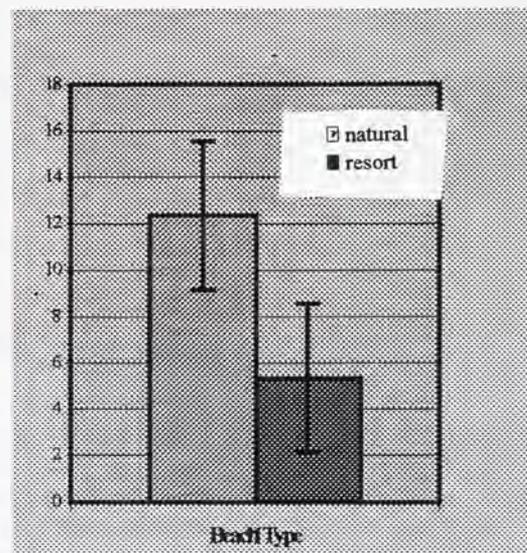
### Results

Species richness and average density (species/1 liter of sand) was higher at every natural beach than every resort beach (Table 1). Average species richness for natural beaches was 12.33 (SD 3.21) and 5.66 (SD 3.21) for resort beaches (Figure 2). This result was significant ( $p < .02799$ ). Opunohu Bay had the largest number of species while Club Med had the lowest. In the beaches with high organic input, Beachcomber natural and Opunohu, species richness was centered well above the waterline. Species richness at the four white sand beaches was concentrated within the intertidal zone (Figure 3).

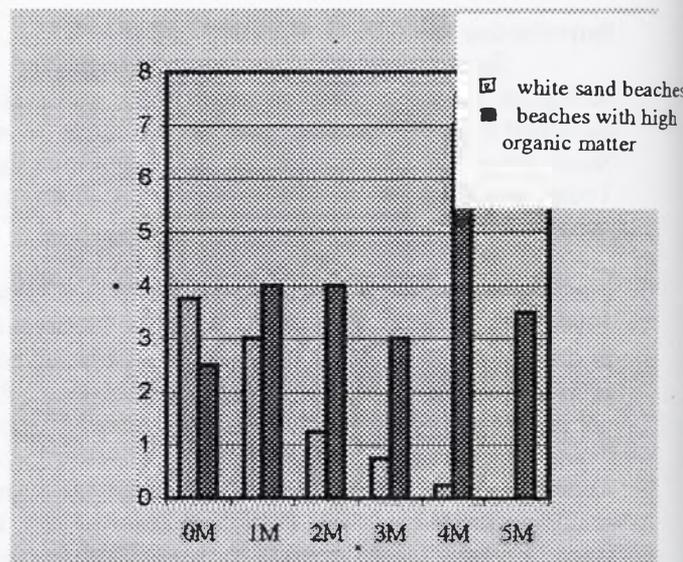
	species richness	average density
Club Med Resort	3	.136 +/- .119
Beachcomber Resort	4	.187 +/- .126
Beachcomber natural	10	7.368 +/- 17.734
Opunohu Bay	16	1.359 +/- 2.159
Temae natural	11	.197 +/- .302
Temae Sofitel resort	9	.187 +/- .126

**Table 1:** species richness and average density for all six sites

Different species in different proportions existed between natural and resort beaches. Natural beaches, mainly Opunohu and Beachcomber, were dominated by amphipods. Oligochaetes and polychaetes were also abundant (Figure 4). Polychaetes dominated at resort beaches, followed by anomurans and insects (Figure 5).



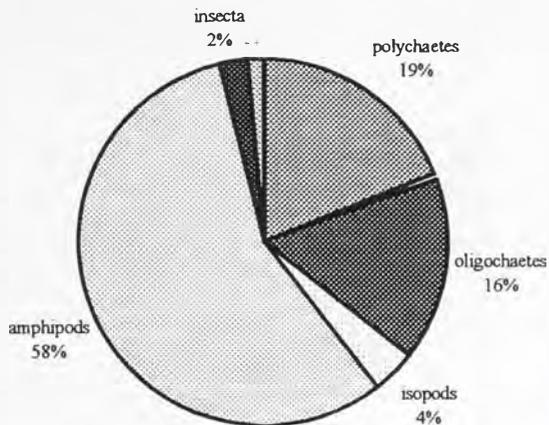
**Figure 2.** Average species richness for natural and resort sites. Average species richness is on the y-axis.



**Figure 3.** Average species richness as a function of distance from the water line for two types of beaches. Average species richness on the y-axis and distance from the water line on the x-axis.

The polychaete families *Pisionidea* and *Neridea* were most common on natural beaches while *Glyceridae*, *Pisionidae* and *Palmyidae* were most common on resort beaches. Opunohu natural and Beachcomber natural had the largest average density.

A cluster analysis shows that Beachcomber natural and Opunohu natural beach had the highest measure of species similarity, 36.8 (Figure 6). The white sand resort beaches, Temae Sofitel Resort and Club Med resort, were grouped together, having a coefficient of 20. Beachcomber Resort artificial beach had a coefficient of 27.2 with Beachcomber natural and Opunohu natural, and these three beaches had a measure of 21.6 with Temae natural. Overall, the beaches showed a large amount of species variation and no beach was very similar to another.



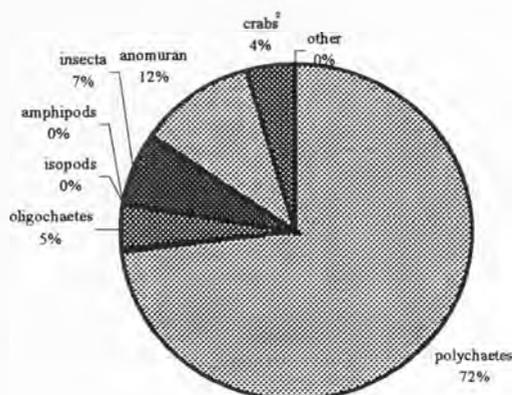
**Figure 4.** Relative abundance of fauna at natural beaches

### Discussion

Species richness was greater at natural beaches than at resort beaches. Natural beaches tended to have a greater amount of organic input, variation in sand grain size, and less human disturbance. Resort beaches had less organic input, more homogeneous sand, and more human disturbance. Each of these factors can account for differences in species richness. Zonation of species richness was different at beaches with high organic matter (Opunohu natural and Beachcomber natural) than at beaches without high amounts of organic matter, the white sand beaches (Figure 3). Organisms at beaches with high organic matter did not have to depend entirely on nutrient exchange with the ocean. As a result, species richness was concentrated well above the waterline, suggesting that the additional inputs of organic debris from trees and plants may be a more important food source for organisms at these beaches than the ocean is. At the white sand beaches, almost all of the nutrient exchange took place at the shore/ocean interface within the intertidal zone. As a result, species richness was concentrated within this zone and decreased as distance increased from this zone. This finding is consistent with other studies (Dexter 1984).

In addition to higher organic input, natural beaches had a greater diversity of habitats in and on top of the sand. Opunohu natural beach had fine sand as well as small rocks higher up on the beach. Polychaetes mainly lived in the fine sand along the shore, while insect larvae lived in the small rocks. At Beachcomber natural beach, amphipods were found living in and under organic debris washed in from the sea and oligochaetes were particularly abundant around tree roots buried in the sand. Temae natural beach had a coarse sand zone at the water line that supported a large population of isopods, and finer sand zone that supported polychaetes. In general, environments with a high number of diverse habitats have high species richness (Begon *et al.* 1996).

Resort beaches had a low input of organic matter from terrestrial sources mainly because they were combed a couple of times per month to remove any debris



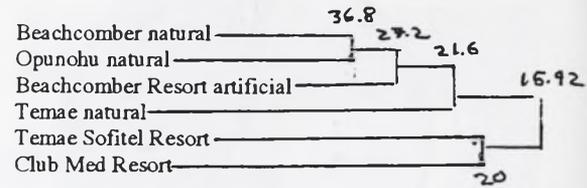
**Figure 5.** Relative abundance of fauna at resort beaches

including decaying *Turbinaria*, tree leaves, and rocks. Not only does this decrease organic input, but it mixes the sand grains together, forming a more homogeneous and uniform environment. Future studies should focus on this type of human disturbance and see how it affects species richness.

In addition to species richness, natural and resort beaches had different sets of fauna (Figure 4 and 5). This can be explained by the feeding ecology of the organisms sampled. Amphipods and isopods are typically scavengers and detritivores, and so thrive in environments high in detritus. Not one amphipod or isopod was found at a resort beach, possibly because these beaches had little or no organic debris. Oligochaetes, found mainly on the natural beaches, are deposit feeders that require substrata rich in organic nutrients. Beachcomber natural and Opunohu natural contained almost all of the oligochaetes. Resort beaches contained mostly animals efficient at extracting nutrients within the highly dynamic intertidal zone, like anomurans and polychaetes. Anomurans are especially adapted to resort beach conditions because they are primarily filter feeders. Many of the polychaetes found at resort beaches had large palps that could also be used for filter feeding (Frouin 1998). Polychaetes have very diverse feeding strategies, so can take advantage of the limited number of food choices at resort beaches, in addition to the large number of food choices at natural beaches.

The cluster analysis showed that every beach was significantly dissimilar to every other, with the exception of Beachcomber natural and Opunohu natural. Temae natural and Temae Sofitel resort beach were the most similar in habitat and conditions, but only had a Jaccard coefficient of 17.6. Temae natural beach was dominated by isopods with a few polychaetes, amphipods, and oligochaetes; Temae resort beach was dominated by polychaetes, and most of them were different from the ones at Temae natural. The main difference between the two beaches was that the resort beach was cleaned of rocks approximately two times a month while the natural beach was not. A study by Frouin 1998, showed that spionid polychaetes on Tahiti were not found in areas of coarse sand and rocks because these sediments did not enable the worms to build semi-permanent mucus tubes used in

Beachcomber natural (1)					
Beachcomber Resort (2)	27.3				
Opunohu natural (3)	36.8	17.6			
Club Med (4)	8.3	16.7	11.8		
Temae natural (5)	23.5	7.1	17.4	16.7	
Temae Resort (6)	5.5	8.3	4.2	20	17.6
	1	2	3	4	5



**Figure 6.** Initial matrix and cluster diagram using Jaccard's coefficient

feeding.

The absence of isopods and amphipods on all the resort beaches sampled suggests that these animals may be particularly susceptible to disturbance. Future studies should look at how amphipod and isopod populations change in response to human-induced mechanical disturbance, specifically raking. These animals are already used as bio-indicators for water pollution (Lawrence and Poulter 1998). The lack of isopods and amphipods and the high abundance of polychaete worms on Moorean resort beaches may be indicative of the homogenization of this habitat. Since species density temporally varies a great deal on sandy beaches, the use of bio-indicators in these environments should be approached with caution (Gourbault *et al.* 1998). An integrated approach using multiple animal groups may be the best way to measure change in such temporally -variable habitats.

Overall, the diversity of beaches and conditions on the island of Moorea made it difficult to make sweeping comparisons between natural and resort beaches. Isolating anthropogenic disturbance as being the main cause in decreasing species richness on resort beaches was difficult to establish. Unlike typical exposed sandy beaches, the natural beaches of Moorea are highly influenced by organic inputs from plants and debris washed in from the ocean. A barrier reef, lagoon, and fringing reef add to the complexity of these systems. The idea that beaches can be fully defined by grain characteristics, wave climate, and tidal regime (McLachlan 1983), may not be applicable to Moorean beaches. In future studies assessing anthropogenic affects in tropical locales, only beaches with extremely similar conditions in common should be compared to each other, to rule out confounding factors. Samples should also be numerous as well as large, to take into account the low species density of sandy beaches. Sand grain size and organic matter content should also be quantitatively measured. The variety of beach types on Moorea makes the conservation of its beaches vitally important. Not only do these beaches provide habitats for a diverse range of animals, but they serve as 'great incubative and digestive systems' (McLachlan and Turner 1993) that help filter the sea water, break down organic matter, and deliver nutrients back into the sea.

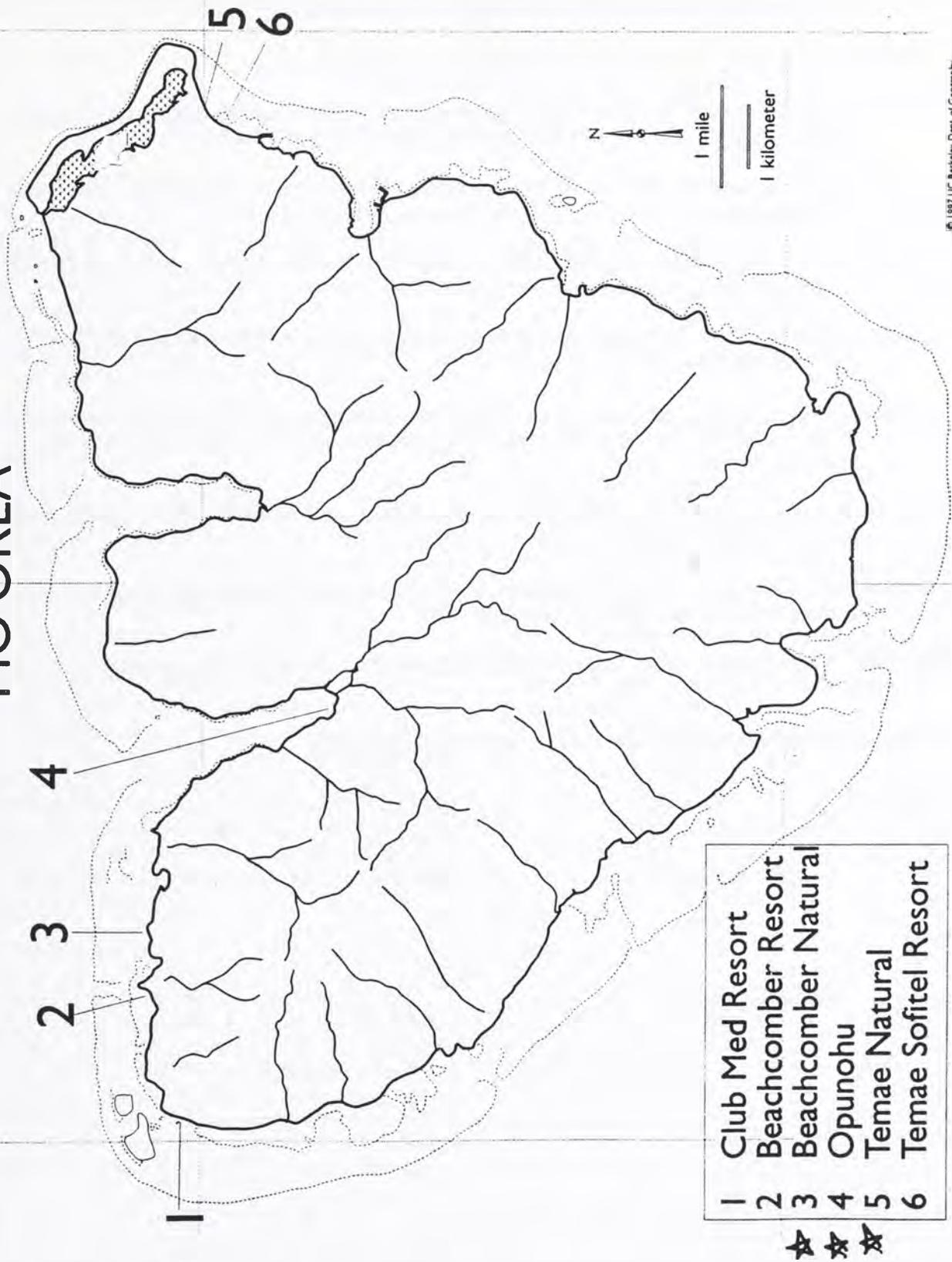
## Conclusions

The beaches of Moorea are varied and complex. The resort beaches on Moorea have lower average species richness and lower average density than the natural beaches. Resort beaches and natural beaches characteristically have different types of fauna and in different proportions. Moorean natural beaches appear to be highly variable in conditions and species, and some are highly influenced by the input of organic matter. The homogenization of resort beaches appears to be the reason for the decrease in species richness. The absence of amphipods and isopods on resort beaches may make those organisms good bio-indicators of human disturbance. Future studies focusing on anthropogenic affects on sandy beaches should be adequately controlled for confounding factors. The need for this work is essential for the conservation of sandy beaches on Moorea and other tropical locales.

## Acknowledgments

I would like to thank John and Debby for the use of the facilities, especially John for showing me the swash technique and in identifying specimens. Tons of thanks to the T.A.s for being patient, especially James. My gratitude is extended to the professors for all their help and classic things they said. Thanks to Jeff Judd for helping me identify worms, and to the people of Moorea, thanks for making my stay on Moorea awesome, maururu.

# MO'OREA



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fig. 1 Beaches sampled

Figure 1. Beaches sampled. Natural beaches marked with a star.

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# Reef Variability with Gard to Wave Regime Temae, Moorea, French Polynesia

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**ABSTRACT.** Measurements of wave energy and reef morphology were taken at two sites on Moorea, French Polynesia. Data collected over the months of October and November show that the most significant factor determining the structure of coral reef communities on the northeast angle of Moorea is physical disturbance from waves. Site comparison on Motu Temae suggests moderate wave stress conditions maintain four well defined reef zones. Increased wave exposure causes variable effects with in the reef zones but the pattern of zonation as a whole is maintained. Site exposure to a high wave regime is sufficient enough to modify the structure of the fore reef by increasing the frequency on the spur and groove system by decreasing average widths. The breaking waves are then filtered by the ridge crest and generate a lagoon al flow parallel to shore. Measurements indicate this flow to be sufficient to modify the percentage of live coral cover in the reef flat.

## Introduction

Apart from the hydrodynamic aspects of wave impact on coral reefs, (Roberts et al. 1975) its effects on the biota cannot be underestimated. Wave surge is an important factor influencing community zonation. (Tunncliffe 1982). While coral workers agree that waves and currents play an important role in carbonate systems, the number of investigations that actually focused on physical processes on reefs of differing geometries is limited. It is therefore the purpose of this study to investigate some of the relationships that exist between form and process in a coral reef environment by comparing the morphologic and biologic structure of two sites where wave energy is considered a dominant process. The variability of coral reefs at these two sites is assessed with respect to the wave climate.

## Site, Material and Methods

Motu Temae is located on the northeast angle of Moorea, French Polynesia (Figure 1). The 3.5-km peninsular projection is unique to the island of Moorea. It represents 4.5 km of barrier reef that is directly connected to the shore in such a way that a narrow reef flat, rather than a deep lagoon separate the coast from the barrier reef. The Motu's proximity to the barrier reef and position relative to the predominant swell direction makes it an ideal site to study wave interactions with reefs.

Two sites were chosen along the eastern third of Temae based on their wave power regimes. Site 1 is situated at Fauupo Point on the eastern most corner of the island. The point is incident to the 1-3 meter seasonal swell from the east-

southeast. Wave energy is concentrated here and the site experiences a high wave regime.

One-kilometer west, adjacent to the airport, site 2 experiences moderate wave stress. The lower wave regime at airport site is due to swell refraction around Fauupo point that dissipates the swell energy changing the shape and direction of the waves. The wave gradient and provided between sites 1 and 2 affords a unique look at wave processes on reef geometry, and sediment distribution.



Figure 1. Study Site, Motu Temae, NE angle Moorea, French Polynesia

### Reef Variability

The overall morphologies were measured for site comparison. The extent of reef visible above water at the airport and Fauupo Point was measured over a two-week period by Top-Con survey.

As a method of identifying the structure of the fore-reef, (the submerged portion of the reef mass extending seaward from the reef crest) the frequency of grooves and the spacing of these features was determined. These parameters were measured by lying a 40 meter transect line parallel to the algal ridge crest from the eastern edge of the first groove visible upon entry. Measurement commenced at what was visually determined to be the seaward extent of the spur and groove. The width of both features was recorded in meters as well as the overall number of grooves to determine the frequency.

The percentage of live coral in the reef flat was compared at the two sites using a line transect method. Random number tables determined the position of three transects along a fifty-meter stretch of beach. The transects were laid perpendicular to the algal ridge for the total distance of the reef flat. The intersection of coral heads was recorded, summed and the coral cover percentage was extracted. The mean coral head diameter was then calculated.

### Wave Regimes

Wave regimes were quantified visually at the two sites over a period of 7 non-consecutive days. Twenty-five waves were counted, catalogued and their heights and period compared to an equal number of waves at the other site. As never more than twenty minutes elapsed between observations at the two sites one can assume both sites were viewed at approximate times in the tidal cycle and relative swell position.

### Statistical Analysis

The site survey and wave measurements were compared and analyzed for significant differences using T-tests.

### Results

#### Reef Variability

The seaward slope of the fore-reefs from the surface down to a few meters is generally cut by a system of more or less spaced grooves separated by spurs (Figure 2). At Temae, as elsewhere, a system of spurs & grooves characterize the reefs on coasts exposed to high wave energy (Guilcher 1988). The grooves are frequent and relatively straight near the land ward extent of the fore-reef. They average 1.8 meters in width. The spurs separating

the grooves are flattened ridges 3.1 meters in average width. They slope seaward and meet the off reef floor characterized by fewer coral heads and coralling algae is abundant.

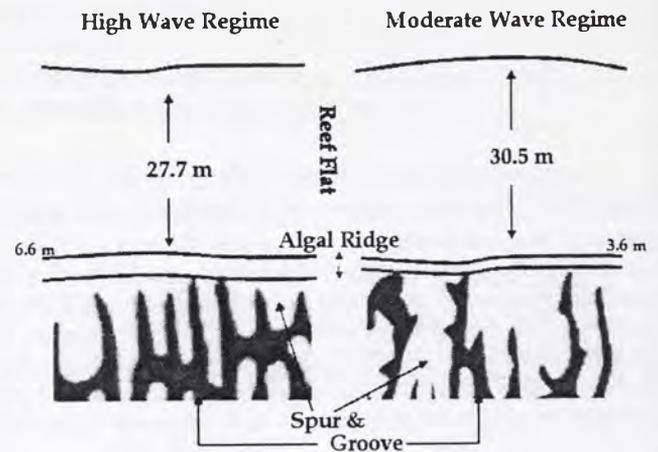


Figure 2. Fore/Back-reef Geomorphology Sites 1 and 2. (Plan View)



Figure 3. Fore/Back-reef Geomorphology Sites 1 and 2. (Profile)

At the moderate energy site, there is a lower frequency of spurs and grooves (Table 1). The flattened tops of the spurs average 4.7 meters and carry luxuriant developments of coral and coralline algae, whereas the bare floors of the grooves, support little coral or algal growth because of scoring action and their erosional nature. The channels average 3.2 meters wide and frequently merge with a zone of sediment accumulation and deep patch reef development.

Parameter	High Wave Regime	Moderate Wave Regime
Groove	1.8 (m)	3.2 (m)
SD	0.4	1.4
n	9	5
Spur	3.1 (m)	4.7 (m)
SD	0.9	1.3
n	8	5

Table 1. Average Spur&Groove Widths in Meters

The upper part of the spur and groove system forms a ridge with a crest at its apex that extends out of the water (Figure 3). This algal ridge is very straight and defined by the breaker line. The ridge

varies in width between the two sites spanning 6.6 meters at the high-energy regime and nearly half that, 3.6 meters at site 2 (Figure 2). The landward limit is characterized by a rather abrupt change in topography dropping .6 and .4 meters to the floor of the back reef at sites 1 and 2 respectively.

The reef flat extends inward from the inner side of the algal ridge. It is floored by coral sand and rubble, algal encrustation and a variety of small coral heads (Table 2). The living coral cover at site 2 is 8.13%. The percentage decreases as you move eastwards to site 1. Where the percentage of live coral is .34%.

Parameter	High Wave Regime	Moderate Wave Regime
Mean Coral Diameter	0.03 (m)	0.14 (m)
n	6	62
% Area Covered	0.34%	8.13%

Table 2. Reef Flat Coral Coverage Sites 1 & 2

#### Wave Regime

The wave heights between sites 1 and 2 were significantly different. ( $p < .05$ ) At the Point, wave attack averaged 40% higher than waves 1 kilometer to the west at the airport adjacent site.

#### Discussion

Wave and current studies conducted have identified a close relationship between physical processes, reef geometry, (Inman et al. 1963; Roberts et al 1975; Davies 1977; Roberts 1980; and others). Since strong trade winds are a common occurrence, the 1-3 meter swells observed probably occurs frequently in any year and one can expect that the wave regime may indeed be a major factor controlling a number of reef processes at Temae.

A significant proportion of the incoming wave energy is extracted by frictional attenuation along the fore reef and, more importantly, breaking activity at the reef crest. (Roberts & Suhayda 1983). A high wave regime intensifies the wave effect the fore-reef by moving the breaker points seaward along the fore reef and consequently affects a larger area and deeper part of the reef. Fairly constant surf, requiring high wave energy and the persistence of the same wind direction are important requirements for algal ridge development. The increased area, intensity and

volumes of water produced by the seaward shift at the high wave regime provides a mechanism for the differences in spur and groove frequency and algal ridge construction between sites.

The same input wave heights are significantly reduced and high frequency waves are produced as waves propagate over the reef crest. The degree to which wave energy is modified or filtered depends on several factors, including overall reef geometry, width of the shallow reef flat, and uniformity of depth across the back reef and width of the shallow reef flat (Roberts & Suhayda 1983). However with no appreciable differences between these factors in the back reefs of the two sites the flow over the reef is responsible for the differences in coral cover.

#### Conclusion

The measurements at Temae did not exhibit significant differences from the results of previous studies on wave current contributions to reef processes such as sediment transport (Roberts 1980), the zonation of corals (Birkland 1974) the water circulation over the reefs (Black 1977) and the geomorphology of coral. The observations did however provide data for further comparisons and suggestions into the plexus of interactions between biological and physical processes involved in morphologic and biologic variability of reefs. The site-specific observations serve to refine the extent to which the process of wave attack operates on and affects the geometric framework provided by the reef. Further studies must be conducted on many different reef types (in different wave energy regimes) before generalities concerning process-response interactions can be formulated.

#### Acknowledgements

Many Thanks to everyone involved at the Gump Research Station, Moorea, this fall. The suggestions of Mr. John Boland were greatly appreciated as was the advice of Profs. David Lindberg, Jere Lipps and Brent Mishler. I am appreciative of Norm Hetland for his efforts in making the surveys possible. I am also extremely thankful for the friendships fostered in the field. In this respect, Andres Lebensohn and Drs. Baker and Brusck proved invaluable.

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# Plant recovery on fire scars in Moorea, French Polynesia

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**ABSTRACT.** Fire is becoming more and more frequent in the tropics. This study examined plant recovery after burns on sites in Moorea, French Polynesia. Fire on tropical islands presents a unique set of circumstances because species diversity is relatively low, and the threat of invasion by exotic species is high. Burn sites examined ranged from one to eight years of age. Paired comparisons were used, placing the control plots in adjacent unburned areas. The study looked at species richness, finding significant differences between burns and controls, the differences decreasing with increasing site age. Fire reduces species diversity, and after eight years, recovery still has not been completed. Similarity in community composition between burn sites was also examined using Jaccard Coefficients. The two older burn sites dominated by *Dicranopteris linearis*, were more similar (Jaccard Coefficient .21). *Dicranopteris*, a native, weedy fern may be arresting succession. The younger site, almost barren, was very dissimilar (Jaccard Coefficients .0256 and .0233). Perhaps the younger site is at an earlier stage in succession. Control sites varied in species composition, probably due to between site differences. Observation of other fire scars on the island indicate that ferns may also contribute to more intense, frequent fires.

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## Introduction

Fire in the tropics has a long history (Turcq, B.A. et al 1998). However the study of fire in the tropics has only recently begun to accelerate, for two main reasons. First, recent studies have found that naturally-caused fires, mostly from lightning, have occurred more frequently in the past than previously assumed (Middleton et al 1997). Second, the increase in human activity in the tropics has led to changes in fire regimes, both at a global level, such as global warming, and at local levels, with activities such as slash and burn agriculture (Uhl and Kauffman 1990). For general reviews of fire in the tropics, see Goldammer (1990) and Mueller-Dombois (1981).

There is no set progression followed in plant recovery after fire in the tropics. Each recovering burn is unique both with respect to preexisting conditions--such as fuel load, canopy cover, etc. (Uhl and Kauffman 1990), and conditions affecting recovery after fire, such as erosion, presence of exotic species, etc (Woods 1989, Uhl et al 1982). The goal of this study was to take a look at what effect burns have on plant recovery after fire on a tropical island. The study examines what species are returning after burns, and how they compare to what existed before the fire. It also examines species dominance, seeking to answer

questions as to which plants are dominating after fires, why, and how this compares to species existing before. One final aspect briefly considered is whether exotic species or native species are more successful in colonizing burns.

## Materials and Methods

The study took place in Moorea, French Polynesia, a volcanic island, found at 144° 50' W and 17° 30' S, 30 km west of Tahiti, in the South Pacific Ocean. A tropical island, its climate is typical of the tropics, with mean annual rainfall ranging from 1500mm to over 3,000mm depending on elevation. Its population of 12,000 mainly inhabits the more level coastal areas (O.R.S.T.O.M. 1993).

Three study sites were selected for use in a paired comparison experiment. Attempts were made to choose sites of various ages with hopes of gaining information on succession. Each site consisted of a previously burned area and a neighboring unburned area for use as a control, the two "treatments" in this study. Care was taken to make sure all variables were controlled for, except the burn itself. Slope angle, slope direction, soil type, and hydrological properties were all taken into account. Age of the burns was determined by interviewing adjacent residents.

Sites that had burned two or more times in recent years were not chosen.

For each site, a site description was compiled, including exact location, date of the fire, size of the burn, topography, slope angle, direction of slope, light information, and substrate type. Size of the control area was difficult to estimate because it was often part of vegetation continuing inland. Therefore, locations given for the controls are where sampling actually took place.

*Site one* (Figure 1) is located on the northern side of Moorea, across the circum-island road from the Beachcomber Park Royal Hotel, 200 meters inland. The burn ( $17^{\circ}29'44''\text{S}$ ,  $149^{\circ}53'35''\text{W}$ ) and its control to the east/north-east ( $17^{\circ}29'50''\text{S}$ ,  $149^{\circ}53'38''\text{W}$ ) are on an approximately  $20^{\circ}$  slope on rocky, hard clay, oxidized basalt soils situated at less than 100 meters above sea level, against a valley wall. The year-old burn extends over approximately 20 vertical meters and is less than 1 Ha in size. The site receives an average rainfall of 1500mm per year (O.R.S.T.O.M. 1993). Heavy erosion is taking place on the almost barren burn site, but in the control the ground has smoother

topography. The slope faces north/northeast and receives direct sunlight for approximately eight hours of the day. This part of the island is in a rain shadow and receives less rain than other parts of the island (O.R.S.T.O.M. 1993). The burned area is mostly bare ground, containing some cover by lichen and occasional plant. In contrast the control is covered mostly with *Lantana camara*. The source of ignition appears to have been on a nearby coconut plantation.

*Site two*, a four-year-old burn, is located approximately 0.5 km north of Haapiti on the southwest part of the island, with the burn at  $17^{\circ}33'17''\text{S}$ ,  $149^{\circ}51'16''\text{W}$  and the control at  $17^{\circ}33'23''\text{S}$ ,  $149^{\circ}52'16''\text{W}$ . It receives 2100mm of rain per year (O.R.S.T.O.M. 1993). Four years ago the fire burned up a ridge for about one kilometer, with the width varying from less than 100 meters at either end to more than 300 meters at intermediate points. The crest of the ridge is rounded. In places, the slope is as great as  $25^{\circ}$ . There is evidence of erosion before plant cover was re-established. The burn is about 4 Ha in size, and covers more than 100 vertical meters,

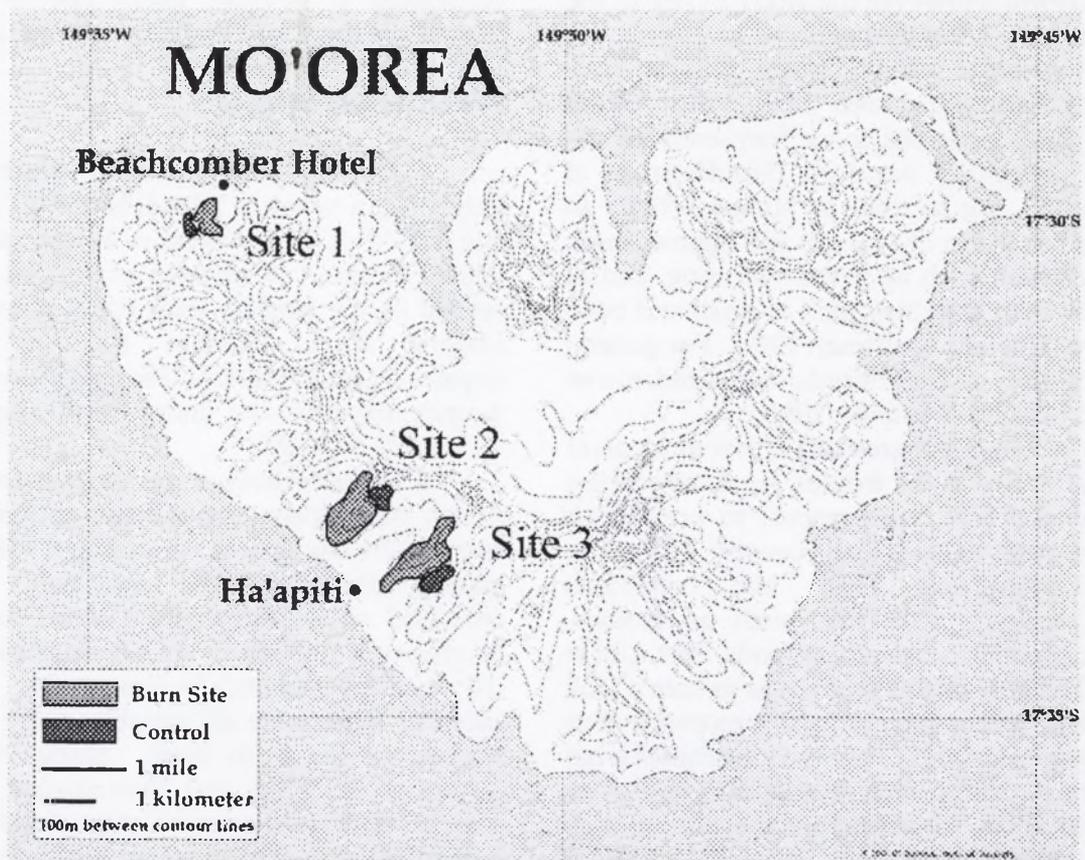


Figure 1. Map of Moorea, French Polynesia, showing locations of study sites.

beginning at 150 meters above sea level. The soil is also basalt, though more broken down, with smaller particles, than site one. The slope faces west/southwest, and because the burn spans a ridge, receives direct sunlight for almost the entire day. Considerably more rain falls on this part of the island. The burned area is dominated by *Dicranopteris linearis*, a fast-growing fern, and by *Metrosideros collina*. The control has an almost complete canopy, with a number of plant species. The east edge of the burn borders a No-no plantation, which, on close inspection confirmed by interviews with landowners, is still burnt regularly for weed control.

*Site three*, (17°33'44"S, 149°51'58"W [burn]; 17°33'48,"149°51'57" [control]) located one kilometer southeast of Haapiti, is eight years old. It begins 50 meters above sea level, where it burned along a ridge for approximately 1.5 km. The site is 200 m wide possibly more at some points and never has a slope of more than 20°. The overall area burnt is 5 Ha. The site receives 2100mm of rain annually (O.R.S.T.O.M. 1993). The northeast facing slope gradually decreases in angle into the fringes of Haapiti. Again the ridge crest is rounded. Similar to site two, the soil is basalt in origin and has a layer of soil. Two strips were observed where extra moisture moves off the hill, though there was no evidence of running water. The ridge faces west and also receives direct sunlight most of the day. The plant composition of the burn includes *Dicranopteris* and *Metrocideros* again. Large amounts of *Cocos nucifera*, *Mangifera indica*, and *Hibiscus tiliacens* can be found in the control. The source of ignition appears to have come from yard waste burning in a nearby cemetery.

To randomly select quadrats at site one, we placed a string down as close to the middle of the plot as possible. It bisected the burn on its longest dimension and likewise the control. Survey sites along this line were chosen using a random number table. If the next random number was odd we went left; or if even, right. Finally, the distance perpendicular to the line was randomly chosen and the exact center of the quadrat placed at its end. Quadrats were rejected if they came within four meters of an edge, and a new distance from the line chosen. The quadrat was placed parallel to the line.

Because of their relatively larger areas, quadrat locations at sites two and three were chosen using compass heading and number of

steps, the number of steps limited to 400. Headings and number of steps were taken from a random number table. After completing work at one quadrat, we would continue from that particular quadrat on our new heading. If an edge or other aberration was encountered, a new heading was selected, and steps repeated. The quadrat was placed with one side parallel to the ridge crest.

The area of the quadrats was 1 m<sup>2</sup>, except for the Site One burn where 2 m x 2 m was used. On the site one burn we used a 1 m x 1 m PVC square, which was subdivided into 10 cm by 10 cm squares. This PVC square was then placed four times around the center point determined by the random number table. For the site one control, and all remaining quadrats, four stakes and a 0.5 m piece of PVC were used to measure out a 0.5 m x 0.5 m square four times around the center point of the quadrat. Next, in each square the presence of species, number of individuals, height of tallest individual of each species, and percent coverage (including bare ground and individuals whose branches reach over into the quadrat) were recorded. It was possible to have more than 100 percent cover per quadrat, because plants were at different levels.

When possible, species were identified in the field. Otherwise notes were taken and pictures drawn for later comparison with field lab herbarium specimens, Jepson Herbarium (University of California at Berkeley) specimens, with photographs in Whistler (1995) and Valier (1995).

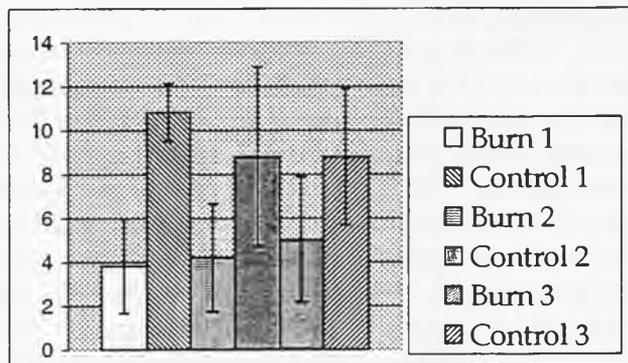
Finally, using Microsoft Excel, data was analyzed for trends in species richness, species dominance, and community similarity. Two-way ANOVAs and one-way ANOVAs were used mainly for species richness analysis, whereas simple comparisons of graphs were used for species dominance. Finally, Jaccard Coefficients of Community were calculated to look for similarity of species composition between burns and controls of all sites.

## Results

At all sites combined, fifty-two species were included in the study, forty-one of which were identified. Seven species were ground dwelling mosses and lichen, eight species of ferns, eight monocots, and twenty-eight dicot species.

Source of Variation	F	P-value
Site	0.2043	0.8167
Burn/Control	25.2298	3.92E-05
Interaction	0.8851	0.4257

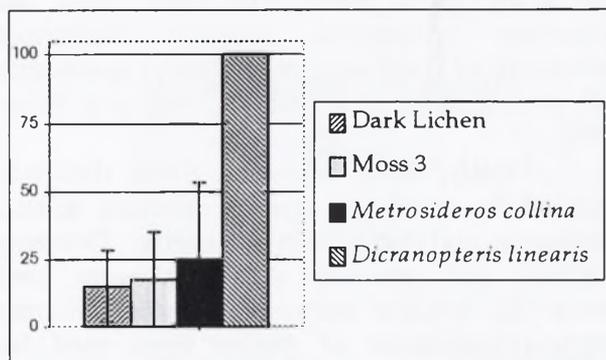
**Table 1.** 2-Way ANOVA results analyzing species richness.



**Figure 2.** Mean species richness of study sites.

Site Analyzed	P-value
1	0.0003
2	0.0411
3	0.1124

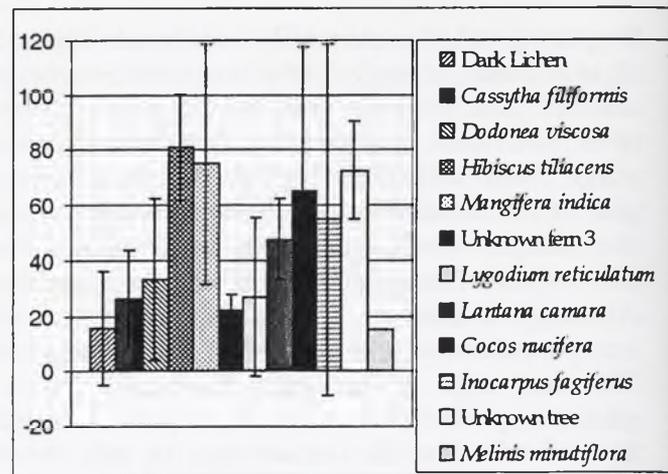
**Table 2.** One-Way ANOVA results analyzing species richness differences between burn and control for each site.



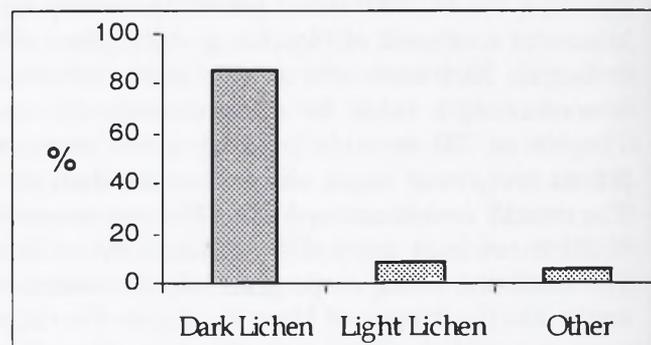
**Figure 3.** Mean percent cover in burns (only spp with > 15% cover included).

Looking at species richness for all sites across both burn and control, a two-way ANOVA revealed significant differences between burns and controls ( $P = 3.9223 \times 10^{-5}$ ), and no significant difference between sites. The interaction was also not significant (Table 1). Figure 2 shows the mean species richness of each burn and control.

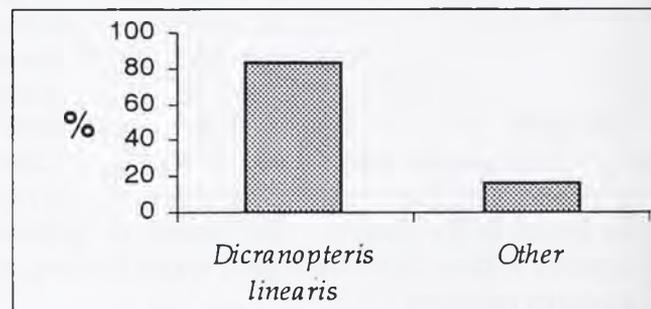
The one-way ANOVA's, looking at differences between each burn and its control



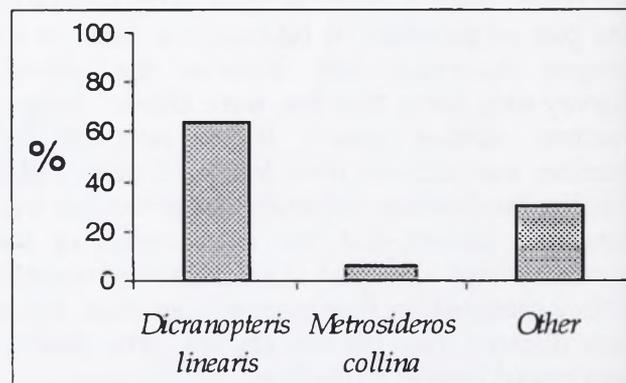
**Figure 4.** Mean percent cover in controls (only spp with > 15% cover included).



**Figure 5a.** Percent cover of species broken down for burn one,



**Figure 5b.** Percent cover of species broken down for Burn two.



**Figure 5c.** Percent cover of species broken down for Burn three.

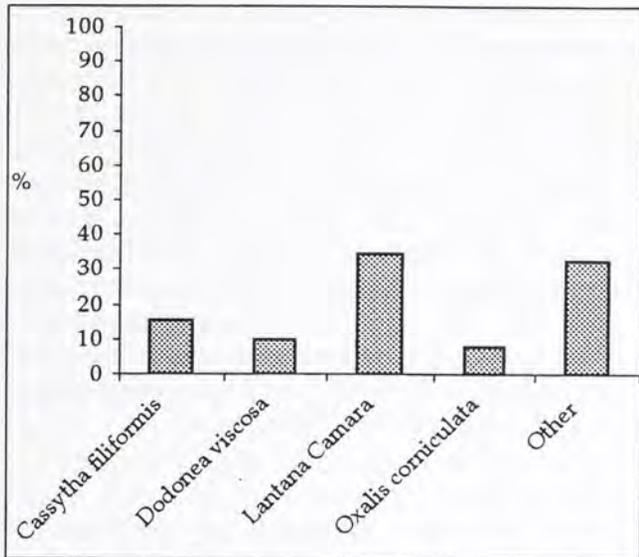


Figure 6a. Percent cover of species in Control one.

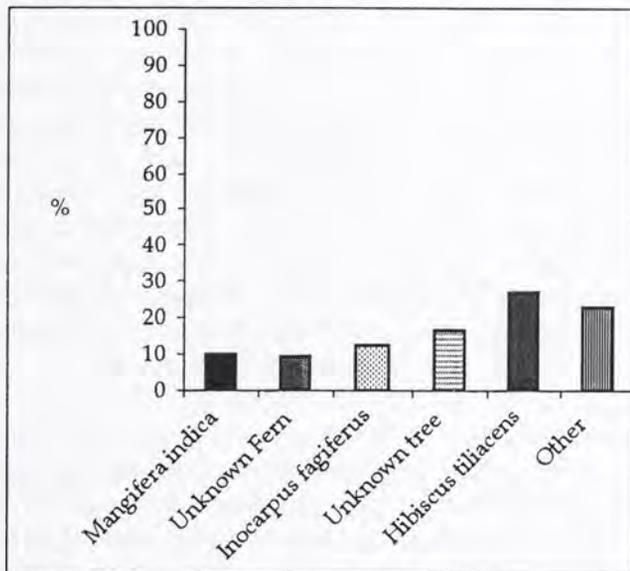


Figure 6b. Percent cover of species in Control two.

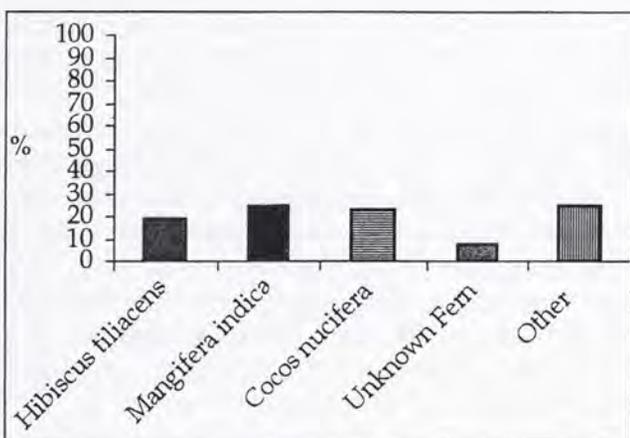


Figure 6c. Percent cover of species in Control three.

Sites Compared	Burn	Control
1 and 2	0.026	0.02
2 and 3	0.211	0.46
1 and 3	0.023	0.04

Table 3. Jaccard Coefficients of Community.

individually, reveal that for site three, the difference between burn and control is not significant (Table 2).

To look for dominance, mean percent cover was calculated for all species. Figure 3 shows mean percent cover for all species with more than 15% cover in burns. In contrast, Figure 4 shows the same, but only for controls. For all burn sites *Dicranopteris* made up 69% of the cover.

For comparison of individual species dominance, Figures 5a, 5b, and 5c show percent cover of species with greater than seven percent cover in burns (those with less than seven percent are listed under "other"), one for each site. Figure 6a, 6b, and 6c show the same for the controls. In the burns, a dark lichen had the most cover in site 1, whereas *Dicranopteris* dominated in sites two and three. Controls, with the same seven percent cutoff, show more species sharing the total cover.

Jaccard Coefficients of Community, using species presence or absence were calculated to determine similarity between communities. Table 3 summarizes the results for burns and controls. Sites two and three were more similar, comparing both burns and controls. The burn and control at site one had very few species in common with their counterparts in sites two and three.

## Discussion

### Post-fire Recovery

The reduced amount of species richness is not what one would intuitively expect after a fire in a tropical forest. The two-way ANOVA showed significantly lower numbers of species in burns than in controls for all three sites ( $P = .00004$ ). This might be expected soon after fire, where depending on intensity of the fire, flames have destroyed almost all vegetation. High intensity fires are known to sterilize soil, causing loss of nutrients, destroying microbes and seed banks, and fatally damaging canopy trees, whose crowns would otherwise be out of reach of the flames (Kauffman and Uhl 1990). In the tropics, however, low intensity fires are more common,

especially in primary forest (Cochrane et al 1999). Often vegetation is left partially intact, and rapid recovery from vegetative resprouting, spore deposition, seed rain and seed banks follows (Hopkins 1984, Uhl et al 1981). In fact, gallery forests in Belize studied by Kellman and Meave (1997) showed *greater* species richness following fires.

In this study, however, no sites showed higher species richness compared to their controls following fire. The almost homogeneous conditions in the burn sites of this study do not fit any standard descriptions very well. The lack of species richness on site one may be due to its young age and heavy erosion. There was no topsoil for seeds to establish themselves in, and precipitation, already reduced due to the rain-shadow, is absorbed and drains off the site quickly following rain. Burns at sites two and three show lower species richness due to dominating effects of *Dicranopteris*, which registered 100% cover at all plots in sites two and three. Kinnaird and O'Brien (1998) also noted that the main effect of fire was a shift from forest towards grasses, creepers and ferns, all secondary species. No significant differences between sites along with no significant interactions made such comparisons possible.

#### *Time Since Burn*

Originally, different age sites were chosen in hopes of making comparisons for analysis of succession. Differences between sites made such analysis difficult. However, a few conclusions can still be offered relating to ages of the sites. Other studies have also shown that using multiple, different-aged sites at one moment in time does not yield accurate results regarding succession, because a change at any stage may end up altering the progression and outcome (Denslow 1980; Uhl et al 1981; Hughes et al 1991). Individual sites should be monitored for a longer period of time. What can be concluded, however, is that the presence of *Dicranopteris* is having one of two possible effects on the recovery of the burn sites: either slowing succession or altering the course of succession towards a different climax state. Maheswaran et al. (1988) suggest that *Dicranopteris* can replace rainforest for an indeterminate amount of time following disturbance. Percent cover data in Figure 5 shows *Dicranopteris* with 84 percent of total plant cover at site 2, and 64 percent of total plant cover at site

3. More recovery would be expected after eight years. Nykvist (1996) observed fern-dominated sites where ferns change from 100 percent of the biomass two years after a burn to ten percent of the biomass eight years after the burn, with woody plant species recolonizing burns. *Metrosideros* is the only other woody plant that appeared in quadrats sampled, showing 6.3 % of the total plant cover in the site three burn. *Acacia* trees were observed at site two and site three, with some individuals four meters tall, but none fell in quadrats. Neither of these tree species are found in their controls, however.

#### *Community Similarity*

A look at the Jaccard Coefficients of Community (Table 2) shows how different the sites actually are. As expected, burns of sites two and three are more similar, as are the controls for those sites. An index, such as Morisita's, which incorporates species abundance, would more accurately show similarity between sites two and three. However, a better index could not be used because calculating the number of individuals of the most abundant species, *Dicranopteris*, was infeasible due to the thick mats it forms and numerous rhizomes. The Jaccard Coefficient results also show why conclusions reached about succession must be thoroughly scrutinized.

#### *Early Successional Species*

Successful post-disturbance colonizers have similar characteristics, especially with respect to controlling essential conditions for plant growth such as light, water, nutrients, and to some degree temperature. *Dicranopteris* possesses characteristics which make it able to dominate in a variety of environments and make it an efficient colonizer, both in the presence and absence of other species (Walker et al 1995). It is an opportunistic plant that has two forms of reproduction that giving an advantage when disturbance, such as fire, opens up space. It is able to reproduce vegetatively through rhizomes within weeks of disturbance, as well as to wind-disperse spores over longer distances (Uhl et al 1981). Its rhizomes, when buried, are fire resistant, another characteristic of early successional species (Maheswaran et al 1988). *Dicranopteris* has demonstrated the ability to invade new areas by shading out competing plants as well. Three light meter readings of zero were noted under as little as 65 cm-high

*Dicranopteris*. The fern can establish on nutrient-poor soils; once established *Dicranopteris* has mechanisms--in addition to shading--for excluding other species. Its thick cuticle prevents rapid decomposition, and blocks light from reaching soils as well (Maheswaran et al 1988). With its large amount of dead matter, *Dicranopteris* concentrates and hoards nitrogen, making it more difficult for other species to obtain this essential nutrient (Maheswaran et al 1988). This dead matter also becomes a fuel source for further fires, which is discussed later (Hughes 1991).

What is unique about *Dicranopteris*? It is native. Ironically, the impetus for much post-fire research stems from invasions of exotic species following disturbance. For example, *Melinis minutiflora*, a problematic species in Hawaii (D'Antonio et al *in press*), showed up in a site two control quadrat. Other individuals of *M. minutiflora* were observed on edges of burns at sites two and three. *Dicranopteris* is most likely excluding this exotic grass from spreading out further onto the burn sites. With increased disturbance, the early successional vegetation shifts from primary forest tree species to secondary tree species to forbs and grasses (Uhl et al 1982). In many cases this also provides exotic species the opportunity to invade, and invasion of exotic grasses in disturbed areas of Hawaii is a major concern (D'Antonio 1999 *in press*). This is an area which may yield valuable information as to bio-control options in the future of Pacific islands, especially in places like Hawaii.

#### *Future Changes in Fire*

Though the burn at site one does not currently have much growing on it, that is likely to change soon. Also, its location on the drier site of the Moorea does not make it immune from future burns. The *Dicranopteris* ground cover on the burns at sites two and three suggests that burns will occur more frequently there in the future: Evaporation takes place more quickly, with more direct sunlight and increased wind movement closer to the ground. The slope also keeps water from remaining in one place. *Dicranopteris* maintains a large percent of dead

biomass, which serves as a fuel (Hughes 1991, F.P.M. 1991). In fact Maheswaran et al (1988) showed that *Dicranopteris* litter in fernlands only lost 15 percent of its mass after one year. This fuel source does not exist in the control areas.

The literature suggests that forests will re-establish and eventually out-compete *Dicranopteris*, though other studies (Uhl et al 1981) have shown faster recovery than on Moorea. In addition, an increasing human population, practicing regular burning of trash and yard waste, will also multiply the chances of ignition. The most recent brush fire, on August 21, 1999, burned a *Dicranopteris*-covered ridge on the eastern side of the island. For the first time in history, helicopter intervention was required. A positive feedback loop has now been established, with fire leading to more fire (Cochrane et al 1999). This phenomenon is common for burns in the tropics, and is mostly associated with the drying of areas following fire, where incomplete or non-existent canopies prevent trapping of humidity (Woods 1989).

#### Conclusions

The impacts of fire on Moorea present a unique set of conditions to be studied. The reduction in species richness for long periods following fire shows a number of things. First, fire does not always have a positive effect on species richness, especially with an efficient colonizer such as *Dicranopteris*. And second, succession following disturbance does not necessarily progress rapidly, the climax state possibly having been altered as well. The native *Dicranopteris* dominates burn sites, and may be able to exclude invasions by other species, including exotics.

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# Learning capabilities of different size *Octopus bocki*

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**ABSTRACT.** I investigated the relation between size and learning capabilities in *Octopus bocki*, an Indo-Pacific pygmy species. I tested 19 subjects in a visual and tactile discrimination experiment. I performed a series of 20 trials per subject (4 training sessions, 5 trials per session). In each trial I simultaneously presented a dark and a white mollusk shell to the subject, and I rewarded attacks on the dark shell (correct responses) with a small piece of crab. I did not reward nor punish attacks on the white shell (incorrect responses). I carried out all experiments at night under red light, since *O. bocki* are nocturnal. Most octopuses were active (moved arms, moved head up and down, crawled) during the experiments. The percentage of correct responses was negatively correlated to octopus size as measured by mantle length ( $r=-0.653$ ,  $P<0.01$ ,  $df=17$ ). The percentage of incorrect responses was not significantly correlated to octopus size ( $r=-0.287$ ,  $P>0.05$ ,  $df=17$ ). The percentage of total responses (correct responses and incorrect responses) was negatively correlated to octopus size ( $r=-0.570$ ,  $P<0.05$ ,  $df=17$ ). There was no significant difference in the mean number of correct responses per octopus between the four five-trial training sessions ( $df=3$ ,  $F=0.408$ ,  $P>0.05$ ), so no actual learning occurred. Younger *O. bocki* demonstrated more exploratory behavior than older individuals, suggesting they are more prone to learn by trial and error. This may be due to imprinting in older, more experienced octopuses. This study is the first to examine associative learning in pygmy *Octopus*.

## Introduction

Invertebrates are very suitable to test the generalities of behavioral theories of learning and the underlying biochemical and physiological mechanisms (Abramson 1994). Cephalopods have very developed sensory and neural systems that enable them to exhibit some of the most complex types of adaptive behaviors found in the nonvertebrate world (Sanders 1975). The demonstration of learning in cephalopods can provide insight into the evolution of cognition (Boal 1991).

Extensive work has been done on the ability of *Octopus vulgaris* to learn to discriminate objects. *O. vulgaris* can readily be trained to choose a target marked with a particular pattern (shape, brightness contrast, texture etc.) in preference to another (Sanders 1975; Wells 1978). This ability has been mainly assessed by techniques utilizing classical conditioning (Young 1961; Maldonado 1963), and very rapid learning has also been shown using operant conditioning techniques (Nixon 1969 cited in Fiorito et al. 1990). Simple associative learning has been repeatedly demonstrated (Sanders 1975; Wells 1978). Other species of *Octopus* have also been used in learning studies, including *O. cyaneus* (Crancher et al. 1972, cited in Fiorito et al. 1990), *O. briareus* (Shashar and Cronin 1996), *O. bimaculoides* (Boal 1991) and *O. rubescens* (Warren et al. 1974, cited in Fiorito et al. 1990). However, I am not aware of a single learning study on any pygmy species of *Octopus*. Furthermore, relationships between

age and learning capabilities have not been addressed in any pygmy species of *Octopus*.

Due to their smaller size, younger octopuses experience a different spectrum of environmental conditions (such as potential predators, possible prey, and suitable den sites) than older octopuses. Therefore, individuals of different ages must have varying needs for behavioral plasticity and adaptability: in other words, for learning. I propose that the demands on younger octopuses to compete, adapt, and otherwise learn to survive in their natural environment are different from those experienced by older octopuses, and in consequence so are their learning capabilities.

*Octopus bocki*, is an Indo-Pacific pygmy species with a mantle length under 30 mm. *O. bocki* has been previously reported only from Fiji and the Philippines (Norman and Sweeney 1997), but it has a much wider distribution. For the present study it was collected from the South Pacific in Moorea, French Polynesia.

In this study I attempted to determine how size, as measured by mantle length and used as a relative indicator of age, relates to the performance of *Octopus bocki* in a simple discrimination experiment. This study marks the first attempt to assess the ability of pygmy octopuses to learn to discriminate objects, a task representative of general processes of associative learning.

## Materials and Methods

### Collection of Octopuses

*Octopus bocki* occurs in relatively high abundance in crevices and cavities in coral rubble around the island of Moorea, French Polynesia. I collected specimens of *O. bocki* from the fringing reef along the west shore of Cook's Bay in Moorea, directly in front of the U.C. Berkeley Richard B. Gump South Pacific Biological Research Station, and from the reef flat on the eastern section of the Vaipahu barrier reef, west of the Avaroa pass at the entrance of Cook's Bay (Figure 1).

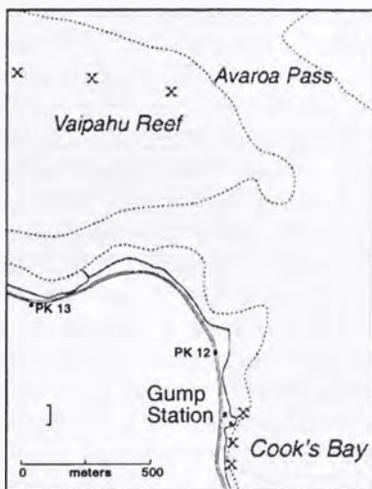


Figure 1. Collection Sites

I only collected animals inhabiting loose, dead, coral rubble using the collection technique described in Cheng (1996). I placed pieces of non-porous concrete blocks on the floor of 80-liter round plastic containers. I collected loose pieces of dead coral rubble weighing up to approximately 30 kg and placed them on top of the concrete blocks to elevate them a few centimeters from the floor of the containers. I allowed the coral rubble to drip dry for a minimum of 30 minutes. Octopuses crawled from their dens in the coral rubble to the seawater that accumulated at the bottom of the containers. After removing the coral rubble and returning it to the reef, I easily secured the octopuses from the pieces of concrete block or the floor of the container.

### Storage of Octopuses

I manually transferred each octopus from the collection container to a storage cup

immediately after collection. I used round transparent plastic storage cups 7.5 cm high and 10 cm in mean diameter (9 cm bottom diameter, 11 cm top diameter) filled to three fourths of their height with 400 ml of unfiltered sea water. I covered each cup with a second identical cup placed inverted over the first and held in place by a small weight (a stone or piece of dead coral). I kept all cups on a wet table in the station's open-air wet laboratory.

Every day at sunrise (0500), I fed each octopus one live crab of carapace width approximately one half the size of the octopus' mantle length. I collected the crabs in the same manner as the octopuses. I did not feed octopuses the morning after they were collected. Instead I started feeding them the second morning after collection, in order to allow at least 24-hours of acclimation free of disturbances.

Between 1400 and 1800 on alternating days I cleaned the storage cups and replaced the sea water in them, transferring the octopuses momentarily to a different cup while doing so. I did not clean or replace the water in the cups of newly collected octopuses until at least 48 hours after collection to avoid disturbances during acclimation.

### Measuring and Sexing Octopuses

Using a plastic caliper, I measured each octopus from a point midway between the eyes to the tip of the mantle. I took mantle length measurements while I transferred the octopuses from cup to cup when cleaning and changing the water in the storage cups. I measured each octopus within an interval starting two days before and ending two days after the octopus underwent experiments.

I sexed most octopuses by transferring each to a petri-dish (height: 1.5 cm; diameter: 10 cm) filled with seawater to about half its height, covering the dish with a lid, and inspecting the octopus under a dissecting microscope (20x total magnification). I identified males by the presence of a groove running along the posterior margin of the third right arm (R3), and a modified suckerless tip, the hectocotylus (Wells 1978).

### Preliminary Experiments

I performed a series of preliminary experiments to determine optimal conditions for the study. The final conditions are described in the following section.

### Discrimination Experiments

I carried out all experiments at night, between 1900 and 0500 hours, since *O. bocki* are

nocturnally active (Cheng 1996). I subjected every octopus to a series of twenty trials, divided into four sessions of five trials each. The four sessions took place on consecutive nights. Five to eight trial sessions are typical for visual and tactile discrimination studies on other species of *Octopus* (Young 1983; Boal 1991; Fiorito and Scotto 1992; Shashar and Cronin 1996).

For each five trial session, I transported the subject in its storage cup to a closed, dry laboratory situated approximately 15 m away from the wet table where the octopuses were kept. I only shone white light on the subject briefly when approaching the wet table with a flashlight, a practice I used in order to avoid turning on the lights and stunning the other octopuses and organisms kept in the laboratory by my colleagues. Inside the dry laboratory I placed the cup with the subject on a beige tabletop, illuminated by a desk lamp fitted with a 60-watt red light bulb and covered with 16 layers of thin red cellophane.

I kept conditions in the dry laboratory as constant as possible throughout all the experiments. I always placed the cup with the subject in the same place on the table and I always sat in the same place relative to the cup. I kept the area of the tabletop surrounding the cup clean of any objects except for the red light lamp, my notebook and a metal tray with small, cold pieces of crab which I used to reward the octopuses.

I allowed the octopuses to acclimate for 10 minutes. Each trial lasted five minutes (Shashar and Cronin 1996), and I gave the five trials in one session at five-minute intervals (Sutherland 1959a cited in Sanders 1975; Fiorito and Scotto 1992; Shashar and Cronin 1996).

On each trial I simultaneously introduced into the storage cup a cold, dark *Pyrene* sp. shell and a cold, white *Cypraea* sp. shell of approximately equal dimensions, hanging by 5 cm lengths of nylon fishing line from a 14 cm long wooden stick. I chose shells as stimuli because they were readily available in many sizes, shapes and colors, they were easily fitted with small pieces of crab, and they have been used as stimuli in learning experiments on other species of *Octopus* (Boal 1991). I positioned both shells in the frontal parallel plane and equidistant from the subject.

Depending on the size of the subject, I used one of two pairs of shells of different size as stimuli. I used the smaller pair (dark shell: 7.5 mm x 4 mm x 4.5 mm; white shell: 6.5 mm x 4.5 mm x 3.5 mm; separation between shells: 42 mm) for animals up to 10 mm in mantle length

and presented the shells 32 mm from the octopus. I used the larger pair (dark shell: 10.5 mm x 5 mm x 6 mm; white shell: 11 mm x 6 mm x 4.5 mm; separation between shells: 55 mm) for animals over 10 mm in mantle length and presented the shells 43 mm from the octopus. I did this in order to keep the size of the stimulus and the distance from the subject to the stimulus somewhat proportional to the size of the octopus being tested.

At the time I introduced the stimuli, I simultaneously moved the shells up and down 3 times per second for 10 seconds. I repeated this procedure 2 minutes into the trial and 4 minutes into the trial. According to Wells (1978), octopuses find shapes that move up and down more attractive than those that don't move or that move from side to side.

On trial 1, 2, 3 and 6 (1<sup>st</sup>, 2<sup>nd</sup>, and 3<sup>rd</sup> trial on session 1 and 1<sup>st</sup> trial on session 2) I introduced a small piece of cold crab into the dark shell to promote attacks (Shashar and Cronin 1996). When the subject attacked the dark shell it ate the crab inside the shell and I did not reward further. On all other trials I presented the shells with no food in them. If the octopus completed a successful attack on the dark shell, I rewarded it immediately. A successful attack was one in which the octopus took the dark shell completely under the interbrachial web and held it for 5 seconds. The reward was a small piece of cold crab touched against the octopus' arms using tweezers. The octopus readily drew in and ate the piece of crab. I did not reward and opted not to punish animals for choosing the white shell.

#### Statistical Analysis

I analyzed the results using descriptive statistics, correlation analysis and two-factor ANOVA without replication from the Data Analysis Tool-Pack in Microsoft Excel 98.

#### Results

Figure 2 presents the types and percentages of responses obtained from the 19 subjects tested during the 20 trials according to the octopuses' mantle length. The percentage of correct responses made by a given subject in the 20 trials ranged from 0 to 40%, with a mean of 8.16 (sd=11.08, n=19). The percentage of incorrect responses ranged from 0 to 15% incorrect responses, with a mean of 2.63 (sd=4.82, n=19). The percentage of total responses (correct and incorrect) ranged from 0 to 55%, with a mean of 10.79 (sd=15.12, n=19).

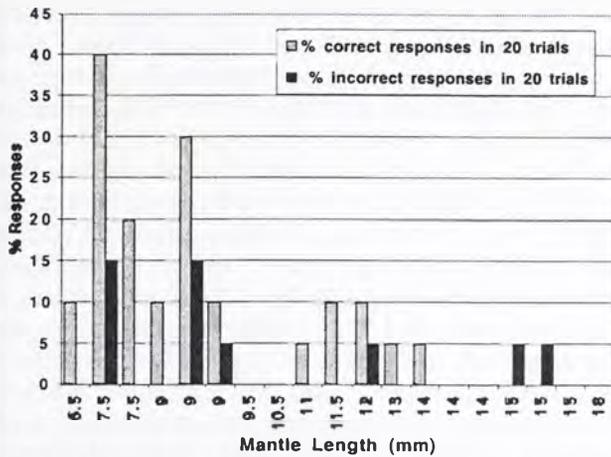


Figure 2. Correct and Incorrect Responses in 20 Trials

Mantle length and % correct responses were negatively correlated ( $r=-0.653$ ,  $P<0.01$ ,  $df=17$ ), as were mantle length and % total responses ( $r=-0.570$ ,  $P<0.05$ ,  $df=17$ ). Mantle length and % incorrect responses were not significantly correlated ( $r=-0.287$ ,  $P>0.05$ ,  $df=17$ ). There was no significant correlation between sex and % correct responses ( $r=-0.260$ ,  $P>0.05$ ,  $df=15$ ), % incorrect responses ( $r=0.175$ ,  $P>0.05$ ,  $df=15$ ) or % total responses ( $r=-0.135$ ,  $P>0.05$ ,  $df=15$ ). Furthermore, there was no significant correlation between the number of days octopuses were kept in captivity before the start of the trials and % correct responses ( $r=0.347$ ,  $P>0.05$ ,  $df=17$ ), % incorrect responses ( $r=0.181$ ,  $P>0.05$ ,  $df=17$ ) or % total responses ( $r=0.312$ ,  $P>0.05$ ,  $df=17$ ).

The mean number of correct responses per octopus per five-trial session was not significantly different between sessions ( $df=3$ ,  $F=0.408$ ,  $P>0.05$ ) (Figure 3). The individual performances over the four training sessions are shown in Figure 4.

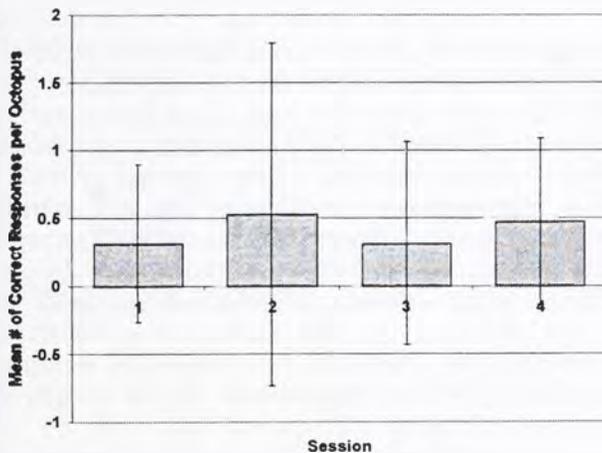


Figure 3. Number of Correct Responses per Octopus per Session (mean  $\pm$  sd)

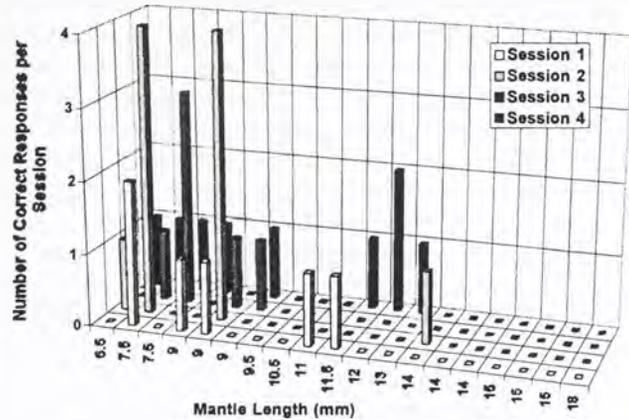


Figure 4. Correct Responses of Individual Octopuses over 4 Training Sessions

Figure 5 shows the type and number of responses from all 19 subjects as a function of trial number. The number of octopuses that responded correctly in a given trial ranged from 0 to 5, with a mean of 1.55 ( $sd=1.15$ ,  $n=20$ ). The number of octopuses that responded incorrectly in a given trial ranged from 0 to 2, and the mean was 0.50 ( $sd=0.83$ ,  $n=20$ ). The total number of octopuses that responded correctly or incorrectly in a given trial ranged from 0 to 5, and the mean was 2.05 ( $sd=1.28$ ,  $n=20$ ).

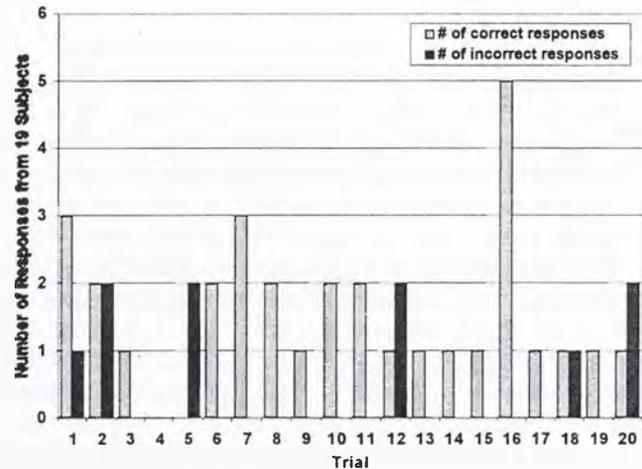


Figure 5. Correct and Incorrect Responses as a Function of Trial

### Discussion

My data showed a significant negative correlation between octopus mantle length and percentage of correct responses, but no significant correlation between mantle length and percentage of incorrect responses. Younger *O. bocki* are more likely than older specimens to repeat an action that is rewarded, but they are just as likely as older specimens to repeat an

unrewarded action. Their higher overall level of activity (both positive and negative responses) suggest that younger *O. bocki* are more active and have a greater tendency to explore their surroundings. The higher percentage of positive responses in younger *O. bocki* suggests they are more likely to learn by trial and error because this kind of learning requires exploratory behavior. However, I did not observe any instance of actual learning in my experiments, an issue I discuss below. The lower levels of activity observed in older *O. bocki* may be due to imprinting having occurred in these more experienced individuals.

Although some octopuses gave many more correct than incorrect responses (Figure 2), analysis of the positive responses given by all octopuses in successive five-trial sessions showed no evidence of improved performance as a result of experience (Figure 3). When I analyzed the number of positive responses given by individual octopuses in the four successive five-trial training sessions, none showed a detectable improvement of performance in successive sessions (Figure 4). Moreover, the number of correct responses from all 19 octopuses did not increase over successive trials (Figure 5). Since learning is defined as a relatively permanent change in behavior potential as a result of experience (Abramson 1994), I judged that no learning occurred in my experiments.

It is possible that the tendency in younger specimens to attack the dark shell was due to an untrained preference rather than to the reward associated with the shell. However, during the preliminary experiments I observed octopuses that when rewarded for attacks on the white shell, attacked the white shell more often than the dark shell in subsequent trials (data not shown). To settle this issue unequivocally, it would have been necessary to carry out a control experiment on a sample of considerable size, in which none of the shells were rewarded. I did not carry out such control due to the limited number of octopuses I was able to collect during the short duration of this field study.

Since the octopuses were collected, fed, and otherwise handled in a consistent manner, the only thing that varied among individuals other than size was sex and the number of days they were kept in captivity before the start of the trials. These two factors did not affect the performance of the subjects, since none of them were significantly correlated to the percentage of correct, incorrect or total responses.

The overall number of responses in this study is much lower than that reported in

typical discrimination learning studies done on normal (no brain lesions) subjects from other species of *Octopus*. The highest percentage of correct responses I obtained was 40%, whereas visual discrimination studies on *O. vulgaris* report typical values over 70% for discriminanda that differed in orientation, brightness, size or shape (Boycott and Young 1957, cited in Sanders 1975). These studies were normally over 120 trials (compared to 20 trials in the present study) and different stimuli were presented successively and one at a time (rather than simultaneously, as in the present study). Sutherland (1959b, cited in Sutherland and Muntz 1959) reports that with difficult discriminations there is a decrease in the number of attacks made, which fall as low as 10% of the trials.

The three main differences between the studies by Boycott and Young (1957) described above and the present study are the length of the experiments, the difficulty of the discrimination and the mode of presentation of the stimuli. It is quite likely that by increasing the number of trials from 20 to 120 (which I could not do due to time constraints) I would have obtained a higher percentage of correct responses. Furthermore, the difficulty of the discrimination might have affected the performance of the octopuses in my experiments. It is hard to assess the difficulty of the discrimination, since the shells used in my experiments combined characteristics of orientation, brightness and shape, whereas the stimuli used in studies of *O. vulgaris* normally differed in only one of these variables during any given experiment.

Finally, Sutherland et al. (1959) report that experiments using simultaneous presentation of stimuli failed to discover a training method more efficient than successive discrimination training. Maldonado (unpublished data, cited in Sanders 1975) showed that acquisition occurred providing that shocks were given for attacks on the negative stimulus as well as food reward for attacks on the positive stimulus. These reports (which I did not encounter until after the end of my experiments) suggest that simultaneous discrimination, especially without punishment for attacks on the negative stimulus, might not produce levels of performance as high as those reported for successive discrimination training, another plausible explanation for the results of the present study.

In future associative learning studies on *Octopus bocki*, it would be interesting to test subjects in a larger number of trials and using

simple geometric figures presented in succession, in order to investigate whether any of these parameters which have proven to be optimal in discrimination experiments on *O. vulgaris* extrapolate to *O. bocki*. In the future it would also be interesting to explore further the learning capabilities of different size *O. bocki* using a larger sample with more representatives of each size class, and including a control of considerable size where attacks on neither of the objects to be discriminated are rewarded. Such a study would expand on the results reported here, and would be useful to further interpret the present study in terms of the natural tendencies of *O. bocki*.

### Conclusion

The present study revealed a tendency in younger *O. bocki* to attack a rewarded dark shell more often than older individuals. Furthermore, this study showed that young *O. bocki* are more likely to repeatedly attack a rewarded dark shell than an unrewarded white shell. Since learning was not observed, it was impossible to assess differences in the learning

capabilities of different size *O. bocki*. However, the results did suggest a higher degree of behavioral adaptability in smaller octopus, as demonstrated by their readiness to perform actions that yielded food more often than actions that had no reward.

### Acknowledgements

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# The Ecology of Coral Reef Fish in the Fringing Reef of Haapiti, Moorea, French Polynesia

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**ABSTRACT.** The ecology of coral reef fish was examined in the lagoon at Haapiti, Moorea, French Polynesia between 10/15/99 and 11/17/99. Four zones were identified within the study site: a sand, a coral head, a reef flat, and a drop-off region. Fish were categorized according to genus and fish distribution was measured by a visual count made while swimming slowly down transect lines oriented perpendicular to the shoreline. Only non-cryptic, diurnal fish were counted. Two studies were done, the first one measured the distribution of fish along a single transect line for the time span ranging from 5am to 6pm. Analysis of variance showed that there was a significant difference for fish distribution by zone, but not by time within a zone. The second study measured the fish distribution during three time periods: sunrise, noon, and sunset. Analysis of variance showed that there was a significant difference in fish distribution for each time period, for each zone, and for each time period within a zone. It is determined that a lull in fish density occurs from 5:00am-5:30am, and 6:00pm-6:30pm and that tidal flux is not a significant factor in fish distribution, while zonation is. Also, a list of observed species is compiled which includes species' habits and habitats.

## Introduction

A lush coralline environment surrounds the shores of Moorea, a high island. Up to now, distributional research has been focused in Tiahura, where a channel has been dredged in the lagoon and the tourism industry has affected the local fish ecology by feeding the sharks and rays. Therefore, the reef in its natural state can no longer be assessed in that area. However, with tourism concentrated around plush resorts, many lagoon areas are left undisturbed. The mangrove patch near Haapiti is one such isolated place and is therefore an ideal site to study the natural distribution of coral reef fish.

There are several reported methods of measuring fish distribution. Studies have been done using nets to catch fish samples (Ley et al. 1999). Distributional counts have also been made using underwater visual assessments (UVAs) (Ohman et al. 1998). This is a method by which a visual count is taken along a transect line, called a transect belt. Finally, by marking the fish with a subcutaneous injection of elastomer, fish can be identified and counted for up to three months (Frederick 1997).

There are conflicting views about the effectiveness of these techniques. A simultaneous comparison between a catch and effort survey (where fish are caught with nets) and a visual census showed that the two studies gave different fish abundances for the same area under the same conditions (Connell et al. 1998). However, another comparison study showed that visual counts, made by using transects of varying widths, were related to each other linearly and suggested that visual studies could be compared given the right conversion factor to adjust for transect width (Chael and Thompson 1997). So, while, there is no one right way conduct a distributional count, a visual count can be an effective and consistent way to measure fish distribution.

When trying to understand fish ecology, it is important to take into account the many factors influencing it. While many studies look at limited aspects of the population density, my study looks at the fish population as a whole, allowing me to make broader generalizations.

Several studies have been done on larval recruitment, which look at the settlement patterns of larval fish onto coral heads (Ohman et al. 1998; Ault, 1998). However, "population dynamics is driven by birth, death, immigration, and emigration" (Hixon 1998), and recruitment studies only addresses the immigration dynamic and not the emigration of older species, birth, or death.

Also, many studies track only a few individual species or a single genus in a study. This leaves a gap in the wealth of knowledge that can be learned by taking a more holistic approach. "Species diversity within a given family appears to be affected more by ecological parameters, such as living coral cover, food diversity, and reproductive behavior" (Galzin and Planes 1994).

In this study I examine the role of tidal flux and light intensity on fish distribution. Moorea has a distinctly tropical environment, where the tidal flux is approximately six inches throughout the year. The tide cycle is twelve hours long, low tide occurs between 5 and 8 am and 4 and 6pm, and the lagoon is anywhere from 500 to 1500 meters long (Galzin and Pointier 1985). This makes for a very small intertidal zone, leaving the water level fairly constant.

Light intensity is also fairly constant throughout the year. The sun rises at 6am and sets at 6pm every day. I thought light intensity might be a factor affecting fish distribution in my study site, especially during the day/night transition, and that this would lead to a decrease in fish density during sunrise and sunset.

There are four areas in the fringing: a sand zone, a coral head zone, a reef flat, and a channel containing a steep drop-off. The topography of the fringe reef leaves the top of the reef flat area exposed during low tide, but I hypothesized that the tide rose enough to allow for the migration of pelagic fish into the coral head zone from the drop-off zone during high tide. I also thought that the high tide would allow fish in the coral head region to migrate into the drop-off zone to feed. It is common for fish to migrate to their feeding grounds. Some Brown Surgeonfish, for instance, make daily migrations of up to 1.5 km and their "initiation of spawning migrations to one spawning site was (also) correlated to the time of sunrise, sunset, and the tidal cycle" (Mazzeroll and Montgomery 1998).

**Materials and Methods**

The study was conducted from 10/15/99 to 11/17/99 in an isolated area of lagoon next to the mangrove patch near Haapiti, Moorea, GPS 17° 30' 29"S, 149° 52' 29" W. See Fig. 1.

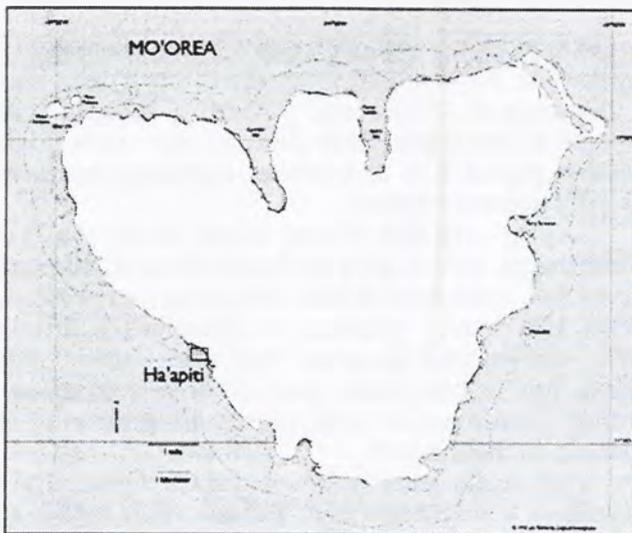


FIG. 1. The map of Moorea with the study site marked, near the town of Haapiti.

Five transect lines were placed perpendicular to the shore, at 20m intervals. To the north, the study site area was buffered from human interference by a barren field. To the south, there was 120 meters of untouched mangrove forest. Four zones were identified within the study site, all within the algal ridge. Starting from the shore and extending towards the algal ridge there was: 1.) a Sand region, which started from the mangrove stand and was between 0 and .5 meters in depth. This region contained small rocks, algae, abundant *Holothuria*, and a few, small, scattered coral heads (<.3m). 2.) Then, there was a Coral Head zone, .5 to 1.5 m deep, which included many large coral heads, and 3.) a shallow Reef Flat zone (~.5m deep) containing mostly small, branched coral heads and algae-covered coral rubble. This was followed by 4.) the Drop-Off zone containing algae

covered coral rubble and branched coral heads. Transect lines were placed at an angle of 20° SW. Twine was stretched along the transect line, starting from the shore and stretching all the way through the sand, coral head and reef flat zones. See Fig. 2.

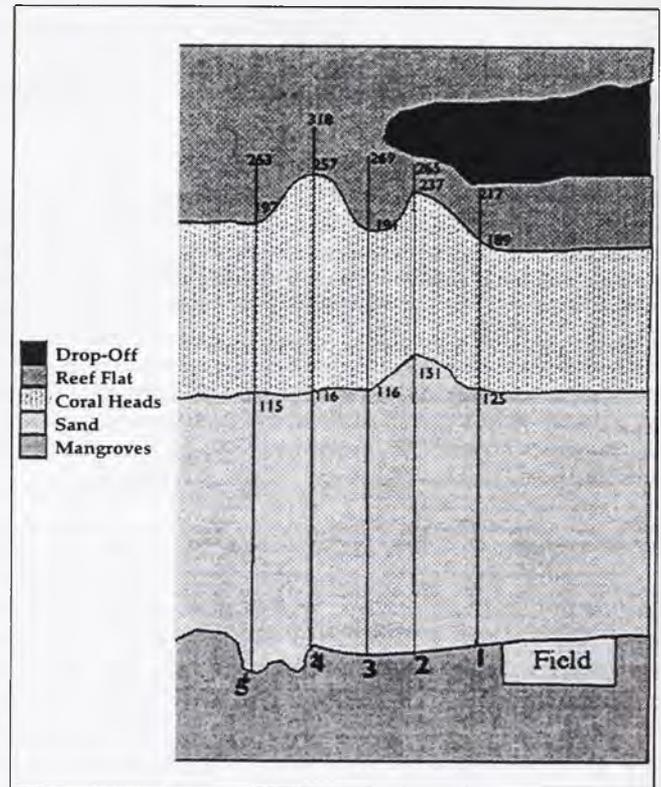


FIG. 2. Map of study site with zones and transect lines.

Only the sand, coral head, and reef flat zones were counted in the study. The deep water obscured viewing in the drop-off zone and an accurate fish count could not be taken. Therefore, only a qualitative assessment of the drop-off zone's population was made.

Fish were identified after extensive preliminary research, and transects were started only after all fish could be easily identified. Due to their cryptic and elusive nature, *Gobiidae* and other small, cryptic fish were not counted, as an accurate count could not be taken of them with the experimental methods that were employed. Included fish species were categorized according to their genera, when possible, otherwise by family.

Individual fish distribution counts were made by swimming down the transect lines slowly and making a visual count of the individuals that were within 1 square meter to either side of the transect line. The transects were completed in a non-random order. Fish that quickly swam through the transect zones were counted as well as fish that were found in the transect line region. Transects took approximately a half-hour to complete. In order to minimize disturbance of the natural fish population, transects along the same line were spaced apart by at least six hours.

### Experiment 1

Fish distribution was measured along the #2 transect line. One fish count was done for every daylight hour, between 5am and 7pm, for a total of fifteen transects. Fish were counted by genera and by zone.

### Experiment 2

In the second experiment, all five transect lines were employed and fish were counted in all three zones. Three times were picked: sunrise, noon, and sunset. Noon was identified as being from 12:00pm-12:30pm. Sunrise was identified as being from 5:00am-5:30am and Sunset was from 6:00pm-6:30pm. A visual count was taken at each of the five transect lines for each time period, for a total of 15 transects. Later, three transects were made from 5:30am-6:00am.

### Results

#### Experiment 1

In the first experiment, analysis of variance showed that there was a significant difference between the sand, coral head, and the reef flat zones. First, I analyzed all the data using a two-way Anova with fish, zone, and time as my three variables. The two way Anova showed that there was significant variance by zone ( $p=.000$ ), but that there was no significant variance by time ( $p=.511$ ), or time by zone ( $p=.997$ ). Taking each zone separately, modified LSD (Bonferroni) tests with significance level .05 showed that there was no significant variance in time for each zone. Total fish density was also calculated for each zone, see Fig. 3, as well as total fish diversity, see Fig. 4.

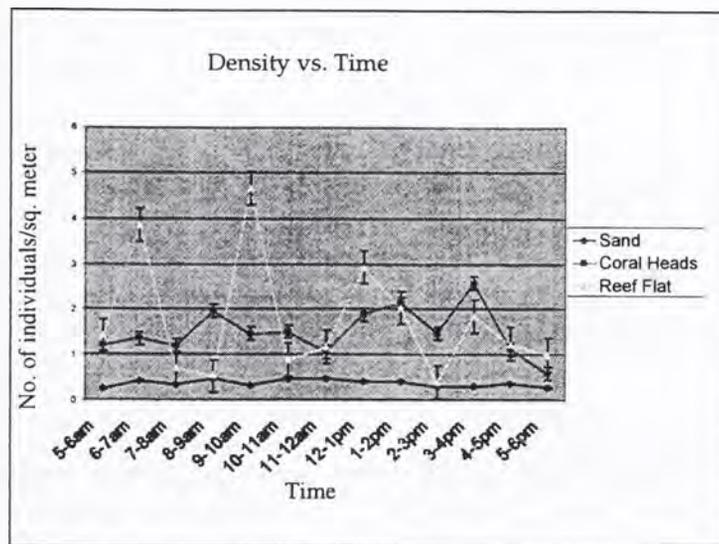


FIG. 3. This graph shows the variation in fish density over the course of a day along the second transect line. Analysis of variance shows that the fluctuations in each zone do not vary significantly over time, but vary significantly between zones.

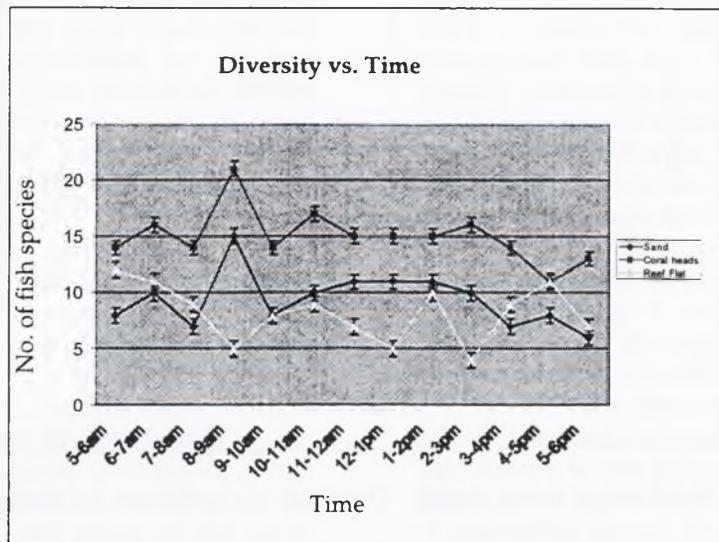


FIG. 4. The diversity of fish over time along the second transect line. There is a significant variance in diversity during the day between zones, but not within zones.

**Experiment 2**

In the second experiment, an analysis of variance was made using time, fish, and zone as the three variables. Analysis by two-way Anova showed that there was a significant difference in fish density by zone and by time ( $p = .385$ ), but there was no significant difference in fish population by time ( $p = .000$ ) and zone ( $p = .042$ ). However, a one-way Anova for each zone showed that there was a significant difference in population by time within each zone. For Sand, ( $p = .04$ ) For Coral Head, ( $p = .003$ ) For Reef Flat ( $p = .028$ ). Total fish

density and total fish diversity was averaged for each zone. See Figs. 5 and 6.

Fish density was also compared between three 5:00am-5:30am transects and three 5:30am-6:00am transects. See figure 7. The results show that the average density of fish from 5:30am -6:00am was similar to the average density found from 12pm-12:30pm in the second study.

A list of fish species found on the reef was compiled, along with their habitat, schooling behavior, recorded location on the reef, and food preferences. See Table 1 in the *Appendix*.

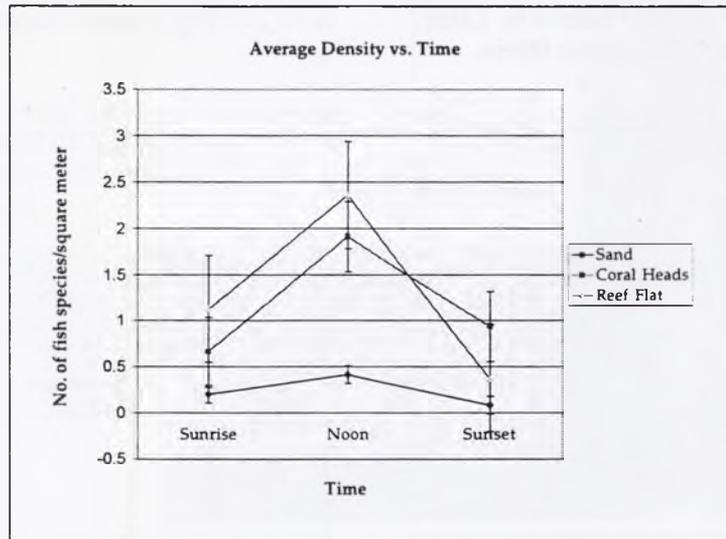


FIG. 5. Average density of fish for sunrise, noon, and sunset. There is significant variance between times for each zone.

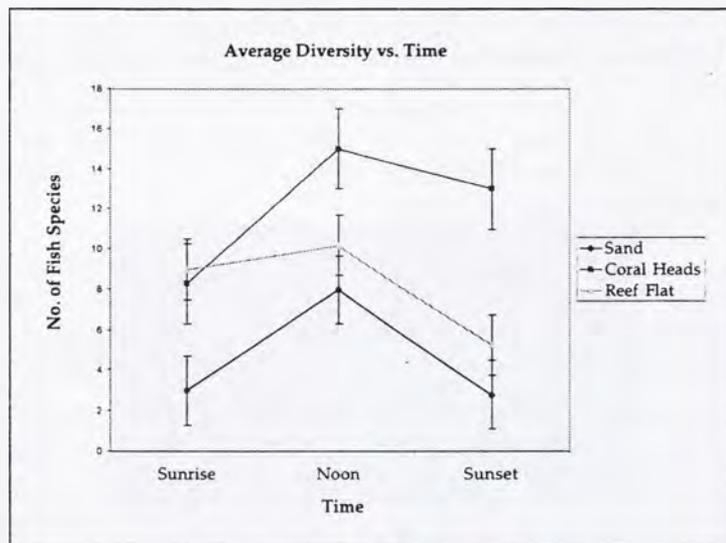


FIG. 6 The average diversity for sunrise, noon, sunset. Diversity is significant for times in each zone.

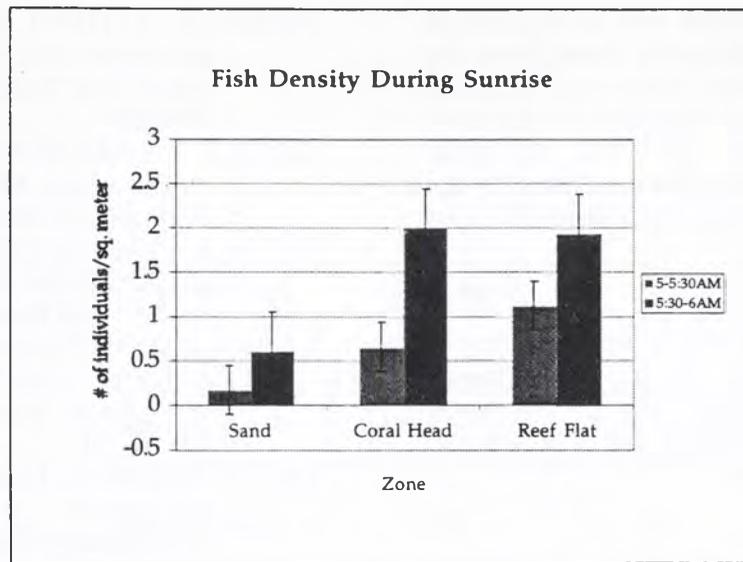


FIG. 7. The average fish density during 5-30am and 5:30-6am. Average density in each zone is significantly different during the two time periods.

### Discussion

There was no significant change in the fish density or distribution in the first experiment, and consequently there was no noticeable affect of tidal flux on fish density for all species. A gradual increase or decrease in total of individual fish density around noon would have indicated an increase in fish migration due to the tide. However, it would have been hard to distinguish between the tidal flux and light intensity, which also rises gradually until it peaks at noon before slowly decreasing.

Looking at the fluctuations of density for each zone, a density increase due to high tide would look like a bell curve. However the data shows almost no fluctuation in density for the sand region, and sharp fluctuations in density for the coral head and reef flat zones. This can be accounted for by fish schooling. In the coral head zone, parrotfish tended to school with other similarly colored fish, especially goatfish. This is not surprising, as small parrotfish can undergo physiological color changes and school with other fish species (Crook, A 1999). I believe that the fluctuations seen in the coral head zone are due to the random chance of coming across schools of fish, a "hit or miss affect" that is inconclusive without further study. In the reef flat zone, the "hit or miss affect" was greater because fish tended to aggregate into larger schools, with members tending to be within the same species.

Also, the tide was not a good determiner of fish distribution. The tide fluctuated, influenced by seasonal changes, such as the onset of the rainy season in November, as well as meteorological changes, such as a nearby hurricane.

In the second experiment, the density between zones tended to be the most significantly different. This supports other data in this area of research,

which states that "spatial variability is more important than temporal variability" and since the fluctuations in density in each zone was not significant throughout the day, experiment 1 provided a good baseline against which to measure the average daily fish density and diversity for each zone.

For Experiment 2, the noon transect provided a good measure of the average density within the whole study site area because the average noon density for each zone was within the standard error of the average density for the zones in experiment 1. The average sunrise and sunset density were found to be significantly low, and the comparison between the density from 5:00 am-5:30 am and 5:30-6am shows that by 5:30 am, the average density in each zone is close to the average density of fish throughout the day. The steep increase in fish density cannot be accounted for by the tidal flux. For the sunset, the fish distribution between 5:30-6pm was qualitatively assessed as having a high fish density and diversity, and it is assumed that the density drop from 6-6:30pm is solely due to the low residual light intensity after the sunset, which mimics the light intensity during the sunrise. In future studies, I would take light intensity measurements throughout the day to show the change in light intensity throughout the day.

The fish list data represents all of the species I could positively identify. It remains incomplete, due mostly to the polymorphic nature of parrotfish. The species listed here do not reflect the full range of parrotfish found in the lagoon, but most other species are represented.

### Conclusions

The day/night transition was found to be a significant factor affecting the distribution of fish,

while tidal flux was not. There was no significant change in fish density or diversity throughout the daylight hours. There was, however, a sharp decrease in fish density and diversity for the half-hour following first light and the half-hour following the sunset. The evidence relating to the migration of fish across the reef flat was found to be inconclusive.

#### *Acknowledgements*

I would like to thank Brent Mishler, David Lindberg, Jere Lipps, Jaime Bartholemew, James Jackson, Meredith Bauer, Norm Hetland, the Gump Station Staff, Jillian Silva, and Richard Bruschi for making this research possible.

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## Appendix

Table 1. Fish species in the study site

Scientific Name	Common Name	Habitat	Social Behavior	Food
Habitat (by zone) S=Sand CH= Coral Heads RF= Reef Flat, Social Behavior no= solitary swimmers yes= schooling (swim with 2+ other fish) pair= swim with 1 monogamous partner				
<i>Abudefduf septemfasciatus</i>	Seargent Major	CH	no	benthic algae, small invertebrates
<i>Abudefduf coelestinus</i>	Convict Damsel	CH,DO	no	zooplankton, algae
<i>Acanthurus triostegus</i>	Convict Tang	S,CH,R,DOF	yes, no	algae
<i>Acanthurus bleekeri</i>	Bleeker's Surgeonfish	CH,DO	no	algae, jellyfish,anemones
<i>Acanthurus bleekeri</i>	Red and Silver Squirrelfish	S,CH, DO	yes	small crustaceans, worms, fish
<i>Aulostomidae</i>	Trumpetfish	S,CH,RF	no	small fish
<i>Bothus panderinus</i>	Flatfish	S, DO	no	benthic animals
<i>Centropyge flavicauda</i>	Lemonpeel Angel	CH, DO	no,pair	algae
<i>Canthigaster benneti</i>	Long-Nosed Globefish/Salamander's Toby	S,CH, DO	no	crustaceans
<i>Carchahinus melanopterus</i>	Black-Tipped Reef Shark	S,CH,RF, DO	no, yes	fish,crustaceans,molluscs
<i>Chanos chanos</i>	Milkfish	DO	yes	cyanobacteria, soft algae, small benthic invertebrates, pelagic fish eggs and larvae
<i>Chaetodon auriga</i>	Threadfin Butterfly	S,CH,RF,DO	pair	coral algae, feeding tentacles of worms
<i>Chaetodon citrinellus</i>	Speckeled Butterfly	S,CH,RF,DO	pair	coral algae, feeding tentacles of worms
<i>Chaetodon semeion</i>	Dotted Butterflyfish	S,CH,RF,DO	pair	coral algae, feeding tentacles of worms
<i>Chaetodon falcula</i>	Saddle Butterfly	S,CH,RF,DO	pair	coral algae, feeding tentacles of worms
<i>Chaetodon bennetti</i>	Bennet's Butterfly	S,CH,RF,DO	pair	coral algae, feeding tentacles of worms
<i>Chaetodon speculum</i>	Ovalspot Butterfly	S,CH,RF,DO	pair	coral algae, feeding tentacles of worms
<i>Chaeodon ulietensis</i>	Pacific Double-Saddle Butterfly	S,CH,RF,DO	pair	coral algae, feeding tentacles of worms
<i>Chaetodon trifasciatus</i>	Redfin Butterfly	S,CH,RF,DO	pair	coral algae, feeding tentacles of worms
<i>Chaetodon flavirostris</i>	Dusky Butterfly	S,CH,RF,DO	pair	coral algae, feeding tentacles of worms
<i>Chaetodon melannotus</i>	Blackback Butterfly	S,CH,RF,DO	pair	coral algae, feeding tentacles of worms
<i>Caetodon ocellicaudus</i>	Spot-tail Butterfly	S,CH,RF,DO	pair	coral algae, feeding tentacles of worms
<i>Chaetodon oxycephalus</i>	Spotnape Butterfly	S,CH,RF,DO	pair	coral algae, feeding tentacles of worms
<i>Chaetodon ornatissimus</i>	Ornate Butterfly	S,CH,RF,DO	pair	coral algae, feeding tentacles of worms
<i>Chaetodon lunula</i>	Racoon Butterfly	S,CH,RF,DO	pair	coral algae, feeding

<i>Chaetodon unimaculatus</i>	One-Spot Butterfly	S,CH,RF,DO	pair	tentacles of worms coral algae, feeding
<i>Chaetodon trifasciatus</i>	Lineated Butterfly	S,CH,RF,DO	pair	tentacles of worms coral algae, feeding
<i>Chaetodon ephippium</i>	Saddle-marked Butterfly	CH,DO	yes	tentacles of worms coral algae, feeding
<i>Chelon vaigiensis</i>	Diamond-Scaled Mullet	S, CH,RF	yes	tentacles of worms filamentous algae, foraminifera
<i>Chlorurus sordidus</i>	Daisy Parrotfish	S,CH,RF,DO	no	algae
<i>Ctenochaetus striatus</i>	Bristle-Tooth Surgeon	CH, RF,DO	yes	algae, invertebrates
<i>Chromis caeruleus</i>	Blue-Green Puller	S,CH,RF,DO	yes	zooplankton
<i>Chromis cyanea</i>	Blue Puller	S,CH,RF,DO	yes	plankton
<i>Dascyllus trimaculatus</i>	Three-Spot Humbug	S	yes	planktonic crustaceans
<i>Dascyllus aruanus</i>	Banded Humbug	S,CH,RF,DO	no	coral algae, feeding tentacles of worms
<i>Diodon hystrix</i>	Purcupine Fish	CH,DO	no	large echinoderms,crustaceans
<i>Dunckerocampus dactyliophorus</i>	Pipefish	CH,RF,DO	no	information not available
<i>Epinephelus merra</i>	Honeycomb Sea Bass	CH, RF,DO	no	crustaceans, fish
<i>Epibulus insidiator</i>	Slingjaw Wrasse	CH,DO	no	crustaceans, fish
<i>Gomphosus varius</i>	Birdfish	CH,RF,DO	yes	crust, other invert.
<i>Heniochus acuminatus</i>	Longfin Banner/Bullfish	CH,DO	no	algae
<i>Labroides diminidiatus</i>	Paradisefish	CH, RF, DO	no	fish parasites
<i>Monotaxis grandoculis</i>	Tropical Porgie/Big Eye Bream	CH	yes	algae
<i>Mulloidichthys flavolineatus</i>	Yellowstripe Goatfish	S,RF	yes	invertebrates
<i>Mulloidichthys vanicolensis</i>	Yellowfin Goatfish	S, CH	no	algae
<i>Ostracion cubicus</i>	Black-Spotted Boxfish	CH,RF,DO	no	algae
<i>Ostracion meleagris</i>	Whitespotted Boxfish	CH,RF,DO	no	didemnid tunicates, polychaetes,sponges, molluscs, copepods, algae
<i>Parupeneus barberinus</i>	Dash-and-Dot Goatfish	S,CH	yes	invertebrates
<i>Parupeneus trifasciatus</i>	Barred Goatfish	S, CH	yes,no	invertebrates
<i>Thalassoma hardwickei</i>	Six-Barred Wrasse	CH,RF,DO	yes	crustaceans, fish, molluscs
<i>Zanclus cornutus</i>	Moorish Idol	CH,RF,DO	yes	encrusting animals
<i>Zebрасoma veliferum</i>	Sailfin Surgeonfish	CH	no, yes	benthic algae

# Aggression, Feeding, Territoriality and Body Size Effects in Geckos (Gekkonidae) of Moorea, French Polynesia

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**ABSTRACT.** I observed the individual behavior and territorial interactions of the Moorean house gecko, *Gehyra mutilata* (Gekkonidae), and monitored its distribution in relation to other Moorean geckos. These geckos had territories which they occupied and defended during feeding hours. Larger geckos chased smaller geckos and won fights with smaller geckos. Larger dominant individuals had defined territories while the activities of smaller individuals were more erratic and less well-defined. Increasing gecko density led to more aggressive behavior. Larger geckos (32-45mm) had smaller, better established ranges and more fights than smaller (15-28mm) geckos. Peak feeding and fighting times occurred between 17:30 and 22:00. Although feeding occurred more often than fighting, fighting was positively correlated with density, while feeding rate decreased as fighting increased. When the feeding site light source was altered, the geckos followed the insects to the newly light-intensified areas of the study site. Of the gecko species present in Moorea, *Gehyra mutilata* was the most abundant overall, and occurred more frequently on and around non-native plants, while *Lepidodactylus lugubris* and *Gehyra oceanica* were more evenly distributed between native and non-native plants. All of this data greatly furthers our knowledge of *Gehyra mutilata*, which has been called "the least studied, widespread gecko in the world." (Fisher 1997)

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## Introduction

The island of Moorea is part of the Society Islands, centered 25 km West of Tahiti. Typical of Indo-Pacific islands, there has been documentation of numerous introductions of old world geckos, family Gekkonidae. (Vaughan et al 1996, Radtkey et al. 1996). One of the prominent non-native species is *Gehyra mutilata*. As insectivorous lizards, they are typically attracted to light associated with human habitation. This circumstance provides an ideal opportunity to observe intraspecific activity, specifically territorial interactions and dominant or aggressive individual behavior. Especially preferred sites are the lit windows of buildings, where insects congregate in the evening.

There are considerable gaps in the reconstruction of the biogeography of the Gekkonidae. The disjunct distribution of many of the more than 700 species can be credited to their

exceptional adaptability and ease of transport by human agency which has enabled them to enjoy a remarkable radiation in all tropical areas. These transported populations have in fact become subjects in naturalized laboratories for the study of their natural history. An important topic worthy of study is the affects of introduced species on the pre-existing species (Petren and Case 1996; Fisher 1996). In order to understand the interspecific interactions, separate data must be collected on each species concerning the species habitat and dietary requirements. Once both species are fully documented there can be a survey of their interaction. This study mainly deals with *Gehyra mutilata*, but includes distribution data on *Gehyra oceanica* and *Lepidodactylus lugubris*. The purpose of this study was to investigate the intraspecific activities, feeding events and territorial behavior of *Gehyra mutilata*. More specifically this paper examines the follow questions: 1) Do larger geckos

win more fights? 2) Does aggression increase as the density of geckos increases? 3) Is a gecko's body size correlated to its range? 4) Do geckos have peak fighting and feeding times? 5) Is feeding and resource partitioning light driven? 6) And finally, how are the three species of geckos distributed?

### Materials and Methods

The study site was located at the University of California, Richard Gump Research Station (~PK 12), on the island of Moorea (17° 30'S and 149° 50' W), French Polynesia. The area is a west-facing wall and window in the recently constructed computer room of the station. I initially identified a population of geckos that capitalized on the available resources in the study area, feeding on insects at the window and surrounding walls. The study took place from September 26<sup>th</sup>, 1999 to November 15<sup>th</sup>, 1999. Data were collected between the hours of 1730 and 2200. These times were based on preliminary reconnaissance and observation. During the monitoring period, the primary location of gecko activity on the west-facing wall was at a window where insects were attracted to the interior light. The total window size was 118 X 150 cm. and it was divided into sixteen 32 X 27 cm panes. The entire window was covered with an expanded steel security grill with 5 X 9 cm openings. The building, window frame and grill were painted white. Distribution data were collected on all three of the species found on the Gump Research Station.

When individuals appeared on the window, their body size was measured, they were photographed, and their feeding activities were observed; in conjunction with feeding activities the numbers and species of prey insects, along with location on the window, was recorded. Their general movements were plotted on the window panes and any intraspecific interactions were observed and recorded. During observations air temperature was measured. Additionally, during observations, insect activity was recorded at thirty-minute intervals. To facilitate identification, individual geckos were sketched and unique markings noted. During observation periods each evening, a convention was established assigning each individual gecko a specific color, which was then used to plot its movements on the window. Arrival and departure times, of individuals, were

recorded. After activity patterns became apparent, the location of the light in relation to the window, was altered. The light was placed in different corners of the window on different evenings.

The study consisted of three parts. The first was the observational data collection, the second was the experimental/ manipulated part and the third was a brief look at the distribution of all geckos on the Richard Gump/ UCB property. The first 2 are explained above.

Part 3: Habitat descriptions for the distribution study of three species of geckos found on the UC Berkeley Gump Research Station, Moorea, French Polynesia.

Six minutes were spent at each site. I searched for geckos with two flashlights and took the same route each time I did the survey. The survey was done six times between the hours of 20:00 and 22:00.

Table 1: Distribution Site Details

Plants present or Habitat:	Specific description:
Crinum Lily	Six bushes. (3-5 feet high)
Three Coconut trees	(small, medium and tall), and a mixed Hibiscus and Palm stand of 4 or 5 trees.
Ornamental hibiscus, bougainvillia, and small shrubs	Along the road.
The dry lab and library outer building walls	Walls and all the slanted roof overhang.
Terminalia tree.	The picnic area, front porch, benches, and the fire pit.
Ti plants and all shrubs or low growing plants	Excludes the building walls.
None	Everywhere on the first floor of the dorm house.
None	Everywhere on the second floor, especially in the back left room (which looks out to the picnic area).

*The three species included in the study and how to identify each:*

1) *Gehyra mutilata*-nocturnal, sexual, insectivorous, non-native, SVL of 40mm, pale pink/white coloration with small brown specks on the lower back/ upper tail region. Generally 2-4 spots.

(Note for future studies: A fourth "gecko", black in color was seen by a classmate: however, its identification was not discovered as I have never seen it, and it was most likely a skink.)

2) *Lepidodactylus lugubris* -parthenogenic, SVL of 40mm, body marked by small darkish m's. Native and found from the coast to the deep rain forest, slight flattened tail and teeth-like scales along the tail, communal nester.

3) *Gehyra oceanica*- up to 200mm (SVL), dark in color, loudest bark of the 3 species found.

**Results**

**Gecko survey**

From all data collected the following graphs and tables were created:

Figure 1 is a picture of *G. mutilata*. SVL is 40mm.

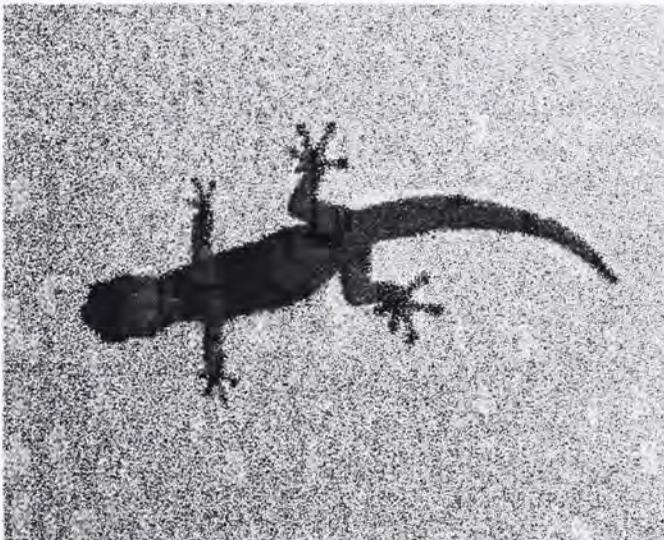


Figure 2: Winners and losers: The pink dots represent the winners body size while the blue represent the losers body size. Notice the overwhelming amount of winners with larger body sizes. Using statistical analysis, there is a chi test value of 4.66759E-67, with a p-value well above .25. This means that the data concludes 99% confident that the results are accurate.

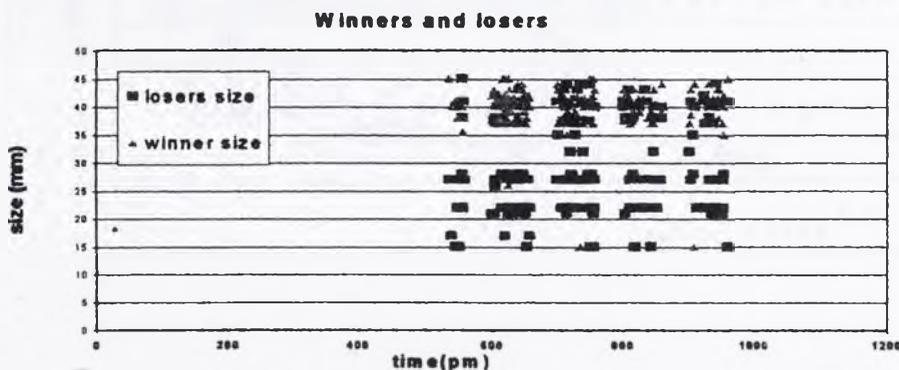
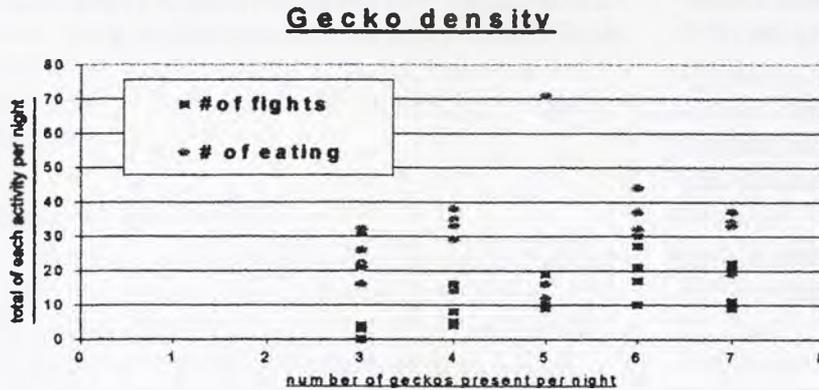


Figure 3A: Gecko density. The lower dots represent the total number of fights per night relative to the number of geckos present in the defined study site.



The upper dots represent the number of feedings that occurred per night relative to the number of geckos present.

Figure 3B: The gecko density plotted relative to the number of geckos present. One point has been removed from the study, as it was an outlier.

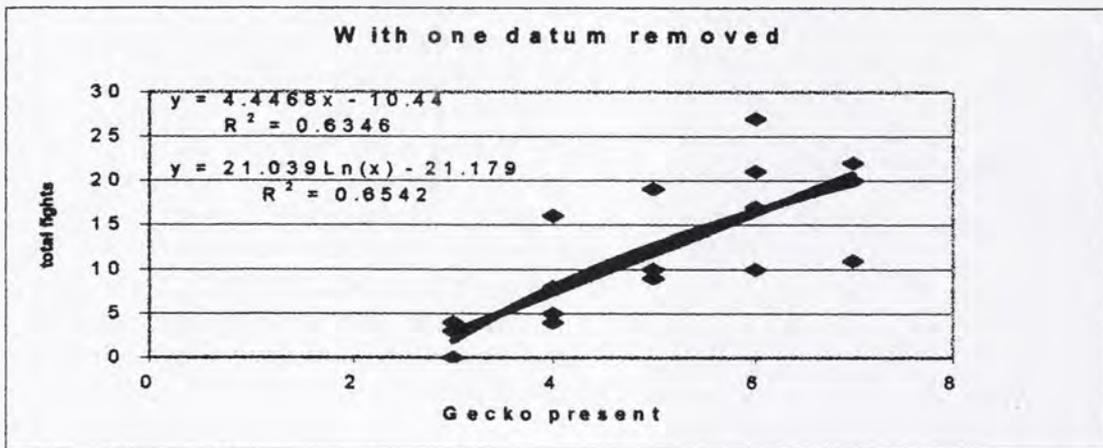


Figure 4: Gecko Body Size and geckos range in (1/4)2 inches. The light, placed in only one of the window panes. (pane#1) The experiment was done for 12 nights, moving the light every three nights, and all data has been compounded to one graph. (correlated Pearson test of range to size of 0.594)

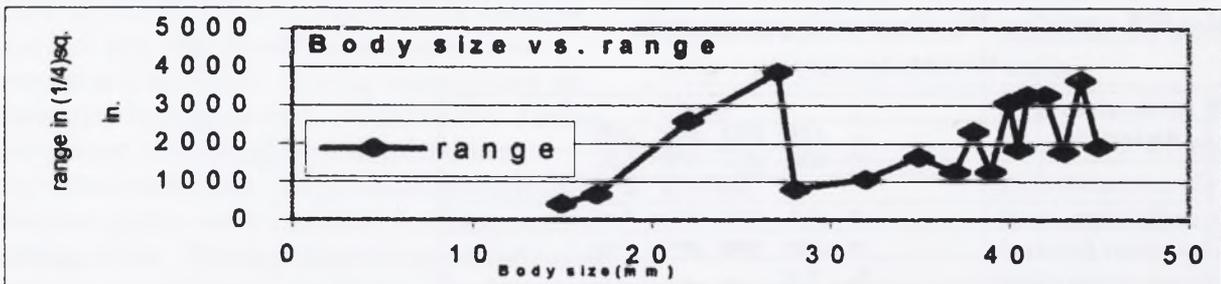


Figure 5A: Peak feeding times. Times are in 10 minute intervals.

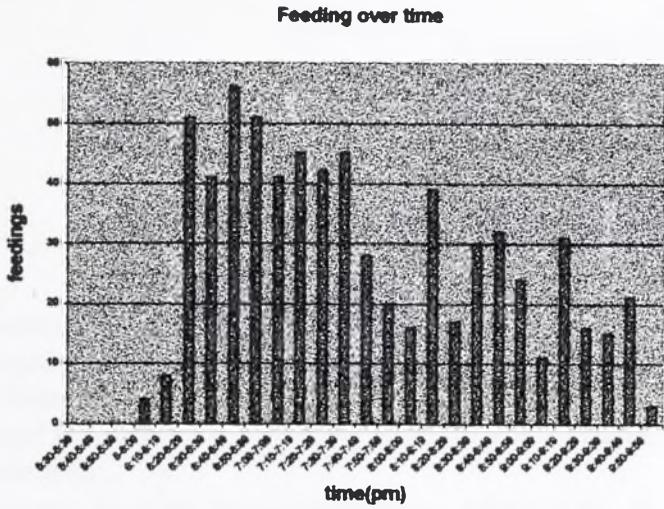


Figure 5B: Peak fighting times. Times are in 10 minute intervals

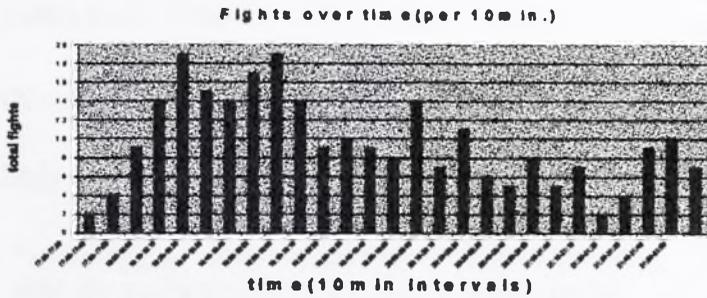


Figure 5C: Typical Night of Data. The feeding and fighting lines overlap at certain points.(7-8pm)

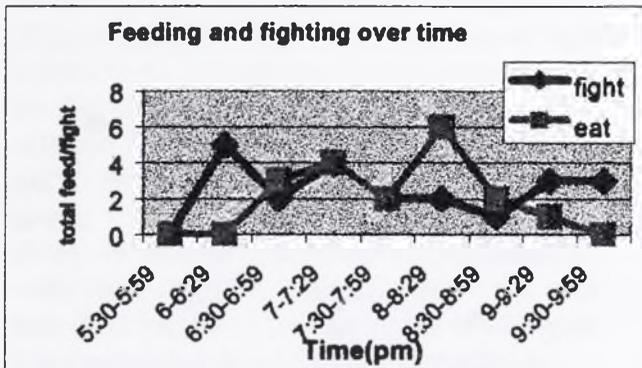


Figure 6: Light intensity over the number of insects, feedings, and fightings. The x-axis represents the 16 windows and their distance from the light. (correlation of fighting and gecko density is 0.494; correlation of food and gecko density is 0.293) Insect density correlation of chi square test is  $9.2038E-188$ , 0, 0 and 2.8685E-201.

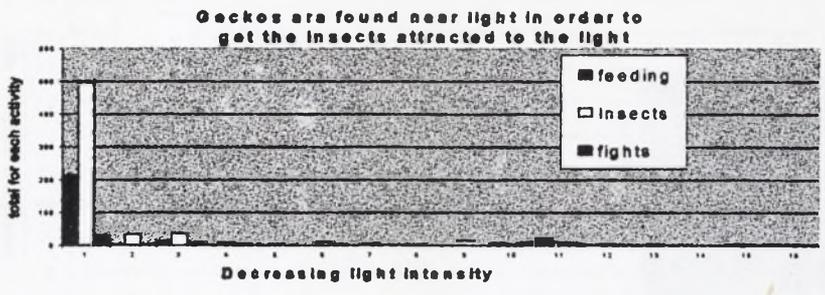


Figure 7: The distribution data for the Gump station.  
**DISTRIBUTION OF 3 SPECIES OF GECKOS**

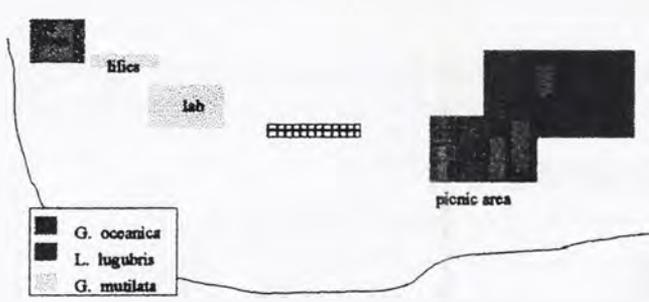
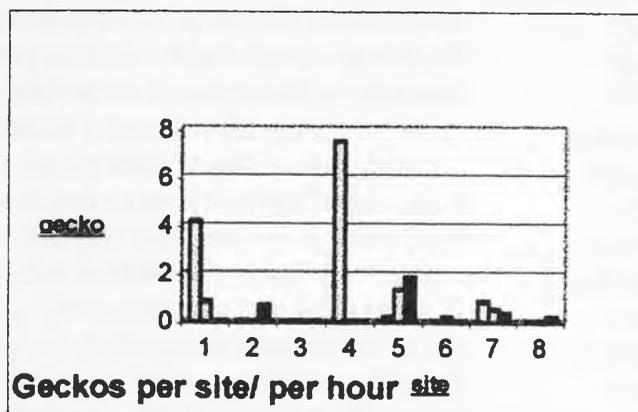


Table 2: Eight designated sites where geckos were monitored on the Gump Research Station.

gecko

Site	<i>G. mutilata</i>	<i>L. lugubris</i>	<i>G. oceanica</i>
lily	25	5	0
trees	0	0	4
shrubs	0	0	0
walls	45	0	0
picnic area	1	8	11
roadside	0	1	0
1st floor	5	3	2
2nd floor	0	8	1
total	76	25	18

Figure 8: The numbers corresponds to the 8 study sites listed in Table 1. #1 is the lilies, #2 the trees etc. The left bar represents *G. mutilata*, the center bar is for *L. lugubris* and right bar represents



### *G. oceanica*

Light meter data was taken 4 times for the 4 corners of the window. The light intensity in the corner where the light was located, was between 392 and 526 on the lux/slow scale of 19990 20000 while the light intensity in the 15 other panes was 0 or below, meaning it was essentially dark, or lacking in light intensity.

For the 23 nights I was present from 17:30-2200:

Earliest fight: 17:35

Latest fight: 21:59

Earliest feed: 18:04

Latest feed: 21:55

### Discussion

#### *Body size and fights:*

Body size influences a gecko's ability to "win" fights. The findings from all data shows that the geckos fights result in the larger gecko "beating", "winning" or dominating the smaller geckos at a highly significant rate. The fights occurred at a rate of 2.51 fights per hour, while feedings occurred at 6.71 feeds per hour (Figure 2 and 5A&B). With the data of fight interactions, I found that the larger geckos were the winners of the fights a highly significant amount of the time. I defined "winner" as a gecko who chases, barks at or bites another gecko. "Loser" is defined as the gecko that ran away, or walked away from a confrontation with another gecko. Figure 2 shows the win lose data for 240 of the 260 fights as 20 fights involved equal sized geckos. Sometimes geckos would simply bark at each other rather than chase each other. One of the disadvantages of barking is that once a gecko barks every other gecko is aware of the "barkers" presence.

The outcome of fights is important to be aware of in order to get a sense of how the geckos resources are divided. If smaller geckos win, it may be that the larger geckos have a lower metabolic demand, but the findings that large geckos win means that large adult geckos spend just as much time feeding as small geckos do. The fact that they fight at all and confront each other shows that geckos do not work as a group and that they are not social. Instead, in terms of proxemics, geckos scurry apart if they get within 3 or 4 inches of one another, and when they do come into contact, barking, chasing and biting occur. This is some of the evidence to demonstrate gecko territoriality. Being sit-and-wait predators, it may be necessary to be staggered around the window so they find enough food to survive. Furthermore, being alone allows them to hunt with more agility and less distraction. In most cases, in natural systems larger animals or plants dominate smaller ones. Larger geckos dominate smaller geckos.

### *Gecko Density in a Defined Area and the Total Numbers (#) of Fights:*

As species are introduced to an area, more demand on the resources is created and the competition for food increases. With increased competition and a heightened demand on the resources, more aggressive behavior will ensue. Although the number of feedings is 3 times larger than the number of fights, fighting was significantly and positively correlated to the number of geckos present. (Figure 3A & 3B). The average number of geckos per night was 4.7, although some nights more would come and attempt to feed, usually unsuccessfully. Large dominant individuals consolidated their territories in the corner of the window with the highest light intensity as well as the most food. When there were more geckos present, more fights would occur. Also, total insect consumption would increase as gecko density increased, simply because there is a higher probability of finding food as more gecko eyes scan and search for it. However, individually the number of feedings per gecko decreased because the geckos were too busy fighting. Therefore, an ecosystem, habitat or area can only sustain a certain number of geckos dependent on the available resources.

Most nights, geckos would enter the feeding area and begin to fight right away in order to "claim" an area. They would defend a territory. Inevitably, each night some geckos would leave for the next window (to the left) or some other place to feed. The competition would be too taxing for the amount of geckos present. It is likely that geckos fight for territory and defend that territory in order to get the best resources possible. Conversely, they do not defend territory that is not insect rich.

### *Gecko Body Size vs. Range( nightly movement)*

Gecko body size was found to be correlated with the amount of territory a gecko will defend. *G. mutilata* fought for territory by chasing, barking or biting other geckos. The larger geckos were also found to win more fights (Figure 2) and therefore control the feeding areas that are optimal or easy for them to find insects (ie. where the light is). Large geckos did not simply defend the largest territory possible: the quality of a territory and

resources found there were more important than the size of the territory. Quality was based on the number of insects found in the area. In Figure 6, we can clearly see that pane #1 was much more insect rich and therefore a higher quality feeding area than the 15 other windowpanes. The 45 mm gecko had a smaller range than the 44mm gecko but the quality of the territory was lowered (Figure 4). As shown in Figure 4, the geckos with a body size of 28mm or below ran about haphazardly, getting chased out of others territories, while the geckos larger than 32mm defended the largest prime insect areas. The big picture here is that the feeding site can maintain a certain number of geckos of differing sizes. I noticed that geckos of mid sizes (35-39mm) would come in each night and get chased off very quickly, while the 15-28mm geckos would hide out and feed in the lower quality areas.

### *Peak feeding and fighting times:*

*Gehyra mutilata* was most active between the hours of 17:30 and 22:00. The first time I observed the geckos was from 17:00 to 5:00 (12 hours) and I was able to conclude, along with what Comendant (1994) found, that the main fighting and feeding times were 17:30-22:00. They would predominantly emerge from their daytime retreats between 17:30 and 18:30. It is notable that the geckos begin to fight prior to feeding (Fig.5). Figure 5 shows the amount of feeding for a typical night. This suggests that geckos arrive each night and look for the highest quality feeding spot, and then begin to fight for the area. The largest geckos win the fights, so we can predict that the largest gecko will be found where the most insects are found. It is important to note the seasonal aspect of feeding and fighting times. The study lasted only 6 weeks, from the end of September to the middle of November. This detail could alter some aspects of the study, but it would not make any of the data less valid.

### *How lights affect gecko behavior*

The species of geckos I studied are nocturnal, and I found it interesting how they were predominantly found near light. (Case et al.1994) Although they are nocturnal, they prefer lit areas. This could be due to geckos eyesight or

an inability to see prey items accurately in darker areas (Refer to Figure 6,7,8 and Table 1) (Note: the geckos are found in areas with strong spot lights and indoor light) Most likely, geckos are found in well-lit areas because of the increased density of insects present on lit windows compared to the amount of insects found in darker areas. Geckos eat insects, which are present in higher density near lights. The graph which shows the data for all of the experimental observations. The x-axis represents the pane in which the light was most intense. Pane 1 represents where the light was placed. The insects went towards the light and so the insects fed more often in the pane where the light was placed. As feeding occurred predominantly in one pane, the fights predominantly occurred in that same pane. Therefore, the geckos followed the food and fighting for the food. The light has a side benefit for the exothermic reptiles: heat. The site of the highest light intensity is also the site of a slight increase in temperature. This temperature was not recorded but it was noted that the window was slightly heated from the lamp. It should also be noted that the room is air conditioned to 70-75 degrees Fahrenheit. Had the room not been cooled, the geckos may have been even more crowded and fought more for the extra warmth. Future studies could measure the effect of limiting light and altering light intensity to determine what geckos do when other insects are present. One important observation I noted was that as the light intensity increased, more large bodied insects flew towards the light, and fewer insects overall were present.

#### *Distribution of the Gump station geckos.*

The final part of my study involved counting the geckos (Figure 7 & 8 and Table 1). I gathered data, presented in Table 1, about the distribution of the gecko. The distribution data is important to the study of geckos in order to get some understanding of the dominant species, and how they divide the Gump Station, or any habitat, into separate feeding territories. The geckos found in the non native plants (lilies) and on the walls of the computer room were the non native species *G. mutilata* while the native geckos were found on native trees in less well lit areas and on the darker walls around the picnic area. The distribution study could be repeated

in order to gain more refined statistical validity, but from Figure 7,8 and Table 1, it is easy to see the distinct differences between the three species. There is no location where all three are found together.

There was only one area where *L. lugubris* and *G. oceanica* were found next to each other (in the picnic area. Their territories did not truly overlap. Rather, *G. oceanica* was found on the porch and bathroom walls, while *L. lugubris* was found in by the terminallia tree. This demonstrates one of the difficulties I had designing my study boundaries. *G. oceanica* fed near the upper walls of the picnic area next to where *L. lugubris* fed. Perhaps *G. oceanica* is found near *L. lugubris* because it is feeding on *L. lugubris*. One of the students, Dave De Marais said he saw the tail of one gecko hanging out of one of the " large gecko's mouth" which I presumed (or deduced) was *G. oceanicas*. (Event took place on October 2<sup>nd</sup>, on the wall by the picnic area.) In summary, of the gecko species in the area *Gehyra mutilata* predominated at the windows. In surrounding vegetation, away from buildings, *G. mutilata* was supplanted by *Lepidodactylus lugubris* and *G. oceanica*.

#### *Sex*

This study does not include the data for sexual differences and male-female interactions as I assumed the species was *L. lugubris*, a parthenogenic species. (While in Moorea, I did not have sufficient data to accurately distinguish which of the two smaller species I observe. I was not certain if they were the same species or two different species.) Male geckos are typically found to be more aggressive than female geckos (Rhen and Crews 1999).

#### *Food*

Geckos preferred moths and would pass by a small fly to eat a moth. Also, they would eat moths that could barely fit in their mouths. Moths were the largest prey item I saw them eat. They took up to four minutes to swallow the larger moths. The insects that geckos most often ate were moths (Lepidoptera), midges, gnats, and black flies (Brachycera). Black flies were eaten at a higher rate, but the moths had more body mass per insect. The moths are at least 50 times the size of black flies.

*G. mutilata* and many other geckos are very comfortable in human habitations, easily exploiting the resources, but they may eventually become

domiciliated, and have a difficult time finding necessary resources when in the wild. Information about what geckos prefer to eat, as oppose to what they do eat, and studies of preferred foods and their mechanism for identifying food would enhance our knowledge of geckos and the insect populations they help control. On one occasion, I saw a gecko lick a beetle's antenna but not eat the beetle. They have preferences in their food selection, but more research needs to be done to determine what they prefer, other than moths. (This data was found to be accurate, although exact numbers were not included due to lack of statistical capabilities.)

### *Fight*

One aspect of intraspecific interactions is the behavior of adults to their own offspring and adults reaction to other gecko's offspring. I noticed two geckos, an adult and a juvenile, would have confrontations more than any two geckos and would be closer together than any other geckos. I was unable to locate any information on studies such as this. The geckos would scurry apart if they got within 3-4 inches of each other. On one occasion, one gecko had another gecko's head, with approximately the same body size, in its mouth. The encounter lasted for 2 hours and 40 min. and ended by the flash of my camera. I used my flashlights and camera flash minimally.

### *Fecal matter:*

The window was littered with fecal matter, and I observed the geckos defecating on the grid with no apparent pattern. To further this study, it would be interesting to see if the fecal matter has some sort of scent marking effect on other geckos. In Carpenter and Duvall (1995) it was found that geckos defecate away from their diurnal resting spot. Their methods clearly explain how this can be done for a future study. Does the feces scent have some sort of mate recognition or individual recognition?

### *Future Research*

Future research in this field could include a comprehensive survey of the distribution of geckos on Moorea, and all of the Society Islands. A comprehensive list of the species of geckos found on Moorea would greatly improve the scope of study of geckos interactions and the

effects of recently introduced geckos on the existing gecko species would be a valuable study in biogeography. Another revealing experiment would be to discover how different colored lights, or different light-intensity might effect geckos, and if they change their body coloring due to the differing lights. Another project could be to measure the effect of moonlight on geckos feeding and fighting habits. Information on how much food a gecko eats in a feeding period could be useful to understand their metabolic requirements and their effects on an ecosystem. Another idea is to determine if geckos are potential or actual pollinators, and if so to discover what effect do they have on flowering plants?

### *Not just a paper about a Gecko.*

How humans effect animal behavior is still not sufficiently studied, and the amount of domiciliated animals we maintain or eliminate with our actions changes the biodiversity and genetic richness of our planet. As we enter the 21<sup>st</sup> century, we are increasingly aware of our control over many aspects of the earth's processes. The behavior of geckos may seem trivial in comparison to the entire earth. However, the behavior of geckos, and particularly the studies of species on islands, are microcosms of the larger landmasses and larger, more complex ecosystems. If we know the needs and habits of each species, we can perhaps live more harmoniously with all species, while at the same time keeping those we call pests balanced within their own system. As more homes are built and more development occurs, the species and populations of geckos which take advantage of humans will inevitably grow greater in number and become more predominant than those species which do not capitalize on humans "insect attracting" habitations. Furthermore, each species affects the other, being either the fed on or the feeder. We humans are not excluded from that food web either. In aboriginal Australia, there are cookbooks with recipes for a gecko barbecue. Also, we can gain useful tools from the study of animal physiology and behavior. Geckos feet have been used by the US military to create instruments that can walk up walls.

## Conclusion

*Gehyra mutilata*'s body size determines the number of fights it will win and therefore how aggressive it is. The number of fights between individual geckos increases as gecko density increases. Geckos have peak times in their feeding and fighting. They begin to fight before they feed, which is indicative or suggestive of defending an optimal feeding territory. Geckos are attracted to light mainly because insects, which are the major food source of geckos, are found by the light. As gecko body size increases, their ranges do not. Rather, large geckos have prime or more insect rich feeding areas or territories while the smaller geckos feed in a larger area where insect density is extremely low (Figure 6 and Figure 4). Geckos defend territories and have a great deal of intraspecific interactions each feeding night.

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# Morning Glories (Convolvulaceae) of Moorea: systematics, distribution, and ecology

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**ABSTRACT.** The flora of French Polynesia is still relatively poorly known compared to other island groups in the Pacific. Little work has been done to gather data on the overall plant diversity of these islands. In this study, the diversity of morning glory species (Convolvulaceae) on the island of Moorea is explored in order to gather information concerning the systematics, the distribution (along with the factors controlling distribution), and the ecology of the local species. 10 Convolvulaceae species were found on Moorea, 6 species from the genus *Ipomoea*, 3 from the genus *Merremia*, and 1 from the genus *Operculina*. A phylogenetic tree resulting from the collection of physical character data while on Moorea shows the relationship between these 10 species. While this phylogeny differs slightly from those previously published, it represents the entirety of the local Convolvulaceae diversity on Moorea making interpretation of the significance of the phylogeny on local ecology possible. The 10 species are shown to be distributed over 3 habitat types with each prevalent species occupying different habitat niches. Ecological association of individual species is explored, often having intriguing connections to species distribution and clade characteristics within the Moorean Convolvulaceae phylogeny. All species found on Moorea are described in detail and dichotomous keys are provided.

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## Introduction

The family Convolvulaceae, the Morning Glory Family, is one of considerable size and species diversity. Beyond this, or perhaps due to this fact, the Convolvulaceae is also a family of economic importance, including food crops such as *Ipomoea batatas* (L.) the sweet potato and other species with edible tuberous roots (*I. pes-caprae* and others not so well utilized as *I. batatas*), ornamental plants (*I. purpurea*, *I. carnea* ssp. *fistulosa*, to name a few) frequently used as ground covers or climbing vines, and species of important traditional medicinal value as well as modern pharmacological use.

The flora of the Society Islands is relatively poorly known in comparison to the flora of other Pacific islands such as the Hawaiian Islands, Fiji, New Zealand, Australia, and New Caledonia. The flora of French Polynesia is currently being worked on by Jacques Florence at ORSTOM in Paris, only the first volume of which is currently available (Florence 1997). The flora of the Societies has been recently dealt with by Dr. Stanley L. Welsh in *Flora Societensis - A Summary Revision of the Society Islands: Mehetia, Tahiti, Moorea, Tetiaroa (îles du vent); Huahine, Raiatea, Tahaa, Bora Bora, Tupai, Maupiti, and Mopelia (îles sous vent)* (Welsh 1998), the only previous works being Drake del

Castillo's 1893 *Flore de Polynésie Française*, written using only the specimens available at the Natural History Museum in Paris, and a 1996 posthumous publication of a checklist of the flora of the Society Islands compiled by Dr. David Stoddart from Dr. F. Raymond Fosberg's rough drafts (Fosberg and Stoddart ed. 1996). Despite Welsh's obvious thoroughness in poring over collected samples at the Bishop Museum in Hawaii and elsewhere, along with visiting the islands, *Flora Societensis* is still not a complete work (nor does Welsh consider it one) with many species that are as yet unknown, not yet known to be present on the Societies, improperly identified, or otherwise.

The Convolvulaceae is no exception to this lack of knowledge, and with the relative number of species known to be established on other island groups of the Pacific, it seems impossible that there could only be a handful of species in the Societies. Of the 17 species listed in Welsh's *Flora Societensis*, nine are to be found on Moorea, plus one unknown to Welsh and identified mistakenly as *I. cairica* by Fosberg (Fosberg and Stoddart ed. 1996), most likely based on a misidentified 1967 specimen deposited at UC Herbarium.

This study was conducted on the island of Moorea, French Polynesia, an island just west of

Dahlgren (1980)	Cronquist (1981)	Cronquist (1988)	Takhtadzhian (1997)	Thorne (1992)
Solanales	Solanales	Polemoniales	Solanales	Solanales
Solanaceae	Duckeodendraceae	Nolanaceae	Solanaceae	Solanaceae
Sclerophylacaceae	Nolanaceae	Solanaceae	Sclerophylacaceae	Solanaceae
Goetzeaceae	Solanaceae	Convolvulaceae	Duckeodendraceae	Duckeodendraceae
Convolvulaceae	Convolvulaceae	Cuscutaceae	Goetzeaceae	Goetzeaceae
Cuscutaceae	Cuscutaceae	Menyanthaceae	Convolvulales	Nolanaceae
Cobaeaceae	Retziaceae	Polemoniaceae	Convolvulaceae	Convolvulaceae
Polemoniaceae	Menyanthaceae	Cobaeaceae	Cuscutaceae	
	Polemoniaceae	Hydrophyllaceae		
	Hydrophyllaceae	Lennoaceae		

Figure 1. Recent Classifications of Convolvulaceae Based on Johnson 1999, and the sources above.

Tahiti, at the University of California at Berkeley Richard B. Gump South Pacific Biological Research Station. This research was conducted in order to ascertain 1) the species diversity within the Convolvulaceae on Moorea, 2) the distribution and preferred habitats of the species present, 3) the phylogenetic relationship of the species, be they "native" or introduced, 4) the general ecology of the species on Moorea.

#### Family Characteristics

The family Convolvulaceae is quite large, having roughly 55 genera and over 1600 species worldwide, *Ipomoea* (700+ spp.), *Convolvulus* (250+ spp.), and *Evolvulus*, *Merremia*, *Jacquemontia*, and *Argyreia* (~100 spp. each) making up the majority of the family (Van Ooststroom 1953; Austin & Huáman 1996; Mabberley 1997).

The family is composed mostly of herbaceous vines with twining stems, climbing or creeping, rarely erect. The leaves are usually simple, petiolate, spirally arranged, entire to deeply lobed, rarely compound, lacking stipules (some species such as *I. cairica* have pseudostipules). The primary leaves of seedlings are deeply 2-lobed in all species, secondary leaves taking on the shape typical of the particular species. The calyx is made up of 5 imbricate sepals, often persistent. The corolla is composed of 5 fused petals, shallowly lobed, often marked by lanceolate midpetaline bands, spirally twisted before opening. The corolla shape is generally campanulate or funnellform, with some cupshaped or salverform. There are 5 stamens, alternating corolla lobes, attached to the corolla tube basally. The anthers are bilocular, laterally or longitudinally dehiscent, but usually have dehisced upon the opening of the flower. The ovary is always superior, usually 2 carpelled often with klausens (false separations), ovules 2 per carpel, and thus usually producing 4 seeds.

The stigma is usually simple, sometimes lobed, the style usually single. The fruit is a capsule, valved or sometimes circumscissile or irregularly dehiscent. Some species are cultivated for their edible roots, medicinal use, and some plants for their narcotic or hallucinogenic properties due to the presence of ergoline alkaloids in certain species. (Welsh 1998; Van Ooststroom 1953; Frey 1995; Mabberley 1997)

In general, family members prefer high amounts of light, being found on the edges of clearings, in disturbed sites, on beaches, or in the canopy. Many species have seeds which are capable of being dispersed by water due to an air cavity within the seed (Van Ooststroom 1953; Mabberley 1997).

Convolvulaceae is probably best known, or perhaps notorious, for the bindweeds (usually referring to plants of the genus *Convolvulus* or sometimes *Calystegia*), aggressive, twining vines that cover and damage crops and are extraordinarily difficult to eradicate. While neither of the above mentioned genera are present on Moorea, two species of *Merremia* that are on Moorea exhibit similar aggressive twining behavior.

#### Taxonomy of the Convolvulaceae.

The taxonomy of the Convolvulaceae is currently, as with many clades, in a state of flux. A consensus has not been reached concerning the taxonomic placement of the family much less the genera and species within the family (Figure 1). Currently, the most common classification of the family would be:

Subclass Asteridae

Order Solanales

Family Convolvulaceae

(sometimes with Cuscutaceae)

(Chase et al. 1993; Dahlgren 1980; Cronquist 1981, 1988; Thorne 1992). Among the Solanales, Solanaceae, the Nightshade Family, appears to

be the closest relative to the Convolvulaceae (with the exception of the closely-allied Cuscutaceae, which is a possible subfamily of Convolvulaceae [Thorne 1992] and one study which suggests *Hydrophyllaceae* is the closer than *Solanaceae* [Johnson et al. 1999]) (Chase et al. 1993; Cronquist 1981; Olmstead & Sweere 1994; Durbin et al. 1995; Soltis & Soltis 1997). With this in mind, *Petunia*, a Solanaceae species shown specifically to be closely related to the Convolvulaceae, was used as the outgroup for the phylogenetic analysis in this paper (Durbin et al. 1995).

Within the Convolvulaceae, and more within the scope of this paper, there are again multiple hypotheses concerning the taxonomy. There is, however, a classical treatment combining the works of Choisy (1845), Hallier (1893), and House (1908), done by Verdcourt (1957, 1963) and Van Ooststroom (1953), and most recently by Austin (1979, 1980, 1991, 1996). The genera present on Moorea fall into two tribes of the Convolvulaceae, *Ipomoeae* and *Merremieae* (also called the Merremoids), two closely related tribes separated on the basis of pollen structure, corolla shape and color, and anther structure, the *Merremieae* having smooth pollen, white or yellow campanulate corollas, and spirally twisted anthers, while the *Ipomoeae* have spinulose pollen, pink, red, purple, sometimes white salverform, funnellform, or campanulate corollas, and straight anthers (Austin 1991; Van Ooststroom 1953).

There are three genera of Convolvulaceae found on Moorea: *Merremia* and *Operculina*, both in the tribe *Merremieae*, and *Ipomoea*, in the tribe *Ipomoeae*. Both *Merremia* and *Ipomoea* have further subdivisions: the 10 species found on Moorea fit into 3 genera, 3 sections of *Merremia*, 1 subgenus, 2 sections, and 2 series of *Ipomoea* (Figure 2) (Van Ooststroom 1953; Austin 1979, 1980, 1996; Miller, Rausher, and Manos 1999).

Parts of this system have been called into question recently based on a phylogeny produced by using ITS and *waxy* genetic sequences within the genus *Ipomoea* (Miller, Rausher, and Manos 1999), but, with the exception of moving *I. obscura* into a new basal group, this has little effect on this research.

#### *Plant Predation, Pollination, and Dispersal*

Most literature on herbivory of Convolvulaceae species not surprisingly deals with pests of the sweet potato, *Ipomoea batatas*.

### Family Convolvulaceae

#### Genus *Operculina*

*Operculina turpethum*

#### Genus *Merremia*

##### Section *Xanthips*

*Merremia umbellata* ssp. *orientalis*

##### Section *Hailale*

*Merremia peltata*

##### Section *Streptandra*

*Merremia mooreana*\*

#### Genus *Ipomoea* L.

##### Subgenus *Eriospermum*

##### Section *Eriospermum*

##### Series *Jalapae*

*Ipomoea carnea* ssp. *fistulosa*

##### Series *Batatas*

*Ipomoea batatas*

*Ipomoea littoralis*

##### Section *Erpipomoea*

*Ipomoea obscura*

*Ipomoea pes-caprae* ssp. *brasilensis*

*Ipomoea violacea*

**Figure 2.** The Moorean Convolvulaceae species placed into the framework of the most current taxonomy of the family. Adapted from Van Ooststroom 1953; Austin 1979, 1980, 1996; Miller 1999; Jarret et al. 1992, McDonald & Austin 1990. \*Provisional Name.

The major insects associated with the sweet potato, are the so-called "Sweet Potato Weevil" (*Cylas formicarius*) and the "Sweet Potato Leaf Miner" moth (*Bedellia somnulentella*), both of which are present in the Society Islands (Paulian 1998) and throughout the Pacific (Spiller & Wise 1982; Zimmerman 1978). *C. formicarius* is known to feed on the stems of many Convolvulaceae family members (Austin et al. 1991), and *B. somnulentella* larvae have been known to destroy the leaves of entire fields of *I. batatas*. The larvae feed on the leaves of *I. batatas* (and other Convolvulaceae species) causing a pitting and yellowing of the leaves (Zimmerman 1978). *Omphisa anastomosalis*, the "Sweet Potato Vine Borer", *Aspidomorpha deusta*, the "Australian Sweet Potato Weevil", and *Eucepes postasciatus*, the "West Indian Sweet Potato Weevil", are other serious pests of the Convolvulaceae, however are not known to be present in the Societies.

Pollinators are various: birds, moths, Curculionid and Bruchid beetles, ants, some species of Hymenoptera, and more. Many species

of morning glory are known to have flowers that are fragrant only at night (Frey, 1995; Van Ooststroom 1953) and attract nocturnal pollinators. Due to the fact that morning glory flowers are usually open for 24 hours or less, their pollination can only happen within a short period of time.

Dispersal of seeds is done by water in many species (*I. violacea*, *I. pes-caprae*, *M. peltata*) or simply by dropping. The seeds of these species are not known to be eaten by rats or birds, nor do they appear particularly palatable (too large, hard, fuzzy, and many are toxic). (Mabberley 1997; Van Ooststroom 1953) All seeds are too large to be effectively carried by wind.

#### *Native vs. Introduced*

One has to be cautious when speaking about native plants on volcanic islands. Like Hawaii, the Society Islands were formed by the Pacific Plate moving over a hot spot, creating a chain of high volcanic islands. In general, native plants are those that were established before the arrival of man, in this case, the Polynesians. It can be very difficult to determine exactly when a plant arrived in the Societies, especially with lack of records, although many can be assumed to have been brought by the Polynesians because of their value as food crops, medicine, or construction material. With the Convolvulaceae, the history is fairly clear and most species can readily be categorized Native or Introduced.

*Ipomoea batatas* - Introduced for food and medicinal use, present before European exploration, native to tropical America.

*Ipomoea carnea* ssp. *fistulosa* - Introduced ornamental, native to tropical America, introduced to Moorea within the last 100 years.

*Ipomoea littoralis* - No agreement on this species, may have arrived before the Polynesians due to its ability to be carried long distances by water, but is also used medicinally by the Polynesians, so may have been introduced. Most likely native because of its habitat preference on the motu (reef islands), but its presence inland is difficult to explain. This species most likely originated in the Americas, being the only member of the *Ipomoea* section *batatas* to be an Old World exclusive. Fosberg believed that *I. littoralis* was introduced accidentally by man at some point.

*Ipomoea obscura* - Native, although first recorded in 1909 in Hawaii, most likely spread from Africa throughout the paleotropics, weedy

and not used by the Polynesians. May have been introduced accidentally by Polynesians, though generally considered native.

*Ipomoea pes-caprae* ssp. *brasiliensis* - Native, dispersed by water, used medicinally and has edible roots, though not thought to have been introduced.

*Ipomoea violacea* - Native, arrived before the Polynesians, dispersed by water.

*Merremia mooreana* - Unknown, species name is provisional, no history will be known for this plant until it can be identified.

*Merremia peltata* - Native, most likely pre-Polynesian, found throughout Asia and Australia, seeds also known to be water dispersed.

*Merremia umbellata* ssp. *orientalis* - Introduced, reason unknown, used medicinally and eaten in parts of the Asian tropics.

*Operculina turpethum* - Introduced. Although native to much of the paleotropics, the plants found on Moorea were obviously planted, most likely for ornamental use or for its medicinal use. Van Ooststroom (1953) considers this plant to have mainly been introduced throughout tropical Asia.

(Welsh 1998; Ooststroom 1953; Petard 1986; Whistler 1992a, 1994; Grepin & Grepin 1984, Austin 1991)

The main question dealing with the native or introduced status of these species is how does their origin affect how they grow on Moorea? Do introduced species exhibit higher degrees of introgression and weediness? Is distribution of the morning glories on Moorea somewhat determined by the plants' native or introduced status? Are native species more closely related than introduced species? These are the types of questions that need to be addressed concerning the morning glories present on the island of Moorea.

## Materials and Methods

### *Distribution Analysis*

Determination of the distribution of the morning glory species was accomplished mostly on foot, roadside distribution being aided by use of vehicles. With the exception of *Merremia peltata*, the native, canopy-dwelling species, the morning glory species were restricted either to disturbed roadside or trailsite sites or the coastal strand. *M. peltata*, having such a wide distribution, boundary points were established around the island indicating the first spot in from

the coast at which the plant was spotted. The strand dwelling species were seemingly restricted to the motu (reef islands) as they were not found elsewhere.

#### *Character Analysis*

Character 1 - Growth Form: Herbaceous Vine; Arborescent. Convolvulaceae is composed almost entirely of herbaceous vines; arborescence only shows up rarely in the family. All Convolvulaceae species on Moorea were either clearly an herbaceous vine or woody shrub, and this character did not appear to be linked to any other physical change.

Character 2 - Anther Shape: Straight; Spirally Twisted. All Convolvulaceae species on Moorea had either distinctly twisted anthers or untwisted anthers. This is also a criterion often used in the separation of the tribes of the Convolvulaceae. All species on Moorea with twisted anthers also had smooth pollen and equal length stamens, but there is no indication that these traits are linked, as a few species have been observed to have spiked pollen and twisted anthers (Van Ooststroom 1953).

Character 3 - Stamen Length: Stamens of Equal Length; Stamens Unequal: 3 long stamens, 2 short stamens; Stamens unequal: 2 short stamens, 3 long stamens; Stamens unequal: 4 long, 1 minuscule staminode. The first three states clearly fit all Convolvulaceae species on Moorea, the fourth is applicable only to the outgroup *Petunia*. As with Character 2, this character is not clearly linked to any other.

Character 4 - Anther Pollen: Anther dehisced upon flower opening, pollen external; Anther not dehisced upon flower opening, pollen internal. All Convolvulaceae species on Moorea have anthers that have already dehisced upon the opening of the flower and have at least some of their pollen held externally. *Petunia* anthers are not dehisced upon the opening of the flower.

Character 5 - Stamen Number: True Stamens 5; True Stamens 4, Staminode 1. Again, this character, like number 4, serves only to separate the outgroup *Petunia* from the Convolvulaceae of Moorea.

Character 6 - Stigma Shape: Simple; Globularly 2-lobed. There are two clear character states among the Convolvulaceae of Moorea involving stigma shape: simple, unlobed stigmas or globularly 2-lobed stigmas, another character that has been used to separate tribes of Convolvulaceae (Welsh 1998, Van Ooststroom

1953). This character appears to be independent of all others, and there is nothing in the literature to make one believe otherwise.

Character 7 - Pollen Grooves: Pollen Not Grooved; Pollen 3-Grooved; Pollen 6-Grooved. The pollen grains of the Convolvulaceae of Moorea are either spinulose or smooth. Within these categories are other characters such as spike arrangement or this one, concerning grooves or furrows on the pollen exine. Spiked pollen can be grooved, however smooth pollen are obviously not be spiked, so have no recordable spike arrangement. The grooves appear to be independent of other characters.

Character 8 - Pollen Spikes: Pollen Not Spiked; Pollen Spiked Randomly; Pollen Spiked in a Tiled Fashion; Pollen Spiked in Discrete Ranks. Within the Convolvulaceae of Moorea, the pollen grains are either not spiked (smooth), spiked with no discernible pattern, spiked in a tiled fashion (usually spiked in hexagon-shaped rings), or spiked in discrete ranks or rows. While the pollen must be spiked to exhibit these characters, these characters are independent of all others.

Character 9 - Pollen Shape: Spherical; 3-6 sided polygon in outline. There are those species on Moorea with hexagonal-discoidal pollen and triangular-discoidal pollen; these two states seem to be variations on the same general type of pollen, which could presumably be broken down into smaller categories, but for the sake of this research, was left intact. The rest of the species have spherical pollen. Pollen size appears to be linked to these two categories of pollen shape, and thus size was not used as a character.

Character 10 - Pollen Spike Type: Spike surrounded by bacula tuft; Spike surrounded by cavities; Spike simple. This character is not known for five species in the present treatment, however, the remaining species fall clearly into the three categories above, based on previous SEM (Scanning Electron Microscopy) analysis (Hsiao 1995; Bhattacharyya 1979; Frey 1995). These characters are independent of spike distribution.

Character 11 - Stem Wings: Unwinged; Winged. Stems of the Moorean Convolvulaceae are either winged or unwinged. Other stem traits such as pubescence, gland presence, etc. appear to be unrelated to the presence of wings, as winged species from other parts of the world are known to be glabrous, pubescent, or glandular (Van Ooststroom 1953).

Character 12 - Stem Hair: Glabrous or Sparsely Pubescent; Long-Pilose to Puberulent. Only one plant was found to have long-pilose to puberulent stems, all others were found to be either entirely glabrous or glabrous to sparsely pubescent. As noted in Character 11, this character is independent from stem wings.

Character 13 - Milky Sap: Absent (or Inconspicuous); Conspicuously Milky. This character obviously depends on the definition of "milky." In this case, any sap that was entirely clear was considered not milky, everything else was opaque and white and thus milky. This is a character that shows up off and on within most genera of Convolvulaceae and is not known to be linked to any other character.

Character 14 - Capsule Dehiscence: 4-Valved, 2-Valved, Circumscissile. Most species in Convolvulaceae have 4-valved capsules, and occasionally there are circumscissile capsules. The outgroup *Petunia* has 2-valved capsules. This character is independent of all others in this treatment.

Character 15 - Seed Number: 4 Seeds; Many Seeds. Capsules are rarely formed on *I. batatas*, and, as no seeds were available on *Moorea*, the seed characters were not scored in this phylogeny. For the remainder of the species, all had 4 seeds per capsule. *Petunia* has many seeds per capsule. This character varies independently of capsule dehiscence mechanism.

Character 16 - Seed Hair - Not Present (Glabrous); Pubescent or Puberulent, margin hair length equal; Pubescent or Puberulent, margin hair length long. All seeds of the species present on *Moorea* fit clearly into these three categories. In no instance was there a species with medium length margin hair, it was either much longer or equal to the rest of the seed hair. This character has no correlation with any other in this phylogenetic analysis.

Character 17 - Leaf Shape: Orbicular to Ovate to Ovate-Lanceolate (sometimes shallowly lobed), cordate to truncate basally, not peltate; Peltate; Emarginate to 2-Lobed; Deeply Palmately 5-7 Lobed. The first character state is the basic leaf shape definition for the family, the remaining three characters are those that break free from these constraints. None of these character states appear to be linked to any other.

Character 18 - Sepal Veins: Veins Inconspicuous; 1 Central Raised Vein; 3-5 Raised Veins. In general, sepal veins were inconspicuous on the species on *Moorea*. However, two species

had raised veins, one with only one central vein, the other with 3-5 raised veins per sepal. This character is clearly independent from all other used.

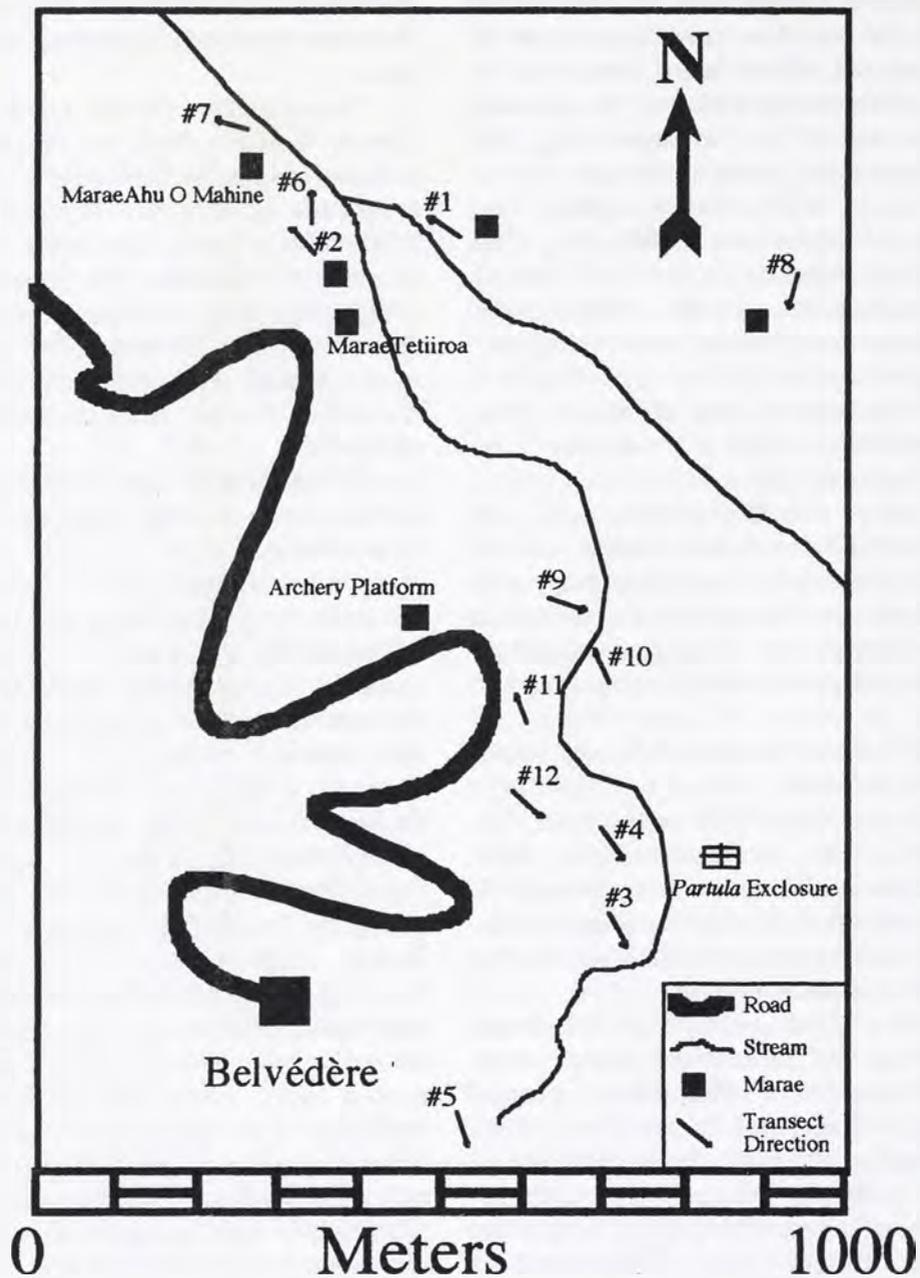
Character 19 - Corolla Limb Color: White or Cream; Yellow; Pink to Purple. White and yellow corollas are ancestral in the family, pink to purple flowers are derived (Austin, 1998). With this in mind, and with the fact that the species of *Moorea* fit cleanly into these categories, this is obviously an appropriate character to use. Flowers of all colors fall into all of the genera represented on *Moorea*, plus this character does not seem dependent on any other character.

Character 20 - Corolla Shape: Dominantly Salverform or Funnelform; Dominantly Campanulate or Cupshaped. This character again relies on term definitions. The definitions for these terms used here are based on those in Welsh (1998). Salverform: corolla tube long and narrow, only somewhat widened near or above the middle of the tube, abruptly flaring near apex into a flattened limb. Campanulate: tube short to fairly long, widened from below the middle of the tube, gradually to somewhat abruptly flaring near the apex; bell-shaped. Funnelform: as it sounds, funnel-shaped; gradually widening upwards, without abrupt flaring. Cup-shaped: widening quickly at the base, widening little above middle. Using these definitions, and on-site observations, the species fit neatly into two categories, cup-shaped being placed with campanulate due to the early widening of the corolla, salverform placed with funnelform due to the late widening of the corolla tube. These characters have no connection with any other in this treatment; corolla colors come in all shapes, despite how it may appear from the species on *Moorea*.

Character 21 - Halophily - Not Halophilic; Halophilic. The term "halophobic" was not used, due to the fact that *I. littoralis* can do well in salty coastal as well as inland environments. The halophilic species are those that live exclusively on the beach in salty substrate. The halophily of these species does not appear to determine or be determined by any other character.

#### *Phylogenetic Analysis*

Selection of the outgroup *Petunia* was based upon results of Durbin et al (1995), showing the close relationship of chalcone synthase gene



**Figure 3.** Map of *M. peltata* transects along the Opunohu River. Arrow direction indicates direction of transect based on compass bearings.

(CHS-B) in *Petunia* to the analogous gene (CHS) of *Ipomoea*, along with results of the consensus tree published in Olmstead & Sweere (1994) showing *Petunia* to be ancestral to other common Solanaceae species such as *Datura*, *Lycopersicon*, *Capsicum*, *Physalis*, and *Nicotiana*, all of which, along with *Petunia*, were available for comparison while on Moorea with the Moorean Convolvulaceae species, and the similar results

(although less detailed with respect to Solanaceae) in Chase et al. (1993) which show *Petunia* to be ancestral to *Nicotiana* and *Lycopersicon* plus being the closest relative of the Convolvulaceae genera used, *Convolvulus* and *Ipomoea*.

Characters used for creating the phylogeny were entirely morphological and were generally fairly prominent characters. Pollen observation

done using basic light microscopy with more detailed descriptions aided by previous palynology studies of Convolvulaceae using SEM (Hsiao 1995; Bhattacharyya 1979; Frey 1995). All character data used (with the exception of the detailed palynology needed for Character 10, plus a well established fact that *I. batatas* produces 4 seeds optimally) was a result of direct observation whenever possible and information from the literature was never used to fill in gaps in observed data to ensure accuracy to the species of Moorea. The shortest length and strict consensus phylogenetic trees were created using MacClade and PAUP. The phenetic analysis was performed manually using Jaccard coefficients of dissimilarity, in this case: 1-(# of character states the same/# of total valid comparisons). Any comparisons involving a "?" or data gap were not counted and subtracted from the number of total valid comparisons.

#### Ecological Studies

For determining the effect of *M. peltata* in the canopy on percent cover and understory species composition, 15 meter transects were laid out at twelve spots in the Opunohu Valley, extending from Marae Ahu O Mahine to just above the Belvedere viewpoint (Figure 3). Percent cover was determined using a GRS Vertical Densitometer at .5 meter intervals along the transect, data being recorded as 0 = no cover in viewfinder, .5 = partial cover in viewfinder, and 1 = 100% cover in viewfinder. Understory species composition data was also taken at .5 meter

intervals, species presence being noted within a meter wide swath centered on the transect tape. Transect sites were chosen specifically to have an equal number of sites with no *M. peltata* cover, moderate *M. peltata* cover, and high *M. peltata* cover ("moderate" being defined as an area where roughly 50% of the upper canopy is covered by *M. peltata*, and "high" being defined as an area with nearly 100% of the upper canopy covered by *M. peltata*).

#### Species Identification and Collection

All species presented in this study were identified in the field using *Flora Societensis* (Welsh 1998), *Manual of the Flowering Plants of Hawaii* (Wagner et al. 1990), *Wayside Plants of the Islands* (Whistler 1994), and *Coastal Flowers of the Tropical Pacific* (Whistler 1980). Furthermore, identification of understory and associated species was aided by photocopies of UC Herbarium specimens collected in the Society Islands, *Plantes Utiles de Polynésie* (Pétard 1986), and *Flore de Tahiti* (1996). Species identifications were strengthened by comparing collected plants to specimens in the UC Herbarium, and by the use of supplemental keys (Austin 1993; Brown 1935; Degener 1946; Fosberg & Sachet 1977; Hillebrand 1888; Ooststroom 1953; Smith 1991; Stone 1970; Webb et al. 1988; Whistler 1992b). All species presented in this report, with the exception of the cultivated *I. batatas*, were collected, pressed, and dried during the course of the study. Voucher specimens are deposited at the UC Herbarium in Berkeley, CA.

## Results

### Key to the Convolvulaceae of Moorea

1. Anthers twisted clockwise, corolla campanulate, white or yellow, pollen smooth
  2. Stems winged, capsule circumscissile  
.....*Operculina turpethum*
  - 2'. Stems not winged, capsule 4-valved
    3. Leaves palmately 5-7 lobed, stem long pilose to puberulent  
.....*Merremia mooreana*
    - 3'. Leaves entire, stem glabrous to short pubescent
      4. Leaves peltate, very broad, plant living in canopy, corolla white  
.....*Merremia peltata*
      - 4'. Leaves cordate, not peltate, longer than broad, low climber, corolla yellow  
.....*Merremia umbellata ssp. orientalis*
- 1'. Anthers straight, corolla salverform to funnellform, rarely campanulate, pink, red, purple, cream, or white, pollen spinulose
  5. Corolla funnellform, purple to pink, sepal with raised vertical veins

6. Sepal with 3-5 raised veins, leaf often 3 lobed, cultivated for tuberous roots  
 .....*Ipomoea batatas*
- 6'. Sepal with 1 central raised vein, leaf small, cordate, found behind beaches or roadside  
 .....*Ipomoea littoralis*
- 5'. Corolla salverform, pink, white, or cream, sepals without prominent raised veins
7. Plant arborescent, corollas pink, sometimes spreading by stolons  
 .....*Ipomoea carnea ssp. fistulosa*
- 7'. Plant a climbing or clambering vine, corollas various
8. Corolla pink, plant growing on beach, leaves emarginate to 2-lobed  
 .....*Ipomoea pes-caprae ssp. brasiliensis*
- 8'. Corolla white or cream, leaf tips acuminate, habitats various
9. Corolla white, tube very long, beach dwelling  
 .....*Ipomoea violacea*
- 9'. Corolla cream with maroon throat, flower small, low climbing, lives in disturbed sites  
 .....*Ipomoea obscura*

*Operculina turpethum* (L.) S. Manso

Large, perennial twining vine with winged stems, often tinged pink on the margins. Leaf blades up to 20 cm long and nearly as wide, orbicular to broadly ovate (at times ovate-lanceolate), entire, basally cordate, ± glabrous, sometimes pilose abaxially. Flowers borne on 1-3 flowered cymes, peduncles usually winged like stems, calyx noticeably pinkish, sepals ovate, the inner rank of sepals longer. Corolla broadly campanulate, tube ~1/2 length of limb, limb white, yellow at base of stamens. Stamens of equal length, pubescent at base of filament, anther spirally twisted. Pollen smooth, 3-grooved, discoid to triangular. Fruit a depressed globose capsule, circumscissile, seeds 4, glabrous.

Observed growing on and with: *Merremia umbellata*, *Wedelia trilobata*, *Hibiscus rosasinensis*.

Found only at one site on Moorea, on west side of Cook's Bay, between Pao Pao and the Gump Research Station, at the crest of the hill, bay side of the road, growing through chain-link fence just at the point the fence takes a 2 meter jog towards the bay.

*Merremia mooreana* Provisional Name

Medium-sized climbing vine, stems thin and long pilose to puberulent, leaf petioles ± glabrous. Leaves exstipulate, deeply palmately 5-7 lobed, margin entire, glabrous, up to 16 cm long, cordate in outline, ± bilaterally symmetrical, lowest lobes slightly unequal, lobes lanceolate. Flowers (only 1 seen) solitary, pedicel length roughly equal to peduncle length, sepals long ovate, covering the length of the tube, dark green-brown, corolla campanulate, limb pure white with yellow at the base of the stamens. Stamens

equal, anthers spirally twisted. Pollen grains smooth, 3-grooved, discoid. Stigma globularly 2-lobed. No fruit found.

Observed growing on and with: *Merremia umbellata*, *Thunbergia fragrans*, *Wedelia trilobata*, *Hibiscus tiliaceus*.

Found only at one site on Moorea, east side of Cook's Bay, 30 meters north of the driveway to the Rotui juice factory (Jus de Fruits de Moorea), bay side of the road, climbing almost solely on the other climbing vines *M. umbellata* and *T. fragrans*..

A sample of the same plant, collected in a nearby location on Moorea (collected June 20, 1967 by Howard M. Smith "Roadside between Faatoai [Papetoai] and Opunohu", UC #1362487) is deposited in the UC Herbarium under the name *Ipomoea cairica* (*I. palmata*, among other synonyms), a plant with similar looking leaves (although *I. cairica* has leaves that are usually cut to the base into 5-7 leaflets) yet has a funnellform corolla (pink to purple, rarely white), differentially lengthened stamens, straight anthers, spinulose pollen, a simple stigma, usually has pseudostipules, and smooth stems. The species found on Moorea is clearly not *I. cairica*.

The keys in Welsh (1998), Wagner (1990), and Van Ooststroom (1953) unanimously lead to *Merremia dissecta*. However, *M. dissecta* has sinuate to coarsely dentate margins, often irregularly lobed, with hirsute petioles. This species is known to have white flowers at times, however usually with a lavender throat. *M. mooreana* also bears a resemblance to *M. tuberosa*, but *M. tuberosa* consistently has bright yellow corollas, is a ± glabrous larger plant, even to the point of being somewhat woody, and the leaf

lobes are oblanceolate. The possibility exists that the species growing on Moorea is a subspecies or variety of *M. dissecta* as no other species known is closer, however more investigation is needed before the true identity of this plant is known.

*Merremia peltata* (L.) Merr.

Large liana, climbing up to 30 meters, flowering and often only producing leaves in the forest canopy, sometimes covering whole trees and entire sections of forest. Grows from a massive underground tuber which supports growth until the stem can get high enough to gather light. Stem up to 5 cm in diameter, coarse when thick, glabrous when young and thin. Leaves are large, basically as broad as long, up to 55 cm long, almost always peltate, ovate to orbicular, basally rounded or cordate, apically acuminate, veins sometimes pinkish. Flowers borne in multi-flowered cymes, usually only one flower open at one time, sepals ovate to oblong, roughly equal in length, dark green to black. Corolla broadly campanulate to cupshaped, white with yellow at the base of the stamens, sometimes having a purple hue, stamens of equal length, basally pubescent, anthers spirally twisted, pollen smooth, 3-grooved, discoid to triangular. Fruit a 4-valved ovoid capsule, seeds 4, brown, tomentose.

Observed growing on and with: *Inocarpus fagifer*, *Syzygium malaccense*, *Syzygium cuminii*, *Syzygium jambos*, *Hibiscus tiliaceus*, *Dioscorea bulbifera*, *Dioscorea alata*, *Aleurites moluccana*, *Angiopteris evecta*, *Mangifera indica*, *Geophila repens*, *Zingiber zerumbet*, *Cordyline fruticosa*, and more.

This species was found covering a huge area of the center of Moorea and showing up in patches coastally. *M. peltata* tends to avoid dry, exposed sites, preferring sites with high rainfall or close proximity to streams, making Moorea's central caldera perfect territory for *M. peltata*.

*Merremia umbellata* ssp. *orientalis* (L.)

Hallier, Verslag Staat Lands

Creeping to low climbing herb, rapidly spreading over large areas. Leaves ovate to deltoid, cordate basally, apically acuminate. Flowers borne in many-flowered umbels, outer sepals shorter than inner. Corolla cupshaped to campanulate, bright yellow, usually flowering along with others in same umbel, upper tip of midpetaline bands often slightly pubescent,

stamens of equal length, anther twisted, pollen smooth, 6-grooved, discoid to hexagonal. Fruit an ovoid to conical capsule, 4-valved, seeds 4, densely hairy.

Observed growing on and with: *Wedelia trilobata* (almost without exception), *Thunbergia fragrans*, *Merremia mooreana*, *Operculina turpethum*, *Passiflora foetida*, *Passiflora ligularis*, *Hibiscus tiliaceus*, *Hibiscus rosasinensis*, *Manihot esculenta*, *Casuarina equisetifolia*, *Carica papaya*, *Tamarindus indica*, *Lantana camara*, *Momordica charantia*, *Dioscorea bulbifera*, *Colocasia esculenta*, *Xanthosoma sagittifolium*, and more.

This species is extremely widespread on Moorea, growing roadside almost everywhere on the island. In contrast to *M. peltata*, *M. umbellata* prefers the drier, coastal spots. Next to roads, where one finds *Wedelia trilobata*, one finds *M. umbellata* as well, thriving particularly well on any protrusion from the mat created by the *Wedelia*.

*Ipomoea batatas* (L.) Lam.

Creeping vine cultivated for its edible tubers (Sweet Potatoes), rarely erect or climbing, stems green, commonly with a purple tinge. Leaves up to 15 cm long, cordate to ovate, frequently 3-lobed, sometimes 5-7 lobed. Flowers infrequent in cultivated varieties, solitary, sepals with 3-5 raised vertical veins, corolla funnellform, purple to pale lavender, the flower throat usually darker, averaging 5 cm. in length. Stamens 3 long 2 short, basally pubescent, anthers straight, pollen spherical, pantoporate, spiked in a hexagonally tiled fashion. Capsules very infrequent in cultivated varieties, ovoid, 4 seeds or often less, glabrous.

Observed growing on and with: Only seen cultivated, with three varieties being grown: brown tubers with yellow-orange flesh (leaves simple), brown tubers with white flesh (leaves 3-lobed), and purple tubers with white flesh (leaves 3-lobed).

This species is not common on Moorea, with few farmers growing the plant for uses beyond their own (most likely for lack of demand). This plant was only observed growing on one farm, although it is known to be growing elsewhere on the island.

*Ipomoea carnea* ssp. *fistulosa* (Mart.) D. Austin (1977) (Commonly *I. fistulosa*)

Woody shrub, up to 5 meters tall with hollow stems, can also be growing vine-like in certain light regimes. Leaves up to 30 cm. long, ovate to lanceolate, changing shape preference seasonally, long acuminate apically, usually truncate basally. Flowers typically solitary, mostly opening and emitting fragrance at night, sepals very short, corolla narrowly campanulate, pink to purple, up to 10 cm long, limb up to 5 cm wide. Stamens 2 long 3 short, basally pilose, anthers straight, pollen spherical, pantoporate, randomly spinulose. Fruit a small, depressed globose capsule, opening by 4 valves, seeds brown, glabrous. Spreads asexually via stolons, rooting at the apical node.

Seen growing on or with: *Citrus maxima*, *Lantana camara*, *Stachytarpheta urticifolia*, *Dicranopteris linearis*, *Psidium guajava*, *Clitoria guianensis*.

Uncommon plant, mostly grown ornamentally, although naturalized in a few spots on Moorea, most notably in the Haapiti valley.

#### *Ipomoea littoralis* (Blume)

Sprawling vine, low climbing or clambering, generally a littoral plant, although can persist at higher elevations in disturbed areas. Stems herbaceous, thin, generally glabrous. Leaves up to 15 cm long, though generally under 8 cm long, glabrous and slightly fleshy at sea level, pubescent and thin at higher elevations, cordate to cordate-ovate, sometimes lobed on young leaves. Flowers solitary, sepals with one central raised vein, corolla funnellform, purple to pale lavender, the flower throat usually darker, averaging 5 cm. in length. Stamens 3 long 2 short, basally glandular pubescent, anthers straight, pollen spherical, pantoporate, spiked in evenly spaced ranks. Fruit a depressed globose capsule, opening by 4 valves, seeds 4, brown, pubescent with bearded margins.

Seen growing on or with: *Ipomoea violacea*, *Ipomoea pes-caprae*, *Cordia subcordata*, *Vigna marina*, *Sophora tomentosa*, *Hibiscus tiliaceus*, *Wedelia trilobata*, *Stachytarpheta urticifolia*, *Rubus rosifolius*, *Dicranopteris linearis*, *Metrosideros collina*, *Hydrocotyle asiatica*, *Passiflora suberosa*, *Inocarpus fagifer*, *Cananga odorata*, *Dioscorea bulbifera*, *Cordyline fruticosa*, and more.

Moderately common plant, found roadside and trailside at elevation and littorally on two of the motu (reef islands).

#### *Ipomoea obscura* (L.) Ker Gawl.

Small, twining vine, prostrate to moderately climbing, stems thin. Leaves up to 9 cm in length, rarely over 5 cm, cordate, entire, grey-green and mucronulate adaxially. Flowers solitary, sepals minute, corolla narrowly campanulate, limb 2-3 cm in diameter, limb cream colored to white, with white to yellow midpetaline bands, throat dark maroon to purple. Stamens 2 long 3 short, basally pilose, anthers straight, pollen spherical, pantoporate, randomly spinulose. Fruit a small capsule, ovoid to globose-ovoid, opening by 4 valves, seeds 4, black, pubescent.

Observed growing on or with: *Wedelia trilobata*, *Thunbergia fragrans*, *Merremia umbellata*, *Tamarindus indica*, *Clitoria guianensis*, *Passiflora foetida*, *Ricinus communis*, *Leucaena leucocephala*, and more.

Very common species on Moorea, found roadside around the entire island, more densely on the north coast, growing in disturbed rocky patches or over low vegetation or fences.

#### *Ipomoea pes-caprae* ssp. *brasiliensis* (L.) Sweet, Ooststroom

Long, trailing vines, growing from a large, edible taproot, growing on beaches, vines often extending down into or near the intertidal zone. Leaves up to 15 cm long, emarginate to 2-lobed, at times truncate, glabrous, light green and stiff. Flowers usually solitary, sometimes found in cymes, inner sepals longer than outer, corolla funnellform, pink to lavender, sometimes white in the throat, up to 7 cm long. Stamens 2 long 3 short, basally pilose, anthers straight, pollen spherical, pantoporate, spiked in a tiled fashion. Fruit an ovoid to depressed globose capsule, opening by 4 valves, seeds 4, pubescent.

Observed growing on or with: *Ipomoea violacea*, *Ipomoea littoralis*, *Vigna marina*, *Cordia subcordata*, *Sophora tomentosa*, *Hibiscus tiliaceus*, *Casuarina equisetifolia*.

Common beach species, found on three of the motu, can spread over large amounts of beach front property.

#### *Ipomoea violacea* (Roem. & Schult.)

(Commonly *I. macrantha* or *I. tuba*)

Trailing or climbing vine, climbing up to 5 meters, living on the back edges of beaches, plant entirely glabrous. Leaves up to 16 cm long, ovate to orbicular, cordate basally. Flowers solitary, opening and emitting fragrance at night, sepals ± equal, corolla salverform, white, tube very long,

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
<i>I. bat</i>	0	0	1	0	0	0	0	2	0	2	0	0	1	0	0	?	0	2	2	0	0
<i>I. car</i>	1	0	2	0	0	0	0	1	0	1	0	0	1	0	0	?	0	0	2	1	0
<i>I. lit</i>	0	0	1	0	0	0	0	3	0	?	0	0	1	0	0	2	0	1	2	0	0
<i>I. obs</i>	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0
<i>I. pes</i>	0	0	2	0	0	0	0	2	0	0	0	0	1	0	0	1	2	0	2	0	1
<i>I. vio</i>	0	0	2	0	0	0	0	1	0	0	0	0	1	0	0	2	0	0	0	0	1
<i>M. mo</i>	0	1	0	0	0	1	1	0	1	?	0	1	0	?	0	1	3	0	0	1	0
<i>M. pel</i>	0	1	0	0	0	1	1	0	1	?	0	0	1	0	0	1	1	0	0	1	0
<i>M. um</i>	0	1	0	0	0	1	2	0	1	?	0	0	1	0	0	2	0	0	1	1	0
<i>O. tur</i>	0	1	0	0	0	?	1	0	1	?	1	0	1	2	0	0	0	0	0	1	0
<i>Pet sp.</i>	0	0	3	1	1	0	0	0	1	?	0	0	0	1	1	0	0	0	2	1	0

**Table 1.** Matrix showing character states (along top) versus species (left side) used to create the phylogeny for this report.

up to 7 cm in length, the limb moderately lobed, up to 5 cm in diameter. Stamens 2 long 3 short, basally pilose, anthers straight, pollen spherical, pantoporate, randomly spinulose. Fruit a globose capsule, seeds 4, densely tomentose with margins long bearded, seeds with air cavity.

Observed growing on and with: *Gardenia taitensis*, *Cordia subcordata*, *Casuarina equisetifolia*, *Ipomoea pes-caprae*, *Ipomoea littoralis*, *Sophora tomentosa*, *Vigna marina*, *Cassytha filiformis*.

Fairly common beach vine, covering a large area on Motu Temae and spots on two other motu.

#### Character Analysis

A summary of the results of the character analysis is given in matrix form (Table 1). More detailed description of the characters found is given below.

**Character 1 - Growth Form.** Only one species found grows in an arborescent fashion, *Ipomoea carnea* ssp. *fistulosa*. The remainder of the species are herbaceous, generally climbing or trailing vines, none of which remain erect without the support of another plant or structure.

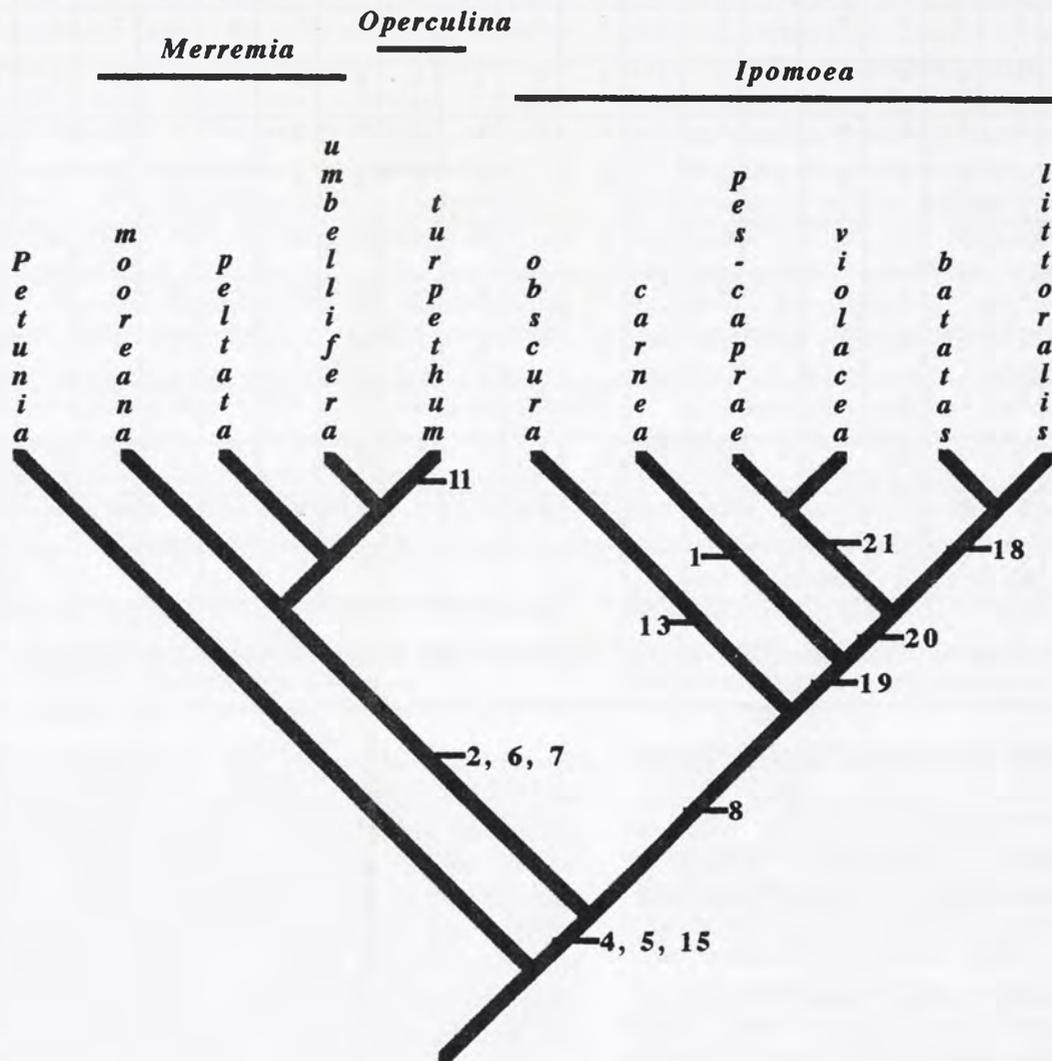
**Character 2 - Anther Shape; Character 3 - Stamen Length.** The same group of species that had twisted anthers also all had equal length stamens. These species, *Merremia mooreana*, *Merremia peltata*, *Merremia umbellata*, and

*Operculina turpethum*, all fall into the tribe *Merremieae* (the Merremoids) which is partially defined by the presence of these characters. The rest of the species, (with the exception of the outgroup) all in the genus *Ipomoea*, had straight anthers and differentially lengthened stamens. However, there were two categories of differentially lengthened stamens: those with 3 long stamens and 2 short stamens, and those with 2 long stamens and 3 short stamens. The similar *I. batatas* and *I. littoralis* emerged as the only species with 3 long stamens and 2 short stamens. The outgroup *Petunia* was the only species with 4 long stamens and one staminode.

**Character 4 - Anther Pollen.** All Convolvulaceae species found on Moorea had anthers that dehisced upon the opening of the flower, and thus had some amount of external pollen, most likely to assist in pollination during the brief window of opportunity for successful pollination due to the short life span of the flowers. *Petunia* anthers are not dehiscent upon the opening of the flower.

**Character 5 - Stamen Number.** As pointed out by Character 3, *Petunia* only has 4 true stamens. All of the morning glories of Moorea have 5 true stamens.

**Character 6 - Stigma Shape.** All of the species in the genus *Merremia* have globularly 2-lobed stigmas. It turns out that *Operculina*



**Figure 4.** Character state changes mapped onto the shortest length tree of the Moorean morning glory species. Genera are shown above their respective species.

*turpethum* also has globularly 2-lobed stigmas, however having only found one flower, this character was never recorded while in Moorea. While it is true that certain members of the Solanaceae have globularly 2-lobed stigmas, *Petunia* does not.

Character 7 - Pollen Grooves; Character 8 - Pollen Spikes; Character 9 - Pollen Shape; Character 10 - Pollen Spike Type. The pollen types within the species on Moorea grouped neatly into two major divisions: Division 1) Pollen grooved, not spiked, 3-6 sided polygon to discoidal; Division 2) Pollen not grooved, spiked, spherical. Within Division 1 there was a subset with 3 grooves (*M. peltata*, *M. mooreana*, *O. turpethum*) and a subset with 6 grooves (*M.*

*umbellata*). Within Division 2 two further criteria were judged: spike pattern and spike type. There was insufficient data by which to group species based on spike type, but three groups emerged based on spike pattern: Spikes Random (*I. carnea*, *I. obscura*, *I. violacea*); Spikes Arranged in a Tiled Fashion (*I. batatas*, *I. pescaprae*); Spikes Ranked (*I. littoralis*). *Petunia* had neither grooved nor spiked pollen.

Character 11 - Stem Wings; Character 12 - Stem Hair; Character 13 - Milky Sap. Only one species was found to have winged stems, *Operculina turpethum*, a member of a genus differentiated from *Merremia* based on little more than capsule dehiscence and stem shape and is a classification that will probably not stand

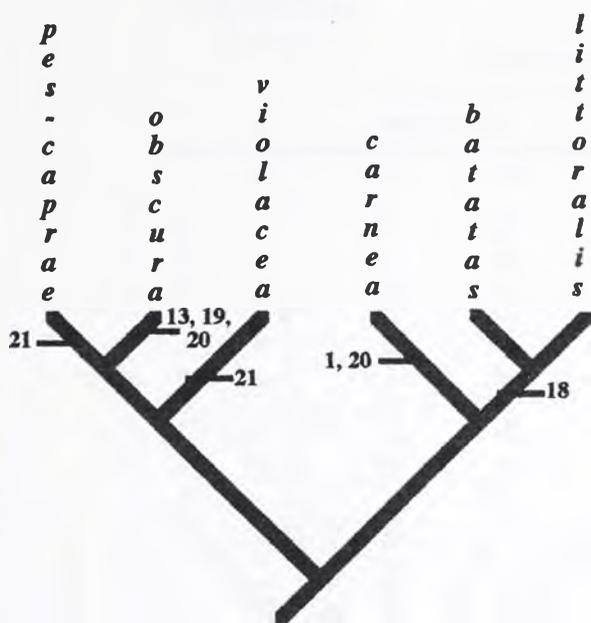


Figure 5. The same character changes in Figure 4 mapped onto the standard phylogeny of the genus *Ipomoea*.

the test of time. Long stem hair was only found on the provisionally named *Merremia mooreana*, although other species were found to have sparsely pubescent stems at times. Conspicuously milky sap was found in the majority of morning glory species, the only exceptions being *I. obscura* and *M. mooreana*.

Character 14 - Capsule Dehiscence; Character 15 - Seed Number; Character 16 - Seed Hair. With the exception of *O. turpethum*, all species had valved capsules. *Petunia* was the only species with a 2-valved capsule, and was the only species with many seeds. All Convolvulaceae species produced 4 seeds, 2 of which had unknown hair length, only one had glabrous seeds (*O. turpethum*), and the rest either had even length hair or bearded margins (*I. littoralis*, *I. violacea*, *M. umbellata*).

Character 17 - Leaf Shape. This character separated out those that differed from the established norm. The one species with peltate leaves was *M. peltata*, with emarginate to 2-lobed leaves was *I. pes-caprae*, and with deeply palmately 5-7 lobed leaves was *M. mooreana*. All of the remaining species has leaves typical of the family.

Character 18 - Sepal Veins; Character 19 - Corolla Limb Color; Character 20 - Corolla Shape. Only 2 species of morning glory on Moorea have raised sepal veins, *I. batatas* with 3-5

raised veins, and *I. littoralis* with 1 central raised vein. All of the species in the genera *Merremia* and *Operculina* had white or yellow corollas, despite the fact that many *Merremia* species have pink to purple flowers elsewhere in the Pacific. Only two *Ipomoea* species had white or cream corollas: *I. violacea* and *I. obscura*. 4 species had salverform to funnellform corollas, a group containing, interestingly, all of the beach dwelling species (*I. violacea*, *I. pes-caprae*, *I. littoralis*) and the sweet potato *I. batatas*.

Character 21 - Halophily. True halophily was only seen in *I. violacea* and *I. pes-caprae*, although *I. littoralis* could live right up to the beach and also inland. The remainder of the species were never found growing in highly salty soil.

#### Phylogenetic Analysis

The PAUP search for the shortest length tree given the matrix in Table 1, produced 10 trees of 40 steps each. Creation of a tree to match the system established by Van Ooststroom (1953), Austin (1979, 1980, 1991, 1996), and McDonald & Mabry (1992), required a tree of 44 steps using the data collected during this research. Mapping only the bipolar state changes onto the tree in Figure 4 and onto the established system (focusing on *Ipomoea*) in Figure 5, it is clear that the previously accepted phylogeny in many cases requires characters to change multiple times.

The strict consensus tree (Figure 6) shows that *I. obscura* and *M. mooreana* were ancestral to their respective clades in all of the created trees. The relationships of the remaining individual species showed no consensus. The most important aspect of the strict consensus tree is that all trees agree that the *Ipomoea* species and the *Merremia/Operculina* species belong to separate clades within the family.

The phenetic analysis (Figure 7) also shows the clear separation between the *Merremieae* and the *Ipomoeae* tribes of the Convolvulaceae. The Jaccard coefficient of dissimilarity between two tribes is .52, whereas the dissimilarity coefficient between the outgroup *Petunia* and the entire array of Convolvulaceae species is .55, making *Petunia* barely less similar to the family than the two tribes are to each other. Within each tribe there is a low degree of dissimilarity: in the *Ipomoeae*, *I. batatas* and *I. littoralis* have a dissimilarity of .11, the largest degree of dissimilarity being .20 between *I. obscura* and *I. carnea*. *Merremieae* is very similar, the lowest

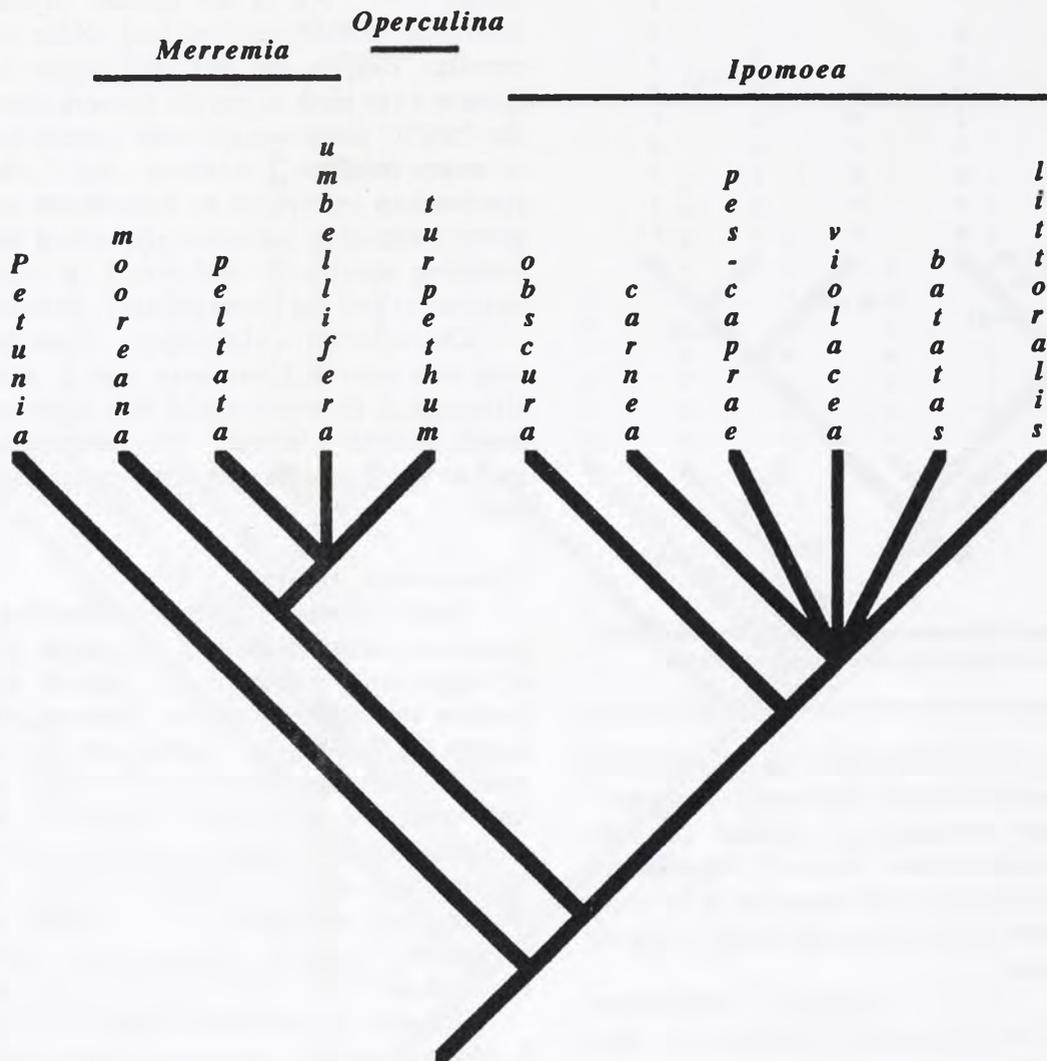


Figure 6. Strict consensus tree of the Convolvulaceae of Moorea using physical characters.

degree of dissimilarity being .16 between *M. peltata* and *M. mooreana*.

Many character states, in fact 20, are clearly distributed within monophyletic (or sometimes monotypic) groups in the resulting phylogenetic tree: Arborescence, straight anthers, twisted anthers, stamens of equal length, anther dehiscing upon flower opening, 5 true stamens, pollen not grooved, pollen not spiked, pollen spherical, pollen 3-6 side polygon, stem winged, stem long pilose to puberulent, capsule circumscissile, 4 seeds, peltate leaves, emarginate to 2-lobed leaves, deeply palmately 5-7 lobed leaves, corolla pink to purple, corolla funnellform to salverform, and halophilic. (Figure 8) Only a small number of character

states are distributed paraphyletically or polyphyletically.

The genus *Merremia* turns out not to be monophyletic from these results. The strict consensus tree also shows a *Merremia* species being ancestral to *Operculina*. Austin (1998a), using a much larger matrix of physical characters and a larger amount of species, also found *Operculina* to be embedded within *Merremia*, making *Operculina*'s already shaky status as a genus even more so. In another study, Austin (1998b) did show *Operculina turpethum* to be in a more ancestral clade than the majority of *Merremia*. More work with a greater number of species, especially molecular phylogenetic work, must be done before throwing out *Operculina* as a

Operculina

Ipomoea

Merremia

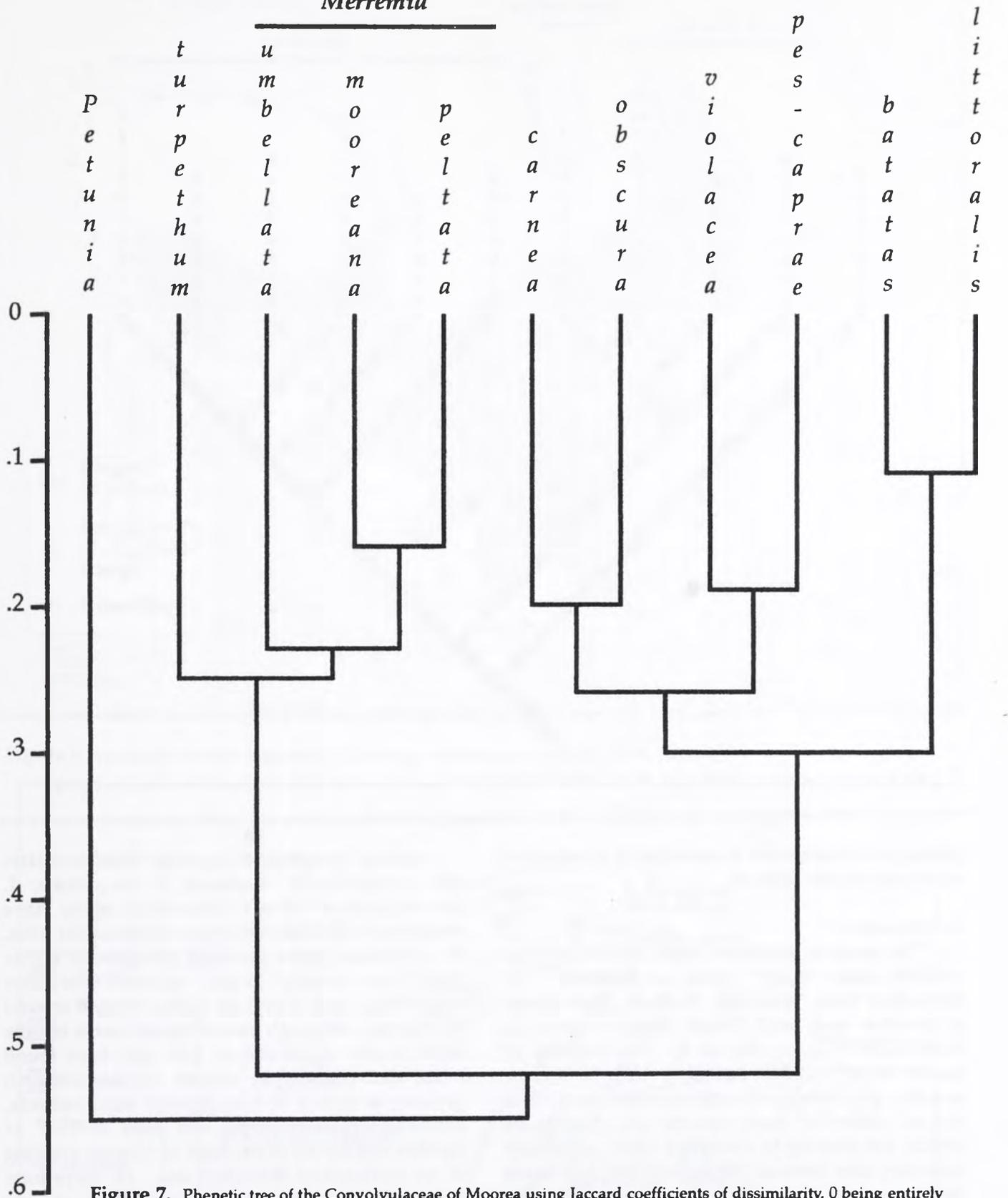


Figure 7. Phenetic tree of the Convolvulaceae of Moorea using Jaccard coefficients of dissimilarity, 0 being entirely similar, 1 being completely dissimilar.

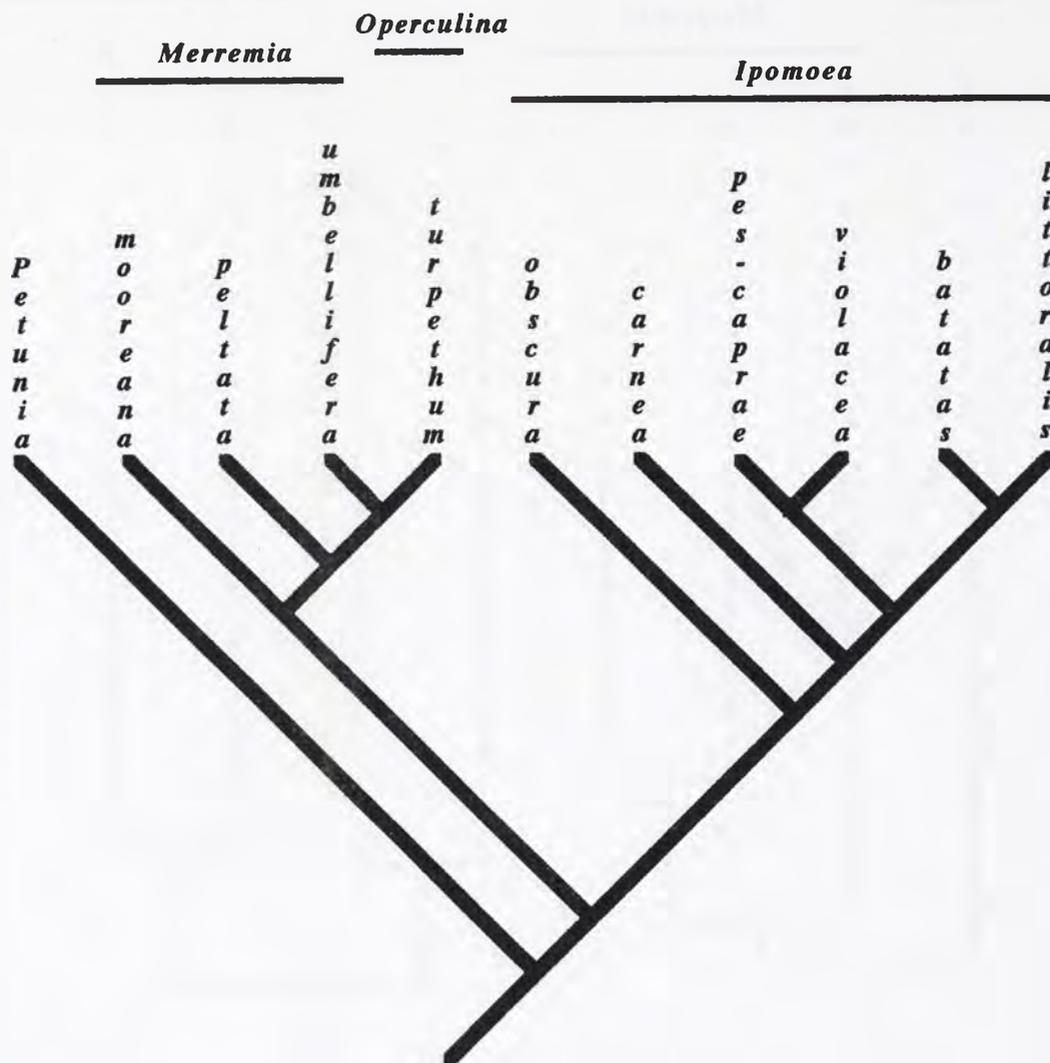


Figure 8. In gray, anthers spirally twisted: one of the monophyletic characters of the Moorean Convolvulaceae phylogeny.

genus, but it seems fair to consider it a subset of *Merremia* for the present.

#### Distribution

The morning glories of Moorea were found to inhabit three major types of habitats: 1) Disturbed Sites - roadside, trailside, burn scars; 2) Beaches and Back Beach Areas - motu; 3) Undisturbed Canopy (Figure 9). The majority of species were found in disturbed sites, a feature usually associated with introduced weeds, and indeed some of these species are introduced weeds, but growing in disturbed sites, especially boundary sites between high cover and low cover (such as would be created by a road or trail) is an affinity expressed by the majority of species in the Convolvulaceae (Van Ooststroom 1953).

Among the species that prefer disturbed sites (*M. umbellata*, *M. mooreana*, *O. turpethum*, *I. obscura*, and at times *I. littoralis*), many have preferences for different types of disturbed sites. *M. umbellata* grows roadside, can grow in either direct or indirect light, climbs over low vegetation, and is spread fairly evenly around the island, although concentrated more on the north coast. *M. mooreana* has only been found twice, once during the course of this research growing in a fairly lush overgrown area roadside, climbing up other vines, and once in 1967 at another site on the north coast of Moorea growing in an undescribed disturbed site. *O. turpethum* was growing alongside *M. umbellata* at one location, in fairly direct light, climbing over low ground cover plants (*Wedelia trilobata*) and a

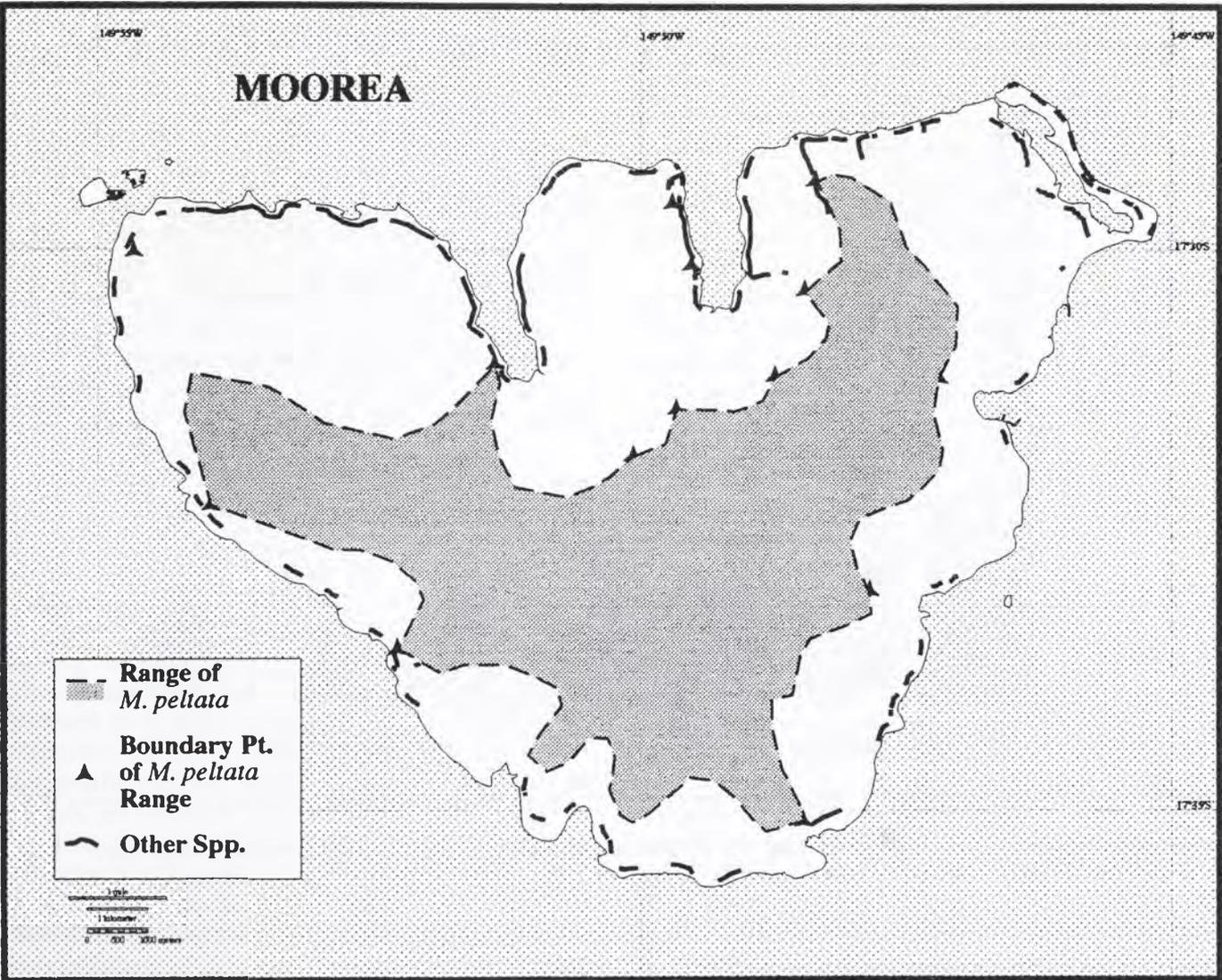


Figure 9. Species distribution on Moorea: roadside spp., beach spp., and canopy sp. *M. peltata*

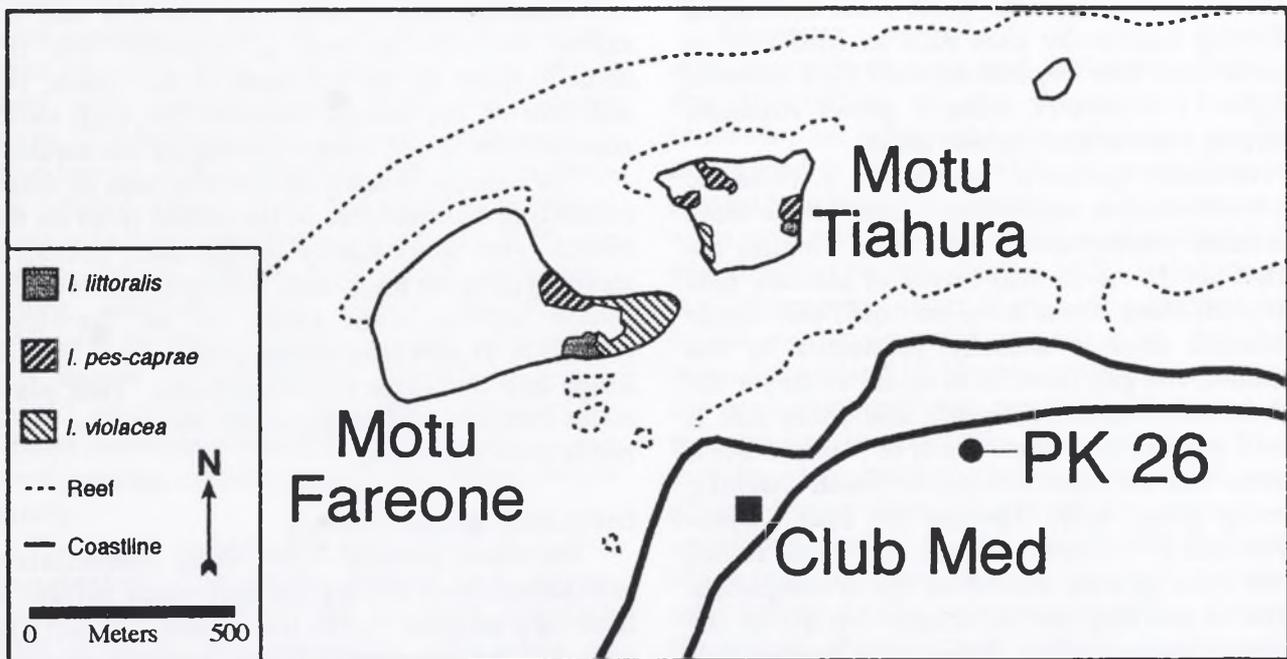
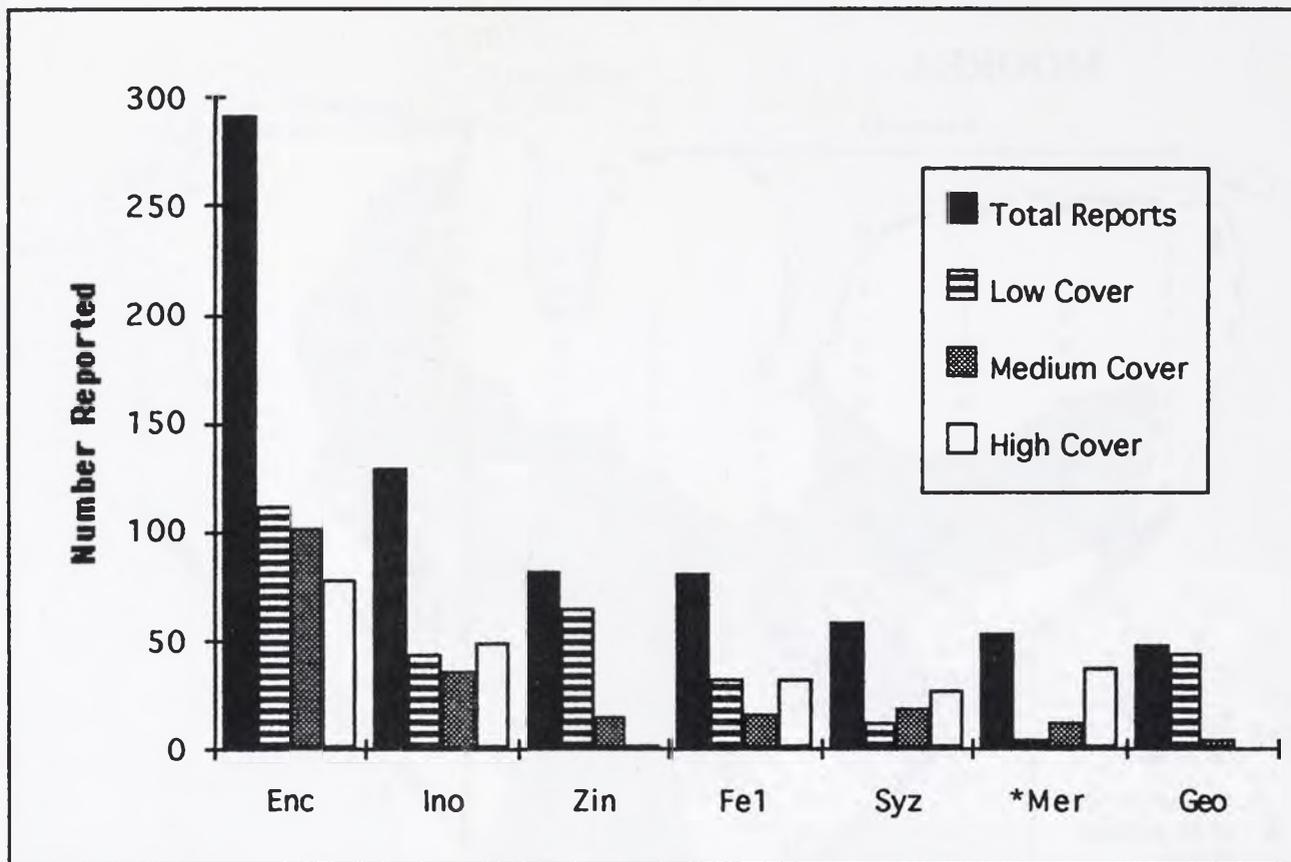


Figure 10. Species distribution on Motu Fareone and Motu Tiahura on the northwest corner of Moorea.



**Figure 11.** Graph of number of reports by species under high, medium, and low *M. peltata* cover. Enc=Encrusting Algae, Ino=*Inocarpus fagifer*, Zin=*Zingiber zerumbet*, Fe1=*Davallia* sp., Syz=*Syzygium malaccense*, \*Mer=*M. peltata* shoots, Geo=*Geophila repens*.

small fence. *I. obscura* has almost as great a distribution as *I. littoralis*, although is not capable of covering such large areas of land, and is also concentrated on the north coast of Moorea, preferring bare rocky sites such as road cuts or areas of very low vegetation with high amounts of light. *I. littoralis*, when it grows roadside, generally lives in dark, moist areas.

The beach species (*I. pes-caprae*, *I. violacea*, *I. littoralis*) grow, interestingly, only on the motu of Moorea. Motu Fareone and Motu Tiahura are located off the north west corner of Moorea, near Club Med, Motu Temae is on the north east corner of Moorea (and is actually connected to the mainland, the gap filled in to create room for the Moorea International Airport), and Motu Ahi is located off the east coast south of Vaiare. Motu Fareone has all three species of beach-dwelling morning glory, Motu Tiahura has both *I. pes-caprae* and *I. violacea* (Figure 10), Motu Temae has all three species, and Motu Ahi is completely devoid of morning glories, despite reports to the contrary (Burford 1995). These three species also

have slightly differing niches on the beach: *I. pes-caprae* will extend farthest down the beach towards the intertidal zone, *I. violacea* will be on the beach itself, but will trail laterally and not extend towards the surf, *I. littoralis* will not actually grow on the fine sand of the beach, but will live on the margin between the high shrub zone and the beach, often climbing on the shrubs.

The canopy species, *M. peltata*, can be found inhabiting the canopies of the tallest trees on the island. This species is by far the most prevalent morning glory on the island, covering much of the central caldera, even going up to the high ridgelines (it was seen growing up to the Vaiare Ridge and the Three Coconuts Pass). This plant needs moisture, and consequently avoids the drier north coast of Moorea.

#### Individual Species Ecology

*Merremia peltata* - One thing immediately noticeable about the species *Merremia peltata* is how well adapted it is to live where it does. The vine has an enormous tuber that can provide

nutrients long enough for a branch to climb its way up into the canopy to get light. Once it gets there, it produces large amounts of very broad leaves to capture sunlight and continues to spread over the canopy. *M. peltata* can be seen covering much of the high-elevation forest of Moorea (Fosberg 1992). One cyme of flowers can have as many as 15 separate buds, no two of which will open at the same time, increasing the time span over which a potential pollinator could successfully pollinate a flower. Another noticeable fact is the utter lack of other common climbing vines such as *Dioscorea bulbifera* and *Dioscorea alata* under *M. peltata* canopy.

In order to assess the effect of *M. peltata* cover on the understory species composition, 12 transects were run under low, medium, and high *M. peltata* cover as described in Material and Methods. The results of these transects are shown in Figure 11. Certain understory species have a strong reaction to differing levels of *M. peltata* in the canopy: as cover increases, the overall amount of encrusting moss drops, the amount of *Zingiber zerumbet* drops off sharply, as does *Geophila repens*, while *Syzgium malaccense* shows an increase in number. Despite these results, the overall percentage cover does not change significantly between the three cover regimes, the mean percent cover value ranging between 86% and 94% with high standard deviation.

*Ipomoea batatas* - *Ipomoea batatas*, the sweet potato, was observed having an insect problem on the one farm visited that was growing sweet potatoes during the course of this study. Three varieties were being grown: 1) A brown tuber with yellow-orange flesh and simple leaves; 2) A brown tuber with white flesh and 3-lobed leaves; 3) A purple tuber with white flesh and 3-lobed leaves. The insect attacking these plants was not present during the day, but was causing severe pitting, yellowing of leaves, wilting, and obviously killing the plants. However, the Brown-Yellow variety showed a high degree of resistance, the Brown-White showed no resistance, and the Purple-White showed moderate resistance, only affected on the plants growing directly next to the Brown-White variety.

The insect to blame is most likely *Bedellia somnulentella*, the Sweet Potato Leaf Miner, known to be present in the Societies (Paulian 1998) although not physically seen while on Moorea as the field was not visited at night. The

other major pest of the sweet potato, *Cylas formicarius*, was found on Moorea living on *Ipomoea pes-caprae*, but was not found on the cultivated sweet potatoes. Furthermore, the damage done to the plants was characteristic of *Bedellia* as is the fact that the affecting insect is dormant during the daytime (Zimmerman 1978).

*Ipomoea pes-caprae*, *Ipomoea violacea*, *Ipomoea littoralis* - These three species grow on or directly up to the beach. This habitat presents some major challenges to survival for a plant: 1) salinity, 2) low soil stability and fresh water retention, 3) exposure to sun and weather, 4) sand burial, 5) seed germination and successful dispersal. *I. pes-caprae* and *I. violacea* can obviously deal with high degrees of salinity, both have extensive root systems and have thick, fleshy stems to help them deal with fresh water supplies. All three species are actually planted as sand-binders do to the fact that they all readily root at leaf nodes and can create large root systems to anchor themselves to the sand. Seed dispersal has a built in mechanism: the ocean. The problem with using the ocean to disperse seeds is low reliability in it actually depositing a seed somewhere viable. All of these species have seeds adapted to floating, some for long periods of time. The fact that these plants have been able to overcome these obstacles ensures that they have little competition for the obviously scant resources, *Vigna marina*, *Sophora tomentosa*, and one of the other species of *Ipomoea* are the only major competitors in this arena.

*Merremia umbellata* - *M. umbellata* distribution is strongly and noticeably related to the distribution of the Composite *Wedelia trilobata*, an ornamental ground cover recently introduced to Moorea. While *M. umbellata* was present long before *W. trilobata*, it is not known to what extent *M. umbellata* had spread around the island before the introduction of *W. trilobata*, nor is it known what effect, if any, *M. umbellata* had on the extremely rapid spread of *W. trilobata* around the island of Moorea. What is evident is the high distributional correlation between the two species. *W. trilobata* does not climb like a morning glory, but spreads along the ground, never getting higher than 750 cm off the ground. *M. umbellata* prefers to grow on higher substrate plants, but will grow along on top of *W. trilobata* until it finds a taller substrate projecting through the mat of *Wedelia* and in most cases cover it completely. This pattern is noticeable around the

entire island. To what extent these two species affect their mutual growth patterns is unknown, but nonetheless it is an interesting ecological phenomenon, an understanding of which could assist in controlling both of these noxious weeds.

#### Pollination Biology

While pollination was not a major focus of this research, these observations are included here simply to further the knowledge of ecological associations with tropical Convolvulaceae species. The most frequently found pollinators of the morning glories of Moorea were ants. Ants of three varieties were found in every species of Convolvulaceae on the island. In most cases, these ants had some amount of pollen stuck to them. A species of beetle of the family Bruchidae was also seen frequently, most notably in *I. violacea*, where they were found living one individual per flower (in each case covered in pollen), and in *I. carnea* ssp. *fistulosa* where they were living together in groups of up to 10 per flower. The introduced honey bee *Apis* was also observed visiting flowers of *Merremia peltata* and *M. umbellata*. While moths and birds are known to pollinate many species in the Convolvulaceae, no moths or birds were seen interacting with Convolvulaceae flowers while on Moorea.

#### Discussion

##### Phylogenetic Analysis

While this study was not extensive enough to justify changes in the accepted phylogeny of the family Convolvulaceae, it does add further support to the removal of *Operculina* as a proper genus name. Beyond that, this analysis adds support to the monophyletic natures of the *Merremieae* and the *Ipomoeae* tribes of Convolvulaceae, based solely on physical evidence. It should be mentioned that a recent study by Miller et al. (1999) phylogenetically analyzed the genus *Ipomoea* based on genetic sequences and came up with some significant differences from the older phylogenies. In many ways, their resulting phylogeny supports the previous system; however, it finds that certain species have been previously placed into incorrect subgenera or sections, plus it finds certain groups to be polyphyletic. *I. obscura* (a result supported by Das & Mukherjee 1997), one of the Moorean species is now believed to be in a new, more ancestral subgenus, in fact the section *Erpipomoea*

previously of the subgenus *Eriospermum* may now be part of this entirely new subgenus. The rest of *Eriospermum* appears to remain intact. Miller et al. suggests 5 as yet unnamed clades or subgenera of *Ipomoea*. Clade 1, the most ancestral would contain the section *Erpipomoea* and a few other groups. Their strict consensus tree could not agree upon the evolutionary order of the remaining 4 clades: Clade 2 contains the old subgenera *Quamoclit*, *Ipomoea*, and two parts of *Eriospermum*, Clades 3,4, and 5 contain the remainder of *Eriospermum*, with the sections basically conserved.

This new data tends to support the findings in this research better than the previous phylogenies; however, that does not make their results necessarily correct. The finding that *I. obscura* may indeed be in a more ancestral clade of *Ipomoea* fits the findings of both the shortest length tree and the strict consensus tree in this report.

One of the questions posed at the end of the Introduction concerned the relative relationships of native versus introduced species. The data from this phylogeny show no pattern in this regard, native species are closely allied to introduced species and vice versa. One possible explanation for this seeming lack of relationship lies in the length of time these plants have been on Moorea. Simply because a plant arrived before the Polynesians does not mean it evolved there. A better method may be to look at whether those that originated in the same area are closely related. Even in this light, there is no evident pattern. In contrast, using the phylogeny of Miller et al. (1999) for only the *Ipomoea* species found on Moorea, you get three clades: 1) American spp.: *I. carnea*, *I. batatas*, *I. littoralis*; 2) Asian spp.: *I. violacea*, *I. pes-caprae*; 3) African sp.: *I. obscura*. This is truly an interesting result. Again, this does not prove that their phylogeny is correct, however it lends an intriguing line of support.

The idea behind creating a phylogeny of the Convolvulaceae of Moorea was to determine whether the results had any local ecological significance. As mentioned before, the plants exhibiting halophily are monophyletic in the Moorean phylogeny. It is not clear where the sweet potato would grow in the wild in its natural form, however from the Moorean phylogeny it could be inferred that it would grow as a littoral species due to its relationship with *I. littoralis* and the two beach species with

which it shares a similar corolla type. The distribution of the species, with the exception of the aforementioned beach-dwelling species maps haphazardly onto the Moorean phylogeny. Weediness is impossible to determine from the phylogeny. Both *M. peltata* and *M. umbellata* are aggressively spreading species, yet so are some species of *Ipomoea*.

Further research into the insect relationships of these plants could also possibly be mapped onto the phylogenetic tree, although the limited results from this study show nothing conclusive. A proper identification of the involved insects would be necessary, as would the drive to stay up all night watching insects.

#### Distribution

The distribution of species on Moorea seems to be controlled by four major factors: 1) Rainfall and water availability, 2) Light availability, 3) Substrate, and 4) Disturbance. Dispersal is also an obvious factor, but no matter how well a seed is dispersed it still must be established in an area that meets the requirements of the species in the four categories above. Whether a species is introduced or native seems to have little effect on its distribution. Introduced species do have a tendency to grow in disturbed sites, however, as mentioned before, the entire family exhibits this tendency, so this result is inconclusive. The seemingly peculiar affinity of the beach-dwelling species for the motu can be explained most likely by the presence of fine-grained natural sand and low disturbance in the form of humans, wave action, or otherwise. Mainland Moorea lacks a beach with these qualifications, and thus lacks the beach-dwelling species.

The rainfall factor is quite important for *M. peltata* which requires high amounts of moisture, hence its high concentration near streams and in the semi-cloud forest on the slopes of Mt. Tohiea, plus its complete avoidance of the north coast, including the crest of Mt. Rotui. *M. umbellata* and *I. obscura* obviously thrive in the drier environment of the north coast, which is also more disturbed due to construction and excavation than the moister, less inhabited south coast.

Almost all species of morning glory on Moorea need large amounts of light, and all, in their own ways, position themselves to receive it. *M. peltata*'s growth form is entirely due to its need for light and its ability to exploit an environment that few others can.

The substrate seems to affect the beach species the most, although *I. littoralis* is very flexible. *I. obscura* does very well on rocky scarps, again exploiting a niche with little competition. *M. umbellata* on the other hand, thrives in richer soil, and cannot survive on rocky scarps like *I. obscura*.

#### Ecology

The study of *M. peltata*'s effect on understory composition is only a preliminary look at the effect of this species that is so obviously important in its habitat. What seems to be happening is that *M. peltata* is maintaining or even exacerbating a pre-existing difficult situation for plant growth, and by doing so reduces competition in its niche. This situation is much more complex than it seems, and would warrant a full study, not just a section of a larger study, to determine more accurately what is happening in this system.

The relationship of *Wedelia trilobata* and *M. umbellata* is another system too elaborate to be fully delved into in this treatment. Due to the importance of weed control, especially in fragile ecosystems like tropical islands, this is another topic that could have some real-world applications and warrants further research to determine 1) if there is a relationship between the two species, 2) what the relationship is, and 3) what can be done to control the spread of the species.

Natural pest resistance in crops is a very valuable direction of research. The mechanism behind the natural pest resistance in some varieties of sweet potato is not known to this author, and, despite its relative lack of importance as a food crop in Moorea, the sweet potato is a major source of food for many parts of the world. Varieties that prove resistant to pests without the intervention of pesticides, biological control, or transgenic technology are very valuable resources and safer and less suspect than any of the other options. While Moorea may not be the optimum site for the study of this question, it is still an important area of study which should be pursued.

#### Direction for Further Research

This paper represents but one small step towards a better understanding of a unique section of the world and an interesting group of organisms. Further research would be aided immeasurably by the production of a definitive

flora of French Polynesia, but until that happens there are many interesting topics in the field of tropical botany that can still be pursued. Tropical islands are the perfect laboratories for the study of evolution of endemic groups and effects of introduced species. While this paper only touched upon these issues, due to it not involving endemic species, much more can be accomplished by studying the introduced and weedy species of morning glory presented in this report.

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## Appendix

### Common and Alternate Names of Moorean Convolvulaceae Species:

<u>Latin Binomial</u>	<u>Tahitian Name</u>	<u>Common Names</u>	<u>Alternate Latin</u>
<i>Ipomoea batatas</i>	Umara	Sweet Potato, Patate Douce	<i>Convolvulus b.</i> , <i>B. edulis</i>
<i>Ipomoea carnea</i> <i>ssp. fistulosa</i>	—	—	<i>Ipomoea fistulosa</i>
<i>Ipomoea littoralis</i>	Paputi, Papati	—	<i>I. denticulata</i> , <i>I. forsteri</i>
<i>Ipomoea obscura</i>	—	—	<i>Convolvulus o.</i> , <i>I. koloaensis</i>
<i>Ipomoea pes-caprae</i> <i>ssp. brasiliensis</i>	Pohue miti	Beach Morning Glory, Liseron Rose	<i>Convolvulus p.</i> , <i>C. brasiliensis</i> , <i>I. brasiliensis</i>
<i>Ipomoea violacea</i>	—	—	<i>I. macrantha</i> , <i>I. tuba</i> , <i>Calonyction album</i> , <i>C. tuba</i> , <i>I. glaberrima</i> , <i>I. grandifolia</i>
<i>Merremia peltata</i>	Pohue	—	<i>Convolvulus p.</i> , <i>Ipomoea p.</i> , <i>M. nymphaeifolia</i>
<i>Merremia umbellata</i> <i>ssp. orientalis</i>	—	—	<i>Convolvulus u.</i>
<i>Operculina turpethum</i>	Pohue Tahatai	—	<i>Convolvulus t.</i> , <i>Ipomoea t.</i> , <i>Merremia t.</i>

### Society Island Convolvulaceae - Representative Specimens:

- Ipomoea littoralis*: 1) Motu Temae, Moorea, November 1994, by Martha Burford, UC #1603240.
- Ipomoea obscura*: 1) Faaa, Tahiti, October 1909, by Leland, Chase, and Tilden, UC #403775.  
2) Faaa Quarry, Tahiti, May 1922, by Setchell and Parks, UC #219643.  
3) Between Faatoai (Papetoai) and Opunohu, Moorea, June 1967, by H. M. Smith, UC #1362450.
- Ipomoea pes-caprae*: 1) Motu Temae, Moorea, November 1994, by Martha Burford, UC #1603234.
- Merremia mooreana*: 1) Between Faatoai (Papetoai) and Opunohu, Moorea, June 1967, by H. M. Smith, UC #1362487, labelled "*Ipomoea cairica*."
- Merremia peltata*: 1) Maara, Tahiti, June 1922, by Setchell and Parks, UC #219666.  
2) Mt. Tahara, Tahiti, May 1922, by Setchell and Parks, UC #219629.
- Merremia umbellata*: 1) Hotuarea Pt., Tahiti, June 1922, by Setchell and Parks, UC #219636.  
2) Road to Arue, Tahiti, May 1922, by Setchell and Parks, UC #219720.

# Photosensitivity and other behavior of the upside-down jellyfish, *Cassiopea* sp.

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**ABSTRACT.** *Cassiopea* is a genus of jellyfish that is densely packed with endosymbiotic algae that are found mostly in the exumbrella and are essential for survival. Jellyfish were placed in an isolated tank of seawater under an artificial light/dark cycle with the light coming from alternate angles. Their movements revealed that the position of the light source influenced how the jellyfish positioned themselves, although it was not clear whether or not the jellyfish relocated themselves in order to maximize light intensity for their zooxanthellae.

The pulsation rates of *Cassiopea* were observed and were found to have an inverse logarithmic relationship with bell diameter. Floating jellyfish were found to have significantly faster pulsation rates than jellyfish at rest.

Bell position influenced the settling ability of the jellyfish. Those placed bell-down on the surface of the water settled in less than a minute, whereas almost all those who were placed bell-up took over twenty minutes to settle. There was no correlation found between diameter and settling ability.

The largest oral appendage lengths were found to be correlated with diameter, the best-fit line to the relationship being a power function. The number of oral appendages were also found to be correlated to diameter, the best-fit line to the relationship being an exponential function.

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## Introduction

Jellyfish come in many different shapes and sizes, but the tropical scyphozoan genus *Cassiopea* is unique in its peculiar ability to live upside down on the floors of tropical lagoons. The bells of these jellyfish have become adapted to settling on the ocean floor by becoming flatter and slightly concave rather than convex like in other jellyfish. This concavity causes there to be a slight suction to the floor, providing some stability against the actively moving water in their environment (Bigelow 1900).

This ability to settle and spend the majority of its life upside down on the floor bottom influences many aspects of *Cassiopea*'s behavior and morphology. These studies examined some aspects of these behaviors and morphologies and their implications.

*Cassiopea* is aided in maintaining a benthic lifestyle by its endosymbiotic relationship with photosynthetic algae living within its mesoglea. This alga has been identified as *Symbiodinium microadriaticum* in some species of *Cassiopea*. These zooxanthellae have the ability to satisfy up to 169% of their host's metabolic demand (Verde, McCloskey 1998). Carroll and Blanquet (1984a) have also suggested that these zooxanthellae may also provide essential amino acids for the jellyfish. The presence of these zooxanthellae affects the behavior of *Cassiopea* in many different ways, one example being that only polyps with symbiotic

dinoflagellates had the ability to strobilate whereas those without could not achieve medusa form (Hofmann, Fitt, Fleck 1996). More importantly, *Cassiopea* is dependent on these zooxanthellae for survival, and thus also dependent on light. If light is not at an optimal intensity, they slowly waste away and die (communication, Lowrie).

Blanquet (1969) found that *Cassiopea* moved to dark areas in the wild would move back to areas with higher light intensities. Those moved to areas with equal light intensity did not move back to their original areas. *Cassiopea* was shown to alter its position in order to maximize light intensity for its zooxanthellae. Studies were done to see if it would also shift its position if light came at a different angle.

Another behavioral aspect of *Cassiopea* that is affected by its benthic nature is its pulsation rate. The act of pulsation (i.e. pulling water into the bell then pushing it out by means of muscular contractions) in jellyfish is a movement associated with active movement through the water. This raises the question of how *Cassiopea*'s sessile nature affects its pulsation rate. This was investigated in a study designed to find a correlation between the position of the jellyfish in the water and the rate at which it pulsed.

After examining how the benthic nature of *Cassiopea* affected different aspects of its behavior, it brought up the issue of what in turn affected its settling ability. A study was done to examine the

hypothesis that the bell position would affect the settling ability of the jellyfish.

Lastly, since there was a lack of information on this species being found in French Polynesia where all the studies were performed, morphological observations and measurements were made. Of particular interest were the paddle-shaped structures (the oral appendages) on the oral arms of the jellyfish that contained a deep shade of blue, a contrast to the light pinkish gray of the bell and arms. Blanquet and Phelan (1987) suggested that the blue, which they coined as "Cassio Blue", was a pigment that filtered out harmful UV radiation while permitting the penetration of photosynthetic active radiation. This has many implications for the nature of the relationship between *Cassiopea* and its zooxanthellae and thus its ability to maintain its benthic lifestyle.

## Materials and Methods

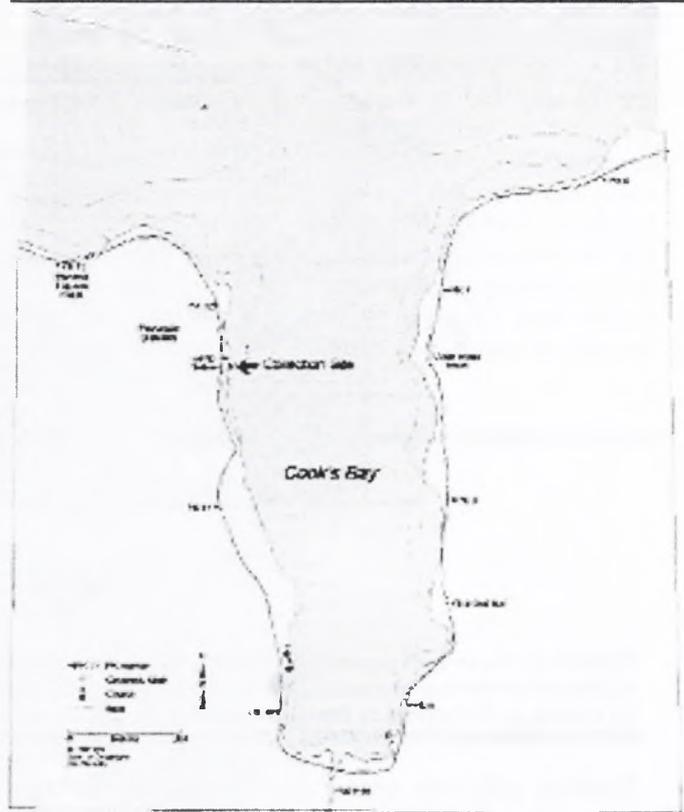
### Collection and Study Site

All studies were conducted using the rhizostome scyphomedusa tentatively identified as *Cassiopea andromeda* (George 1979). Until further confirmation of this, the subjects will be referred to as *Cassiopea* sp. The study was conducted on the island of Moorea, in French Polynesia. Specimens were acquired at the collection site located off the dock of the Richard Gump field station in Cook's Bay. (Figure 1) They were all found in shallow waters 2-3 m deep. The experiments were conducted between the months of October and November 1999. When not in use in experiments, the specimens were kept in a large outdoor cement tank measuring with freshly circulating seawater directly from Cook's Bay.

### Light Affinity Study

A tank of non-circulating seawater was placed in the darkroom of the Gump Station. An artificial light/dark cycle with 12 hours of light and 12 hours of dark was set up using a lamp with a 40 W bulb. The cycle was set to coincide as closely as possible with the natural light/dark cycle in Moorea as to allow the test subjects to adapt more quickly to the artificial environment. The placement of the light source acted as the variable in this experiment. (All of the jellyfish used in this study were approximately the same size, around 9-10 cm. This was done to prevent size being a variable in the study.) Three sets of trials were run with the light source positioned at the top of the tank, at the side of the tank and with the light source coming from under the tank. In each set, all of the sides with the exception of the one with the light source were covered with cardboard to

prevent light coming in from any other angle. (The



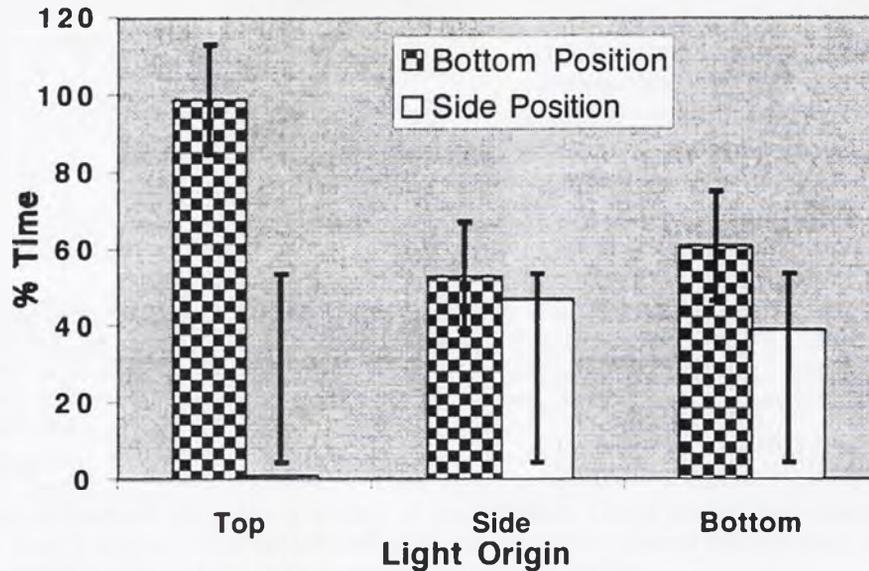
**Figure 1.** Collection site of *Cassiopea* in Cook's Bay on the island of Moorea, French Polynesia.

top of the tank did not have a surface offered for the jellyfish to rest on because previous observations had indicated that the jellyfish preferred to stay near the bottom of the tank.) In each trial, a jellyfish was placed in the tank and allowed 24 hours to adjust to the artificial environment. The jellyfish's location in the tank was then checked and recorded every hour for the next 24-hour period, i.e. one full light/dark cycle.

### Pulsation

Individual jellyfish were placed into a tank of non-circulating seawater (23 cm deep) and their pulses were counted for ten minutes. Afterwards, they were removed and measured for bell diameter (in centimeters) and placed back in their holding tank. The average pulse rate (in minutes) was calculated for each subject and compared to the bell diameter to see if there was a correlation between the size of the jellyfish and the average pulse rate per minute.

The pulse rates between swimming *Cassiopea* and those resting on the bottom of the tank were compared. Individual swimming jellyfish were observed for ten minutes as their pulses were



**Figure 2.** The overall percentage of time spent in the bottom of the tank or the side of tank for each set of trials. There was no significant preference in positioning when light was on the side or the bottom (t-test,  $p > 0.05$ ) but there was a significant preference for resting on the bottom of the tank when light origin was at the top of the tank. (t-test,  $p < 0.05$ ) Error bars show  $\pm$  standard error.

Resting jellyfish were also observed for ten minutes as their pulses were counted. The subjects were then removed from the tank and measured for bell diameter. Average pulse rates per minute were then calculated for both groups. The pulse rates for the swimming jellyfish were then compared with those of the resting jellyfish.

#### *Bell Position and Settling Ability*

Five jellyfish of different bell diameters ranging from 8.5 cm to 15 cm were used for this study. In the first set of trials, they were placed bell up on the surface of the water. In the second set of trials, they were placed bell down on the surface of the water. Each time, they were observed and timed until they settled in a resting position on the bottom of the tank. The average of the times for each set of trials were calculated and compared with each other. If the jellyfish took longer than twenty minutes to settle, the jellyfish was removed from the tank and the settling time recorded as twenty minutes. The times of differently sized jellyfish were also compared to see if there was a correlation between bell diameter and ability to settle.

#### *Morphology*

Rather than measuring every oral appendage on the jellyfish and then taking the average length, only the largest oral appendage

of each jellyfish was measured to find a correlation between appendage length and bell diameter. The largest oral appendage was invariably situated at the center of the jellyfish on the manubrium. The length of the appendages was then compared with the respective bell diameter to find a relationship.

The number of oral appendages on each jellyfish was also compared with bell diameter. Only the oral appendages with the dark blue pigment in them were counted. (There were small clear oral appendages without the blue pigment all less than a centimeter long.) The numbers of oral appendages found were then compared with the numbers found on other different sized jellyfish to see if there was any kind of correlation between diameter and oral appendage number.

#### **Results**

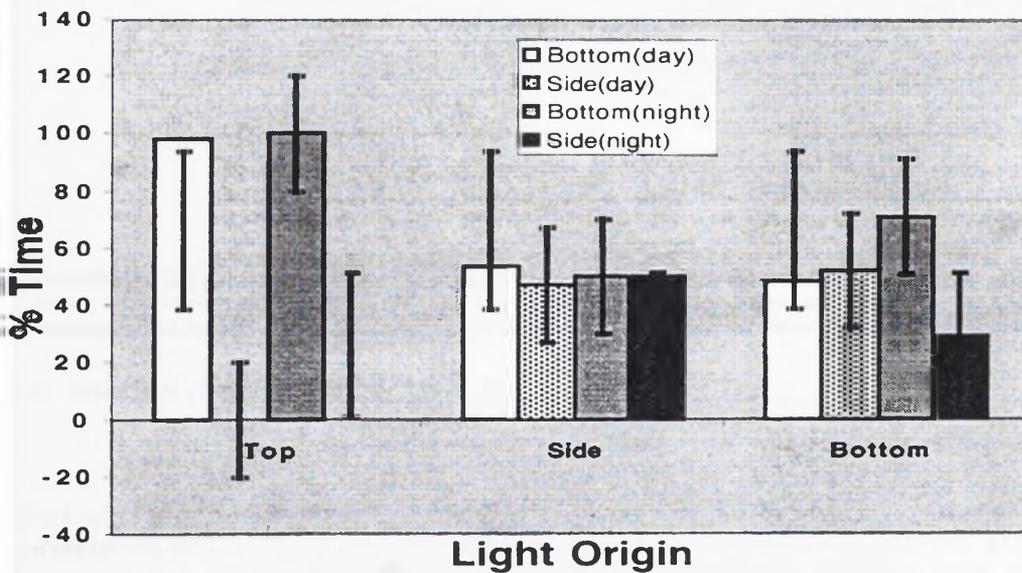
##### *Light Affinity Study*

The jellyfish were found in only two positions within the tank: Either resting on the bottom of the tank, or attached to the side of the tank near the bottom. During all of the trials, regardless of where the light source was, the jellyfish were never seen more than five centimeters up from the floor bottom when they were suctioned to the side of the wall. When they did move, it was not by swimming, but by sliding themselves along the glass. For each trial,

the data were combined to see the overall time spent in each position. This data was then combined with the others from the same set of trials to see if there was an overall preference for one position over the other. (Figure 2)

When the light source was positioned at the top of the tank, there was a statistically significant preference for resting on the bottom of the tank (t-test,  $p=4.98E-07$ ). On the other hand, when the light source was at the side and the bottom of the tank, there was no statistically significant preference for one position over the other (t-test,  $p=0.45$  and  $0.28$ , respectively.).

To see if there was a preference for positioning during the day and night in each set of trials, the percentage of time spent in each position was calculated. (Figure 3) When the light source was positioned at the top of the tank, there was no significant difference between the way the jellyfish were positioned during the day and the way the jellyfish were positioned during the night. (t-test,  $p=0.21$ ) There was also no significant difference in the trials where the light source was positioned at the side of the tank (t-test,  $p=0.31$ ) and where the light source was positioned at the bottom of the tank (t-test,  $p=0.28$ )



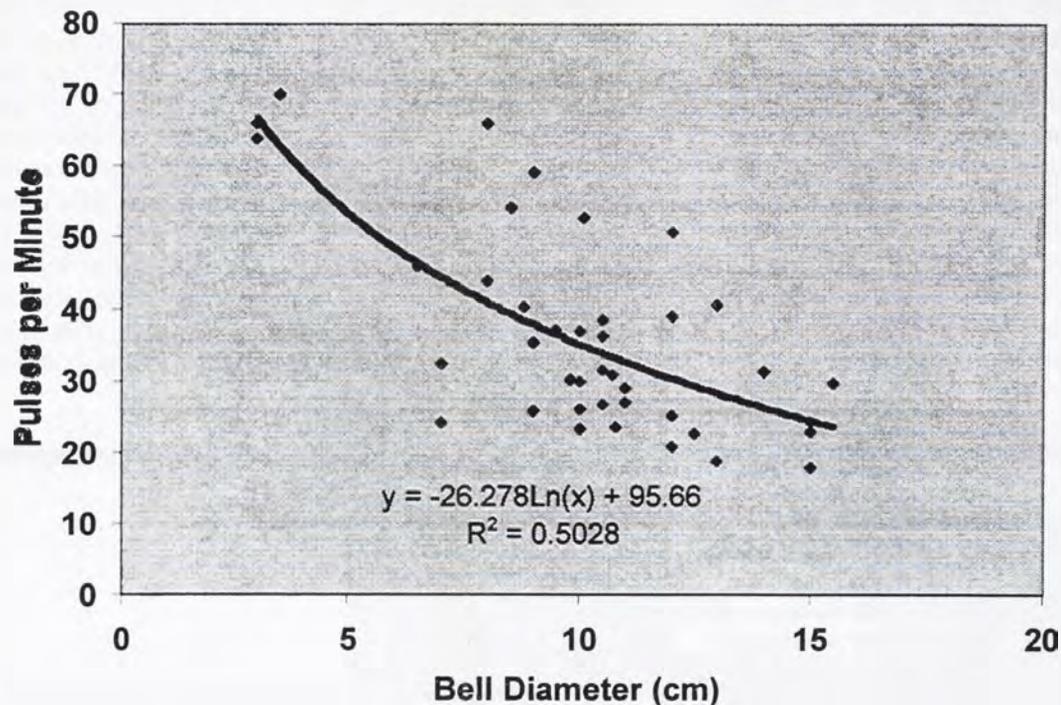
**Figure 3.** Percentage of time spent in each position during the day and night of each set of trials. There was no significant difference between the percentage of time spent in any position during the day and that same position during the night in any set of trials. (t-test,  $p>0.05$ ) The error bars show  $\pm$  standard deviation.

#### Pulsation

A plot of pulsation rate against *Cassiopea* bell diameter revealed an inverse logarithmic relationship (Fig. 4). A correlation was found between increasing bell diameter and decreasing pulse rate. ( $r=0.709$ ) The best-fit curve for the relationship between the pulsation rate and diameter was an inverse logarithm function,  $y = -26.278 \ln(x) + 95.66$ .

A plot of the pulsation rate of swimming *Cassiopea* against bell diameter was compared to

a plot of the pulsation rate of resting *Cassiopea* against bell diameter. (Fig. 5) There was a significant difference found between the pulse rates of floating jellyfish and those of resting jellyfish. (ANOVA,  $p=0.00157$ ) However, there was no strong correlation found between the respective pulse rates and bell diameter. The correlation between bell diameter and floating pulse rate was weak ( $r=0.31$ ) along with the correlation between bell diameter and resting pulse rate. ( $r=0.44$ )



**Figure 4.** Pulsation rate of *Cassiopea* as a function of bell diameter. There was a strong correlation found between the diameter of the bell and the pulsation rate,  $r=0.71$ . The best-fit curve for this relationship is an inverse logarithmic function.

#### *Bell Position and Settling Ability*

When the jellyfish were placed bell up on the surface of the water, it almost invariably took the subject over 20 minutes to achieve resting position on the floor of the tank with the exception of one jellyfish that reached the bottom in 14 minutes. When the jellyfish were placed bell down on the surface of the water, they all took less than a minute to reach the bottom of the tank. The difference between the times it took for bell up and bell down jellyfish to reach resting position were statistically significant (t-test,  $p=8.0161E-05$ )

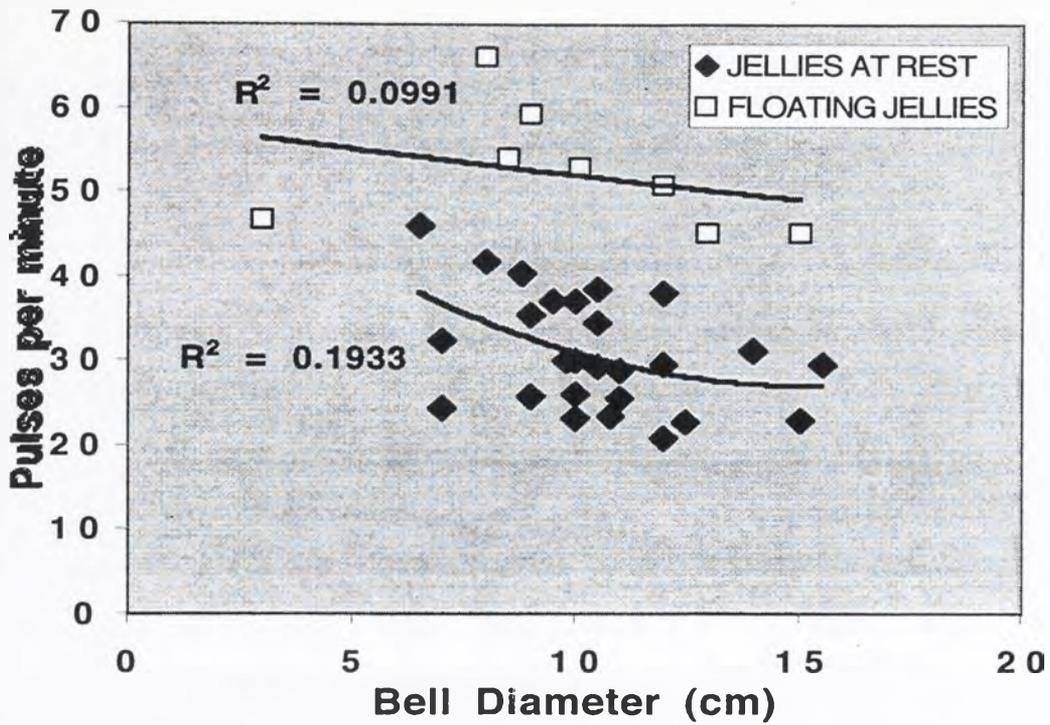
The bell diameter of the jellyfish were also measured and plotted against their respective settling times when placed bell down to see if there was a relationship between the two. (Fig. 6) There was no strong correlation found

between the diameter of the jellyfish and its settling speed. ( $r=0.23$ )

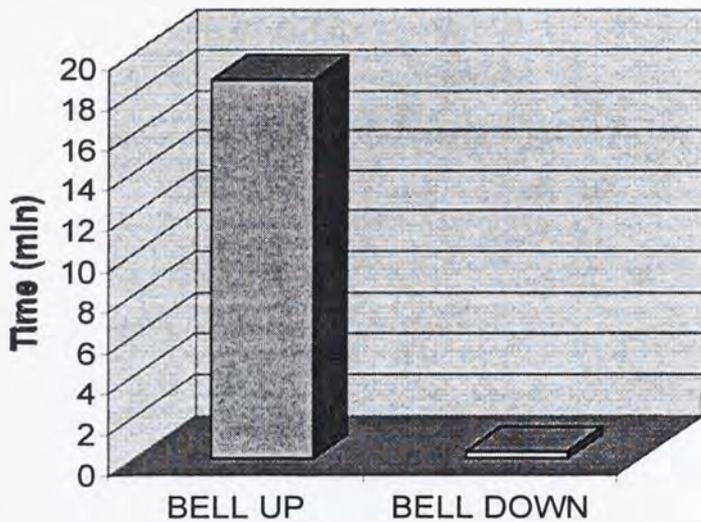
#### *Morphology*

Paddle length was plotted against the bell diameter of the jellyfish (Fig. 7). The correlation between the paddle length and the bell diameter was strong, with  $r=0.88$ . The best-fit curve for the relationship between the paddle length and diameter was found to be a power function,  $y=0.0982x^{1.4199}$ .

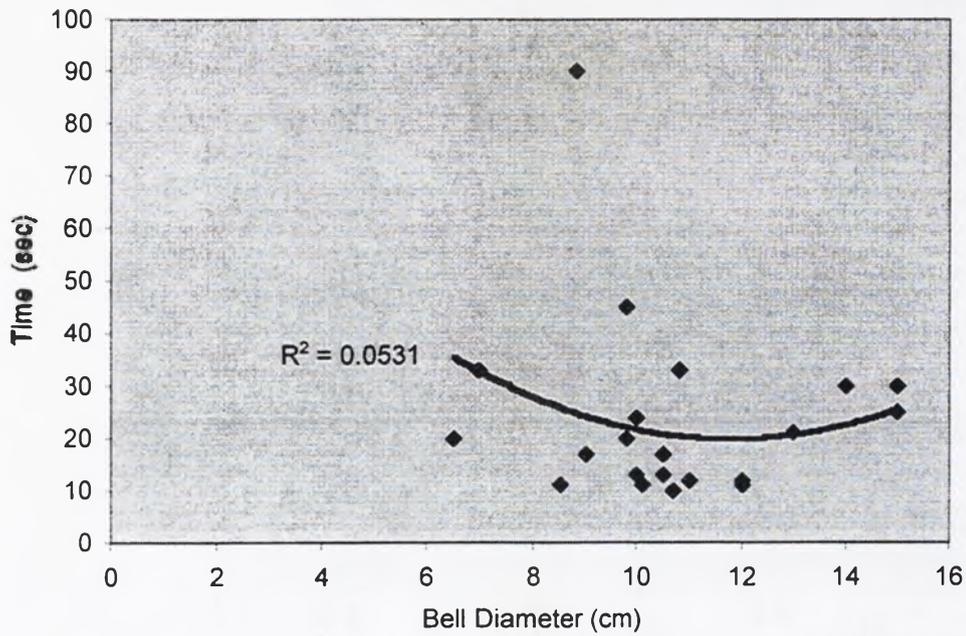
The numbers of paddles counted were also plotted against the respective bell diameters of the jellyfish. (Fig. 8) The best-fit curve for the relationship between the number of oral appendages and the bell diameter was found to be an exponential function,  $y = 29.579e^{0.1148x}$ . There is a strong correlation between the number of oral appendages and the diameter of the bell. ( $r=0.94$ )



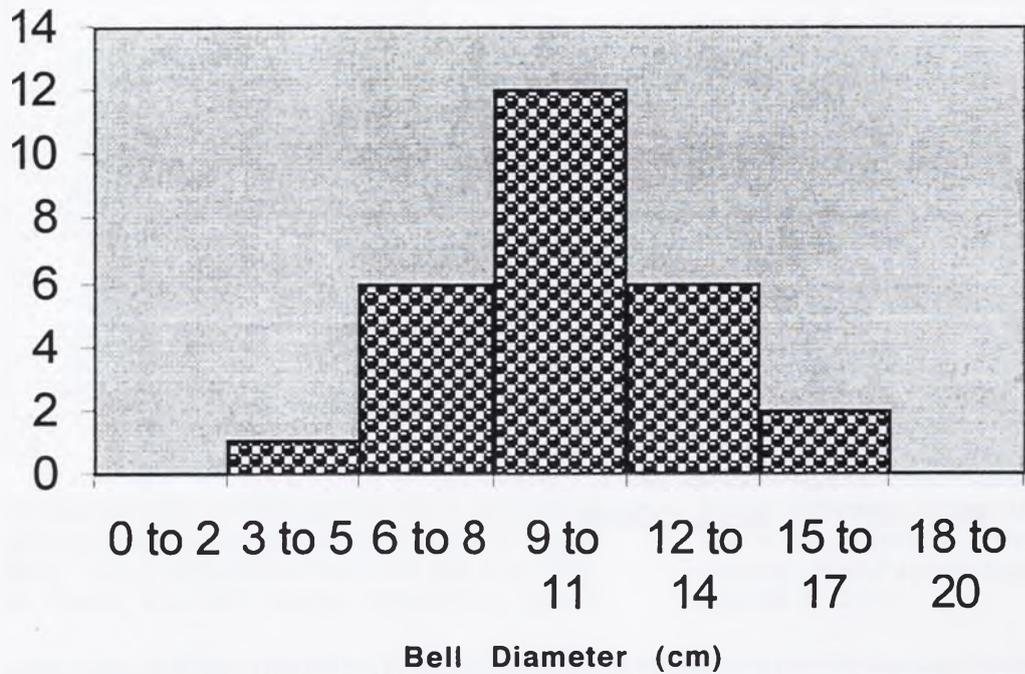
**Figure 5.** Floating pulse rates were found to be significantly higher than resting pulse rates. (ANOVA,  $P < 0.01$ ) but there was no strong correlation found between bell diameter and floating pulse rates and resting pulse rates. ( $r = 0.31$ ,  $r = 0.44$  respectively)



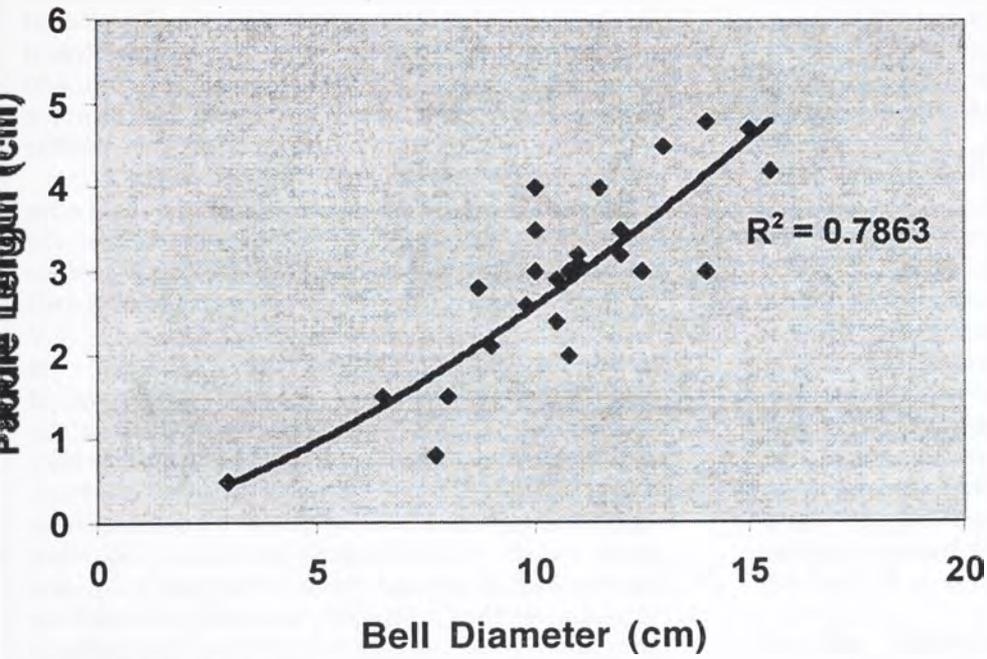
**Figure 6.** There was a statistically significant difference found between the times it took for bell up and bell down jellyfish to achieve settling position on the bottom of the tank. (t-test,  $p = 8.0161E-05$ )



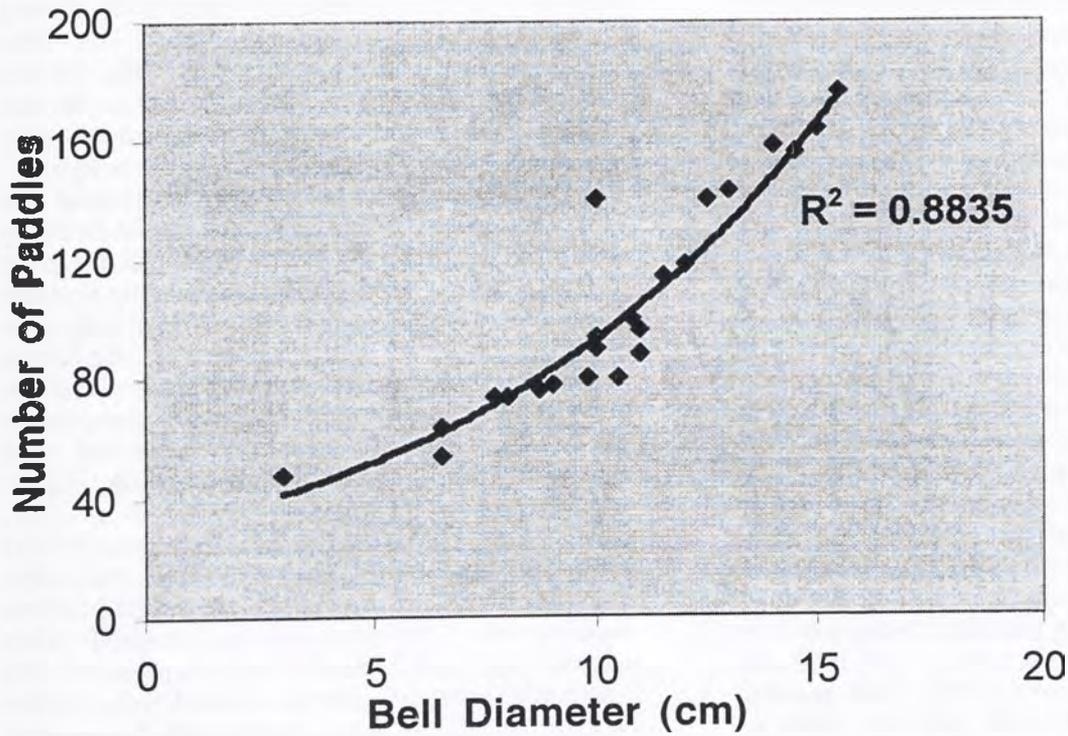
**Figure 7.** There was no correlation found between the diameter of the jellyfish and the time it took for it to settle when placed bell down on the surface of the water. ( $r=0.23$ )



**Figure 8.** Size distribution of *Cassiopea* found in Moorea. Sizes ranged from 3 cm to 17 cm, with most of the individuals in the 9 to 11 cm range.



**Figure 9.** The longest oral appendage length as a function of bell diameter. There was a strong correlation found between the diameter of the bell and the length of the longest oral appendage found in the center of the oral arms. ( $r=0.88$ ) The best-fit curve for this relationship is a power function.



**Figure 10.** The number of paddles as a function of bell diameter. There was a strong correlation found between the diameter of the bell and the number of oral appendages. ( $r=0.88$ ) The best-fit curve for this relationship is an exponential function.

## Discussion

### *Light Affinity*

When the light source was at the top of the tank, the jellyfish had a statistically significant preference for the bottom of the tank as opposed to the side of the tank. However, the other trials had more ambiguous results. The jellyfish divided their time almost equally between the bottom and the side of the tank. This can easily be misconstrued as *Cassiopea* having no preference between the side and the bottom of the tank when the light source is on the side or the bottom of the tank. However, if the jellyfish prefers to sit on the bottom when light comes from above (as in nature), then it must be deliberately choosing to move to the side of the tank when the angle of light is different. Thus, the location of the source of the light influences how and where the jellyfish chooses to position itself.

The way that these jellyfish position themselves under alternate angles of light may not be a technique for maximizing light intensity for their zooxanthellae. Had they chosen one position over the other, we might be able to infer that the stance chosen maximized the photosynthetic ability of their zooxanthellae. However, since there was no statistically significant preference this may not be the case. It is also important to remember most of the zooxanthellae are concentrated in the bell, and the jellyfish are always found bell down on the ocean floor in the wild.

If *Cassiopea* is able to attenuate the necessary intensity to its zooxanthellae without having to expose its umbrella directly to the sun, then perhaps the angle at which the light comes is not important for achieving the maximal photosynthetic rate.

This does not explain why the jellyfish choose to adjust their positions to move onto the side of the wall when the light source was at the bottom or the side of the tank. One explanation may be that *Cassiopea* aligns itself according to the direction of the source of light in order to tell the difference between up and down. A suggestion for further studies would be an investigation into the mechanism and methods that *Cassiopea* uses to orient itself. One possible study could be to observe jellyfish cultured without zooxanthellae under differently angled light sources using the experimental design used for this study to see if they adjusted their positions. This may indicate if the jellyfish actually do shift their positions to maximize light intensity for their zooxanthellae. If the jellyfish without zooxanthellae do not orient

themselves any differently between the different trials, then the zooxanthellae is the factor that causes them to adjust themselves differently. If they do change their orientations according to where the light source is placed, this is more evidence for *Cassiopea* aligning itself towards the light as a means of orientation.

Another explanation might be that the jellyfish is actually positioning itself to avoid the light. As explained previously, Cassio Blue (the blue pigment) in the oral appendages and bell may act as a light filter to avoid damaging UV radiation for both the jellyfish and its zooxanthellae. In the species of *Cassiopea* found in Moorea, Cassio Blue is concentrated in the oral appendages of the jellyfish and is not very visible in the bell or the oral arms. Therefore, light coming from the side or the bottom of the tank would shine directly at these parts that may not have as much protective pigment as the oral appendages. The jellyfish may actually be positioning themselves away from the light to avoid sunburning the zooxanthellae and themselves.

There was no statistically significant difference found between the way the jellyfish positioned themselves during the light hours and the way they positioned themselves during the dark hours during any of the trials. This corresponds with Blanquet (1979), whose findings showed that in nature, *Cassiopea* do not change their position during the course of a day to adjust to changing incident-light intensity.

Further studies should concentrate on the way *Cassiopea* orients itself, and whether those with zooxanthellae adjust their positions to angled light sources in the same way that those without zooxanthellae. It might also be beneficial to introduce the size of the jellyfish as a variable in these experiments since all of the jellyfish used in this particular study were in the same size range. It has been observed that smaller *Cassiopea* have a significantly higher algal density than larger jellyfish (Verde, McCloskey 1998). If the smaller ones orient themselves differently than the larger ones, this may indicate whether algal density plays a factor in the way *Cassiopea* orients itself. This would be most easily performed at an institution where *Cassiopea* is bred, since in the wild it is difficult to capture smaller specimens due to compromised visibility in the muddy and deep waters.

### *Pulsation*

The inversely logarithmic correlation found between diameter and pulse rates can be explained by the fact that the smaller jellyfish

have higher metabolism rates than the larger ones. (Verde, McCloskey 1998) This inverse relationship between metabolic rate and animal size is a common biological phenomenon evident in both vertebrates and invertebrates. The increased pulsation rate of smaller jellyfish is a function that increases the ventilation of the surface epithelium to maintain higher metabolic rates. (Blanquet 1979) The higher algal density of smaller jellyfish may serve to provide the necessary oxygen for the increased metabolic rate.

The difference between the pulse rates of swimming jellyfish and resting jellyfish is statistically significant. This is indication of how *Cassiopea*'s benthic nature affects its behavior, its pulsation rate in this case. Settling on the floor of the ocean significantly slows down the pulse rate of *Cassiopea* due to the fact that it is no longer attempting to force itself through the water. The purpose of pulsing while in resting position is only to pull in fresh water and push away stagnant water (Gohar, 1960). Therefore it is more energetically efficient to slow down its pulse rate when not swimming.

There was no strong correlation found between pulse rate and bell diameter in this study. The limited size range of jellyfish used in this study may explain the lack of correlation. The relationship between pulse rate in jellyfish as shown in the previous study is inversely logarithmic. This is shown in the sharp drop of pulsation rates of jellyfish ranging from 0-5 cm as opposed to the more gradual drop in pulsation rates from jellyfish larger than 5 cm (Fig. 3). No jellyfish with bell diameters of less than 5 cm were available for this study so only the gradual drop in pulse rates as bell diameter increases is evident. If there were data for jellyfish under 5 cm, an inverse logarithmic curve would probably have become evident.

#### *Bell Position and Settling Ability*

There was a statistically significant difference found between the settling ability of bell-up and bell-down jellyfish. The jellyfish placed bell up on the surface of the water may not have been able to shift their position due to the surface tension of the water. The mucus released by the jellyfish may have further increased the inability to break the surface tension of the water. Also, since jellyfish can not isolate movement on any part of their bell, it becomes more difficult for them to completely turn themselves over to achieve the resting position on the ocean floor.

Diameter was found to have no significant correlation with the ability to settle when placed

bell down in the water. Interestingly, only very small *Cassiopea* have actually been seen swimming in the wild (personal observation 1999, Bigelow 1900). If smaller jellyfish have the same difficulty or ease of settling (depending on the bell position) as larger jellyfish, there should be a reason why only the very small ones are actually seen swimming. It is not due to any kind of territoriality of larger jellyfish, even though they aggregate. Blanquet (1979) found that intraspecific contacts in *Cassiopea* produced no apparent effects. Perhaps they are seen swimming because they are more easily swept up off of the ocean floor due to their smaller diameter. A study could be done on the stability of differently sized jellyfish using a wave tank and observing what sizes of *Cassiopea* are more likely to get swept off the side or the floor of the tank due to wave action.

#### *Morphology*

The number and length of the oral appendages were both found to be strongly correlated with bell diameter. Because these oral appendages are the main source of the Cassio Blue in *Cassiopea*, this means that the Cassio Blue is also strongly correlated with bell diameter. This is interesting since smaller jellyfish actually have more zooxanthellae than larger jellyfish. It would be logical to assume that the more zooxanthellae living in the jellyfish, the larger amount of Cassio Blue needed to attenuate and filter the light is. The fact that the larger jellyfish actually have more blue pigment seems almost counterintuitive. But it is necessary to remember that the blue pigment may also protect the jellyfish itself from damaging UV radiation. Perhaps the increasing amount of Cassio Blue as the diameter increases should be associated with the greater need of protection from UV light for the jellyfish itself and not just its zooxanthellae. This still supports the hypothesis that Cassio Blue acts as a light attenuator and filter. It is also interesting to note that since the surface area of the bell grows exponentially ( $area = \pi r^2$ ), the exponential growth of the number of oral appendages may simply be directly correlated with the growth of the surface area of the bell.

#### **Conclusion**

Continuous observations of the jellyfish revealed that *Cassiopea* does alter its position depending on where the source of light is. Specific positions could not be correlated with specifically angled light sources except for when the light source was at the top of the tank. In this situation, the jellyfish spent approximately 99%

of the observed time at the bottom of the tank. Conclusions on whether or not *Cassiopea* does this to maximize light intensity towards its zooxanthellae are unclear.

The pulsation rate of *Cassiopea* was found to be inversely correlated with the bell diameter. Swimming jellyfish were found to have significantly larger pulse rates than resting jellyfish. The position of the bell also influenced the ability of the jellyfish to settle on the bottom of the tank. Jellyfish placed bell down on the surface of the water achieved resting position significantly faster than those placed bell up on the surface of the water

The number and length of the oral appendages were found to be strongly correlated with bell diameter. Because these oral appendages are the main source of the Cassio Blue in *Cassiopea*, this means that amount of Cassio Blue in *Cassiopea* is also strongly correlated with bell diameter.

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# The Impact of Fire on Invertebrate Macrofauna in Moorea, French Polynesia

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**ABSTRACT.** Three fire scars aged 1, 4, and 8 years old were assessed to determine the macro-invertebrate composition on Moorea in French Polynesia. Unburned regions alongside the scars were used as controls. Data collected included taxonomic, functional, and ecological definitions of specimens identified. The goals of the study were to: 1) explore how vegetative alteration by fire would affect faunal composition, 2) determine which faunal groups may be more or less prone to the impact of fires, and 3) generate a list of invertebrates and begin to categorize them for conservation purposes. Of the 80 morphological species collected, 7 Classes were represented including Insecta (30 species) and Arachnida (35 species). No concrete conclusions can be made without further replication of the study. However, comparisons between vertical stratification and species composition give support to the spatial heterogeneity hypothesis and distribution of fauna throughout the layers suggest that the litter macrofauna may be at highest risk with the onset of fire.

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## Introduction

The frequency of fire is typically believed to increase with decreasing moisture. So the threat of fires igniting within the humid tropics is rarely considered. Until the 1970's ecologists still believed that tropical fires were a rare phenomenon, most likely induced by lightning. It was soon ascertained through soil samples and anthropological studies that people had been starting fires for centuries in order to clear land for homes, pasture, or crop (Woods 1989; Turcq et al. 1998). But with increasing population growth, brush fires have been occurring with relatively higher frequency the world over, including tropical regions.

During the drier months of the year, Moorea has had up to 10 brush fires, all of which were ignited by land clearing and trash disposal activities (interview Hanz Fauura, 1999). Most of the fire scars observed on the island occurred on slopes, which are more susceptible to burning due to the higher rate of drainage creating an overall drier microclimate (Woods 1989). Thus the regenerative processes of fire scars is more subject to erosion, which slows the recolonization of the site. The plants, which ultimately succeed in recolonizing the burn, may or may not harbor the qualities needed to repropagate the original faunal organisms. Thus, the faunal composition and abundance is dependent on which plants lead succession and how they vertically stratify (i.e., by deposition of litter and formation of canopy leading to changes in microclimate and three-dimensional complexity) their immediate environment through time.

Most studies dealing with fires focus on the affects of fire on plants and floral succession. Relatively few studies have discussed how the faunal

community structure responds to fire as a whole. Furthermore, the terrestrial invertebrates remain virtually unstudied on Moorea. Accordingly, my first goals were to collect macroinvertebrate specimens on Moorea and explore the idea that the burns will alter the landscape and thus the insect communities. If the faunal composition and diversity is dependent on which plants lead succession and how they structurally alter the environment, then the initial faunal colonizers and survivors which dominate after the fire will experience a turnover in species abundance and richness as susceptible to the regeneration of the plant community. My second goal was to examine the groupings of the colonizers: of all the species collected, are any of the groups they represent, taxonomically, functionally, or ecologically, more or less prone to the effect of fires?

## Materials and Methods

### *Site Selection*

Numerous burn scars were observed visually from the roadside. Subsequent excursions were made to the various sites keeping in mind the following questions: Is the burn site large enough to take samples from the median of the scar in order to avoid any edge effects? Is a control site with a similar elevation and slope nearby? Is the site accessible by foot and can the hike be made in two hours or less? If the land is privately owned, can access be gained? Can the age of the burn be determined? Was the site only burned once? If each of these questions was affirmative, the site was chosen. After speaking with locals, three sites were chosen. In attempt to consider the general affects

of time, the burn sites chosen are at least three years apart in age.

#### Site Descriptions

Each site was assessed in order to compile a brief description including location (with GPS reading), altitude, precipitation, cause and date of burn, soil characterization (Munsell Color rev. ed. 1994), dominant floral species, and the vertical stratification of the microenvironment. Figure 1 contains a map of Moorea indicating the locations of each site.

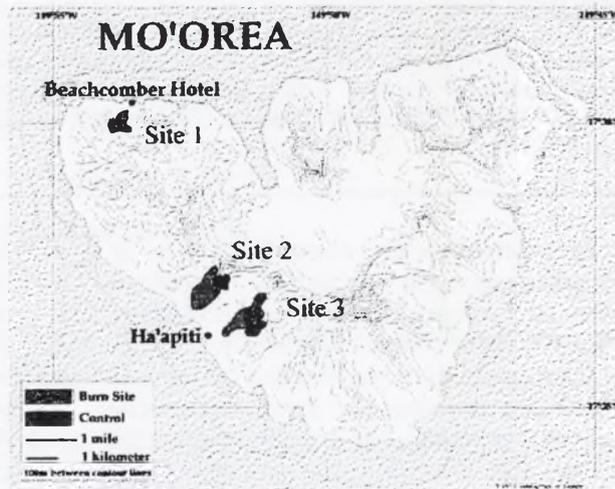


Figure 1. Map depicting study sites.

**Site 1** - Burn Site 1 is located across from the Beachcomber/Park Royale Resort less than 100 m above sea-level near the north-west corner of Moorea (S 17° 29' 44", W 149° 53' 35"). It is found on the driest part of the island accumulating 1500 mm of rain per year (O.S.T.R.O.M. 1993). The burn occurred less than one year ago and is located on privately owned land. The cause of burn is undetermined, though it appears that it may have been caused by a fire intended to clear a plot of land. The site is highly eroded exhibiting numerous drainage channels. The soil is coarse, completely lacking in organic material, and weak red (10R 4/4). The strata include dry, rock/soil and a layer of rubble 2 cm thick with a predominant particle size of 1 cm<sup>2</sup>. The ground was 88.5% (± 6.76) bare with a covering of dark and light lichen types.

Control Site 1 (S 17° 29' 50", W 149° 53' 38") is dominated by *Lantana camara* shrubs supporting the epiphyte *Cassytha filiformis*. The soil has 10% organic material and is dusky red (10R 3/3). There are 4 vertical strata: 1) the *L. camara* and *C. filiformis* shrub layer, 2) the ground layer including *Emilia fosbergii*,

*Oxalis corniculata*, and *Mimosa pudica*, 3) the litter layer composed of fallen branches and debris exposing bare ground, and 4) the soil layer.

**Site 2** - Burn Site 2 is located in Haapiti approximately 150 m above sea level on the western side of Moorea (S 17° 33' 23", W 149° 52' 16"), closer to the apex of the triangular island. It is found on a relatively wetter portion of the island, attaining an annual precipitation of 2200 mm (O.S.T.R.O.M. 1993). The fire was ignited by the burning of land downslope from the study site to clear for a no no (*Morinda citrifolia*) plantation. This site exhibits an irregular topography with drainage channels and eroded pockets spanning up to 2 meters across. Despite the intermittent clumps of *Metrosideros collina* regenerating from stumps, the native fern *Dicranopteris linearis* dominates the site and provides 100% cover. The soil is compacted by shallow roots and contains 60% organic matter. The color can be described as very dusky red (10R 2.5/2). The ferns provide a three-layer strata: 1) the living portion of ferns (up to 40 cm thick), 2) the dead foliage or upper litter (up to 70 cm thick), 3) the indistinguishable decaying foliage and soil layer (up to 10 cm thick)

Control Site 2 (S 17° 33' 17", W 149° 51' 16") has a tree canopy providing 80% cover and is dominated by *Hibiscus tiliacens*, though *Mangifera indica* (mango) and *Inocarpus fagiferus* are also prevalent. The soil is 20-25% organic and is reddish black (2.5YR 2.5/1). The vertical stratification is divided into 5 layers including: 1) tree saplings, 2) epiphyte ferns and ground ferns providing complex three-dimensional structure (30-60 cm above ground), 3) ground cover and logs (10-20 cm above ground), 4) upper litter of dead leaves, branches and debris (2 cm thick), 5) lower litter with decaying matter (2 cm thick), and 6) soil.

**Site 3** - Burn Site 3 (S 17° 33' 44", W 149° 51' 58") is also located in Haapiti. It is approximately 100 m above sea level and receives 2100 mm of rain per year (O.S.T.R.O.M. 1993). The fire occurred 8 years ago and was ignited by trash burning. This site resembled Burn Site 2 in vegetation cover and topography, though the *D. linearis* growth is neither as high nor as dense. In addition to the scattered clumps of *M. collina*, *C. filiformis* is present throughout the site growing atop the native fern. The soil is compacted by shallow fern roots and contains 45-50% organic matter. The color can be described as dusky red (2.5YR 3/2). The ferns here also provide three layers: 1) living fern (up to 25 cm thick), 2) upper litter of dead foliage (up to 40 cm thick), and 3) decaying foliage/soil (up to 10 cm thick).

Control Site 3 (S 17° 33' 48", W 149° 51' 57") has a high canopy providing 90% cover and is dominated by *M. indica*, though *H. tiliacens* and *Cocos*

*nucifera* are also prevalent. The soil is 15-20% organic and is very dusky red (2.5YR 2.5/2). The vertical stratification includes 5 layers which are: 1) the ferns, 2) the ground cover, 3) the upper litter with fallen hibiscus and mango leaves, 4) the lower litter with fern debris and decaying matter, and 5) the soil layer.

#### *Data Collection*

I took 2 samples per day from approximately 7:30am to 11:30am to avoid loss of specimens due to heat. Ten 1 by 1 m<sup>2</sup> quadrats were taken from each site, five from each the burn and the control. This study was self-limited by two factors: 1) the range of collection, and 2) invertebrate type included. Collections were taken from 1.5 m above ground, to accommodate saplings and shrubs yet ignore trees, to 4 cm below ground, which was the deepest I could dig without chiseling in the first burn site. Insects reliant on their wings for transportation (i.e., all members of the Orders Diptera and Hymenoptera, except ants) were disregarded on the basis that they may be visiting and/or can easily escape once their habitat is disturbed. Also, insects less than 1 mm in size were ignored during the study. For Site 1 burn and control, a transect line was laid through the median of the plot and quadrats were chosen from random x and y directions. However, for Sites 2 and 3, this proved to be cumbersome due to the large size of both burns. Thus, quadrats were chosen based on random numbers generating a compass heading and number of steps to be taken.

Once the plots were determined and measured out, an area was cleared around the plot to create a vegetative island thereby lessening the possibility of insect escape. Then with assistance from another field researcher, we searched through each layer counting and collecting invertebrates, making note of the substrate and layer type. All new specimens were placed in a vial. Once the ground was cleared and the litter was bagged, we dug a ¼ by ¼ m<sup>2</sup> plot to sample the soil.

Once out of the field, the litter and soil were taken apart, and if necessary sieved, and the individuals found were recorded. This was done within 24 hours of collection to minimize escape from or predation within the collections. Removing any outlying groups or anomalies, the number of individuals found in the soil were averaged between each set of five plots and then multiplied to equal 5 m<sup>2</sup>. I then sorted through the

invertebrates and separated them by morphology. A voucher specimen of each morphological species was given an identification number and then stored in ethanol.

#### *Data Analyses*

After identifying all species to at least the level of Class (most could be placed in family groupings) based on the morphological species concept, the invertebrates were sorted by ecological, functional, and taxonomic groups (Wilson and Taylor 1967; Kaston 1972; Bland 1978; Perrault 1987). The presence/absence of species was used in a Q-mode cluster analysis to determine the overall similarity between the burns and controls studied. Graphical analyses were employed to determine qualitative differences between groupings.

#### **Results**

##### *General Observations*

A total of 80 species were collected (Tables 1, 2, and 3). The 7 Classes of invertebrates represented are: Annelida, Araneae, Chilopoda, Diplopoda, Gastropoda, and Malacostraca.

Considering the total species composition at all study sites (Figure 2), the controls all had more than 500 individuals whereas the burns had less than 300 counted individuals, the youngest burn having only 31 individuals. The number of species also is more numerous in the controls as compared to the burn sites. Focusing on faunal composition found only in the burns, there was an increase in the number of individuals with time. For example, the number of individuals almost doubled between the 4-year and 8-year old sites with an increase from 16 to 22 species.

It was expected that the highest similarity would be between each burn and its respective control. After employing a Q-mode cluster analysis, the dendrogram constructed revealed less than 50% similarity between all burn-control pairs (Figure 3). The 4-year old burn and its control depicted 42.2% similarity. Burn and control plots from site 3 paired at 35.5% similarity. Sites 2 and 3 grouped together at 26.5% similarity. Lastly, the control for Site 1 paired first with the Haapiti sites, rather than pairing with its adjacent burn.

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**Table 1.** Collected specimens representing the Class Arachnida.

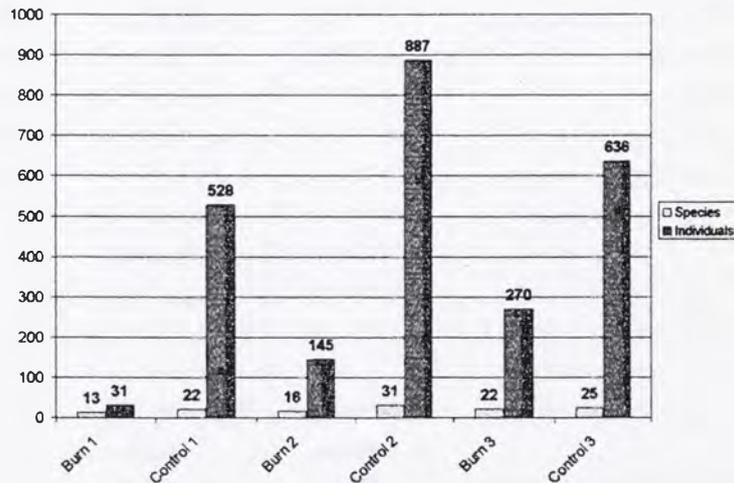
ID#	Family	B1	C1	B2	C2	B3	C3	Functional role	Layer	Other comments
<b>Order Acari</b>										
59	Onibatida				x		x	scavenger	lower litter	
<b>Order Araneae</b>										
<b>Ground Spiders</b>										
3	Dysderidae	x						predator (ambush)	rock rubble	hunts from retreat
5	Dysderidae	x						predator (ambush)	rock rubble	hunts from retreat
15	Dysderidae	x						predator (ambush)	rock rubble	hunts from retreat
24	Dysderidae		x					predator (ambush)	upper litter	hunts from retreat, also #39
33	Dysderidae		x			x		predator (ambush)	upper litter	hunts from retreat, also #40
37	Dysderidae		x					predator (ambush)	upper litter	hunts from retreat, also #38
52	Dysderidae					x	x	predator (ambush)	upper litter	hunts from retreat
84	Dysderidae			x				predator (ambush)	upper litter	hunts from retreat
58	Heteropodidae						x	predator (pursue)	upper litter	crab spider
4	Scytodidae	x						predator (ambush)	upper litter	spitting spider
12	Scytodidae	x	x					predator (ambush)	upper litter	spitting spider
43	Scytodidae					x		predator (ambush)	upper litter	spitting spider
74	Scytodidae			x				predator (ambush)	upper litter	spitting spider
<b>Web Spiders</b>										
42	Araneidae					x		predator (trap)	fem top	vertical orb between fem shallows
79	Pholcidae			x				predator (trap)	ground cover/fems	irregular web in lower-mid strata
85	Tetragnathidae			x				predator (trap)	fems	<i>Leucauge sp.</i> , vertical orb between fems; also #92
87	Tetragnathidae			x				predator (trap)	fems	<i>Leucauge sp.</i> , vertical orb between fems
88	Tetragnathidae			x				predator (trap)	fems	<i>Leucauge sp.</i> , vertical orb between fems
65	Theridiidae					x		predator (pursue)	upper litter	free-living amongst hibiscus leaf litter
89	Theridiidae			x				predator (trap)	fems	<i>Argyrodes sp.</i> , kleptoparasitic, horizontal low webs
95	Theridiidae			x				predator (pursue)	ground cover/fems	<i>Argyrodes sp.</i> , free-living, eats other spiders
70	Ulobonidae		x	x		x		predator (trap)	fems	irregular web in mid strata
77	Ulobonidae		x	x				predator (trap)	fems	irregular web in mid strata; also #90
76	??				x			predator (trap)	ground cover/fems	webs 10 cm above ground
<b>Jumping Spiders</b>										
1	Salticidae	x						predator (pursue)	rock rubble	pounces on prey
2	Salticidae	x						predator (pursue)	rock rubble	pounces on prey
6	Salticidae	x						predator (pursue)	rock rubble	pounces on prey
7	Salticidae	x						predator (pursue)	rock rubble	pounces on prey
23	Salticidae		x					predator (pursue)	upper litter	pounces on prey
53	Salticidae			x	x	x	x	predator (pursue)	fems	pounces on prey, also #80
69	Salticidae					x		predator (pursue)	fems	pounces on prey
72	Salticidae		x	x				predator (pursue)	upper litter	pounces on prey
<b>Order Schizomida</b>										
57	??					x		predator (pursue)	lower litter	buries itself in lower litter

**Table 2.** Collected specimens representing the Class Insecta.

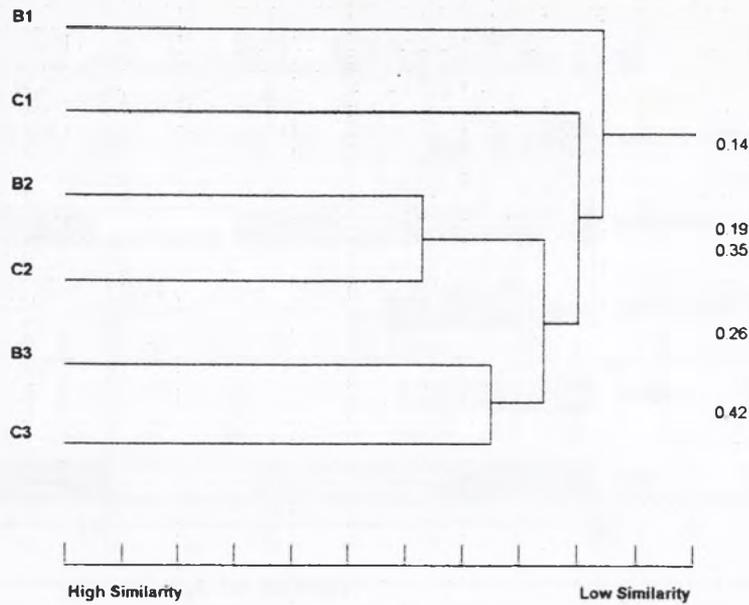
ID #	Family	B1	C1	B2	C2	B3	C3	Functional role	Layer	Other comments
<b>Order Coleoptera: Beetles</b>										
17	Coccinellidae: Lady Beetles	x						x predator (pursue)	shrub (base)	eats aphids and small insects
60	Curculionidae: Weevils							x herbivore	upper litter	eats all parts of plants
26	Scolytidae: Bark Beetles	x						detritivore	soil	found near roots
35	Tenebrionidae: Darkling Beetles	x						herbivore	soil	burrowed 1-3 cm below ground
<b>Order Dermaptera: Earwigs</b>										
31	??	x						scavenger	litter/top soil	
<b>Order Dictyoptera: Cockroaches</b>										
29	Blattidae	x						detritivore	soil/litter	
51	Blattidae							x detritivore	lower litter/soil	
54	Blattidae			x	x	x	x	detritivore	lower litter/soil	
71	Blattidae			x	x			detritivore	lower litter/soil	
73	Cryptocercidae			x				detritivore	soil/litter	eats decaying stems/roots
<b>Order Hemiptera: True Bugs</b>										
21	Delphacidae: Planthopper	x						herbivore (juice)	shrubs (leaves)	
27	Delphacidae: Planthopper	x						herbivore (juice)	litter/shrub (base)	
41	Largidae: Largid Bug	x						herbivore	shrub	ant mimic
28	Miridae: Plant Bug	x						herbivore (juice)	shrub	
32	Pentatomidae: Stink Bug	x						herbivore	shrub	
91	Pentatomidae: Stink Bug				x			herbivore	shrub	
86	Reduviidae: Thread-legged Bug				x			predator (ambush)	upper litter/ferns	Subfamily Emesinae
<b>Order Hymenoptera</b>										
<b>Family Formicidae: Ants</b>										
49	Subfamily Dolichoderinae							x x herbivore	upper/lower litter	<i>Technomyrmex albipes</i>
48	Subfamily Formicinae			x				x herbivore	upper litter	<i>Anoploepis longipes</i> ; dominant in disturbed habitats
55	Subfamily Formicinae							x x herbivore	litter/top soil	<i>Brachymyrmex sp.</i>
78	Subfamily Formicinae				x			herbivore	soil/litter/ferns	<i>Paratrechina sp. (vaga?)</i>
14	Subfamily Myrmicinae	x	x					x x herbivore (harvest)	rubble/litter/shrub	<i>Monomorium destructor</i>
61	Subfamily Myrmicinae			x	x			x predator	soil/upper litter	<i>Strumigenys sp.</i> ; small colonies; eats primarily collembolans
9	Subfamily ??	x						scavenger??	rock rubble	
25	Subfamily ??			x				herbivore??	litter/soil	
64	Subfamily ??							x herbivore??	upper/lower litter	
81	Subfamily ??				x			herbivore??	soil/litter/ferns	
<b>Order Orthoptera</b>										
8	Gryllidae: Crickets	x						herbivore	rock rubble	
66	Gryllidae: Crickets							x herbivore	upper litter	
<b>Order Psocoptera: Psocids</b>										
44	Lepidopsocidae			x				x detritivore	lower litter	eats decaying organic matter and dead insects

**Table 3.** Collected specimens representing the Classes Chilopoda, Diplopoda, Gastropoda, Malacostraca, and Oligochaeta.

ID #	Order	B1	C1	B2	C2	B3	C3	Functional role	Layer	Other comments
<b>Class Chilopoda: Centipedes</b>										
22	Scolopendromorpha	x		x	x	x		predator (pursue)	soil/litter	1/10 full size (no adults found)
<b>Class Diplopoda: Millipedes</b>										
11	Spirobolida	x						scavenger	soil	needs moist soil, many dead on burn site
63	Spirobolida			x	x			scavenger	soil/lower litter	always sheltered by moist litter/soil
46	Spirostrepida			x	x	x		scavenger	soil/lower litter	
36	??			x	x	x	x	scavenger	lower litter	
<b>Class Gastropoda</b>										
62	??				x		x	detritivore	upper litter	<i>Ovachlamys fulgens</i> ; fast-moving land snail; on hibiscus leaves
93	??				x			detritivore	lower litter	land slug; on rotting leaves
30	??			x	x	x	x	detritivore	upper litter	<i>Subulina octona</i> ; also #94
82	??				x			detritivore	upper litter	micro-land snail; mid-upper layer primarily on hibiscus leaves, but also inocarpus and pandanus
<b>Class Malacostraca</b>										
18	Isopoda	x				x	x	scavenger??	soil/litter	pill bug, rolls into ball
19	Isopoda	x						scavenger??	soil/litter	pill bug, rolls into ball
45	Isopoda			x	x	x	x	detritivore??	soil/lower litter	pill bug, does not roll into ball
67	Isopoda					x	x	scavenger??	upper litter	pill bug, does not roll into ball; mid-upper layer near shrub bases
<b>Class Oligochaeta</b>										
50	??					x	x		soil	earthworm; also #75??; no voucher
75	??			x	x				soil/litter	earthworm; also found in root/litter layer below ferns and above soil
<b>Class ??</b>										
83	??				x			detritivore??	lower litter	worm/leach??; on rotting leaves; no voucher



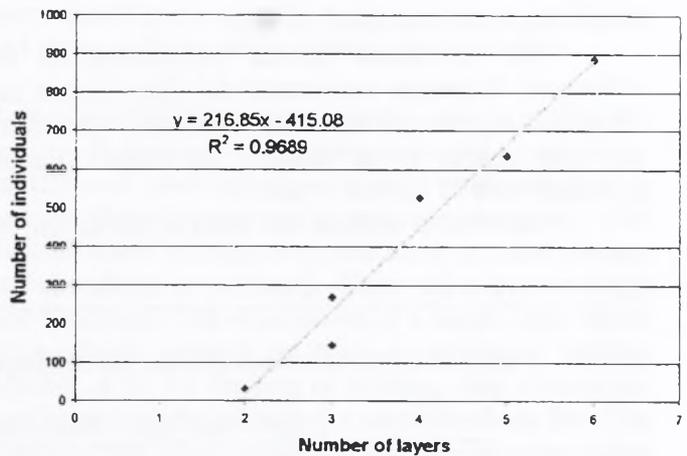
**Figure 2.** Number of species and individuals found at study sites grouped by burn and control pairs. Burn 1 occurred one year ago, Burn 2 occurred 4 years ago, and Burn 3 occurred eight years ago.



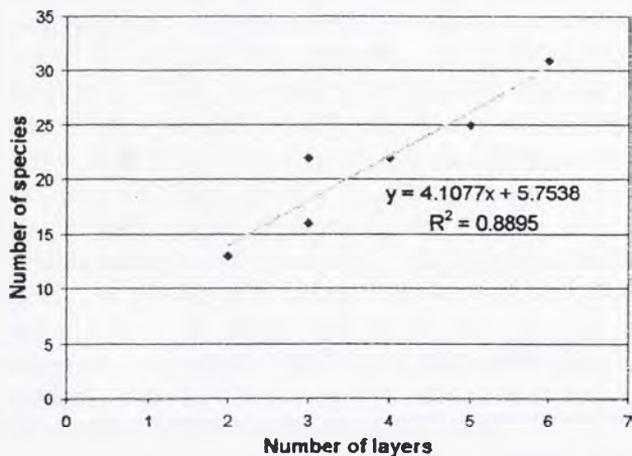
**Figure 3.** Dendrogram constructed from Q-mode cluster analysis depicting the overall similarity between sites (B = burn, C = control; 1 = Site 1, 2 = Site 2, 3 = Site 3).

*Role of Habitat Heterogeneity and Ecological Groups*

The importance of vegetative structure on recolonization by macroinvertebrates was investigated further by comparing the number of species/individuals with vertical stratification. Figure 4 depicts a positive correlation between species richness and the increased number of layers. Figure 5 demonstrates a stronger correlation between the number of individuals plotted against the number of strata, yielding a  $R^2$  value of 0.965.



**Figure 5.** Scatter plot indicating the increase in number of individuals with increase in number of layers ( $R^2 = 0.9689$ ).



**Figure 4.** Scatter plot indicating increase in species number with increase in number of layers ( $R^2 = 0.8695$ ).

Since habitat and community structure can include both dead as well as living components, it was important to consider the role of ground litter or humus layers. Of the 80 species collected, 45 were found in the litter (Figure 6). Thirty-one of these species were found to reside only in the litter and on no other substrate.

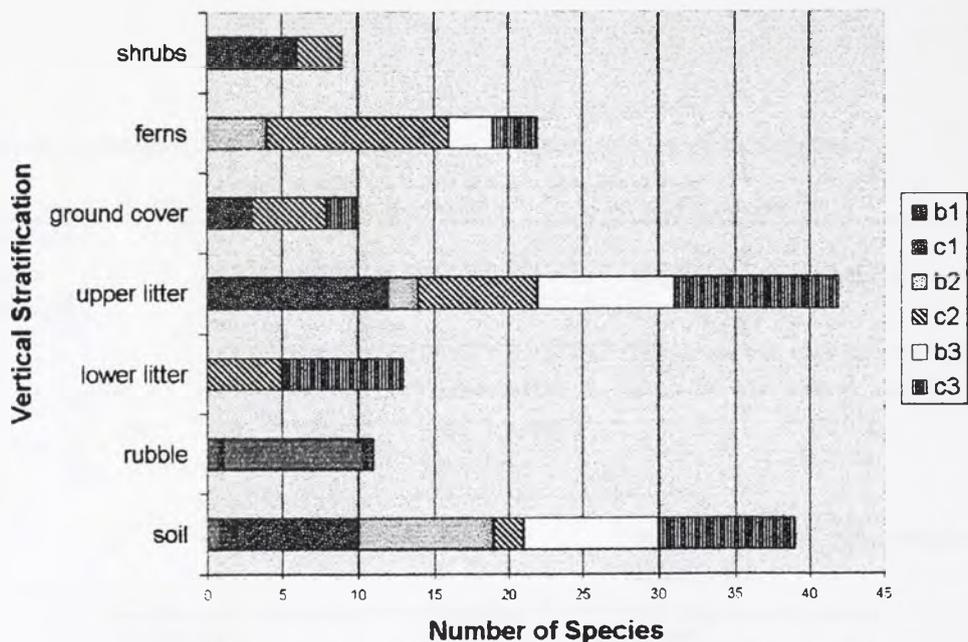


Figure 6. Graph depicting the number of species composing each spatial stratification at all six sites.

*Functional and Taxonomic Groups*

Of the seven classes represented in the collection, 30 species represented the Class Insecta and 37 species represented the Class Arachnida. However, the most diverse group included the spiders (Family Araneae) with 35 species (Table 1).

In order to describe the effect of fire on trophic

levels, specimens were divided into the following functional groups: predators, herbivores, detritivores, and scavengers. The predators were further subdivided into pursuers (those that actively hunt for prey), ambushers (those that sit and wait for prey, or semi-passive hunters), and trappers (those that capture prey indirectly i.e., by utilizing a web or snare). Table

Table 4. Species composition as divided into functional groups (S = number of species; I = number of individuals).

Functional Group	Site 1 - Burn		Site 1 - Control		Site 2 - Burn		Site 2 - Control		Site 3 - Burn		Site 3 - Control	
	S	I	S	I	S	I	S	I	S	I	S	I
predator	9	15	7	36	6	20	15	119	8	34	8	67
ambusher	5	6	5	27	2	4	2	9	3	14	1	7
trapper					1	1	8	44	1	2	1	2
pursuer	4	8	2	6	3	15	5	67	4	18	6	58
herbivore	2	7	8	183	1	68	3	199	4	157	6	225
detritivore			2	83	5	35	8	457	5	40	4	127
scavenger	2	9	5	226	3	14	4	97	4	20	6	206
worm					1	8	1	15	1	19	1	11
Totals:	13	31	22	528	22	145	31	887	22	270	25	636

4 delineates the species composition in terms of functional groups in each study site.

The vast array of spiders collected allowed for this group to be further divided in terms of ecological guilds. The spiders were separated into three groups. The first group, ground spiders, included the Families

Dysdera, Heteropodidae, Scytodidae, and two free-living specimens representing Theridiidae, typically a family of web-spinners. The second group, jumping spiders, represented the Family Salticidae. The third group, web spiders, included the Families Araneidae, Pholcidae, Tetragnathidae, Theridiidae, and Uloboridae.

Each group represented the layer on which its members were commonly found i.e., ground spiders in the lower strata, web spiders in the upper strata, and jumping spiders in the mid-stratification, often entering the

lower strata. Table 5 summarizes the spider composition at each site.

**Table 5.** Spider composition at each site (S = number of species; I = number of individuals).

Spider	Site 1 - Burn		Site 1 - Control		Site 2 - Burn		Site 2 - Control		Site 3 - Burn		Site 3 - Control	
	S	I	S	I	S	I	S	I	S	I	S	I
Ground	5	6	4	30	2	4	2	6	3	16	3	14
Jumping	4	9	1	3	2	10	2	16	1	5	2	3
Web					1	1	8	44	1	2	1	2
Totals:	9	15	5	33	5	15	12	66	5	23	6	19

## Discussion

### General Observations

Though an obvious increase in number of individuals increased with successive time after the burn, no significant increase in species richness is demonstrated. This accords with other invertebrate studies indicating that fire affects species composition and not diversity (Kunte 1997; Andersen 1991).

To explore the differences between burn and control pairs on the basis of species presence or absence, cluster analysis proved a useful general assessment of similarity. Site 2 demonstrated the highest similarity, the burn having 14 shared species and only 2 unique species. This could indicate successful recruitment from control into this burn of intermediate age. The control had the greatest species richness of all studies sites, and thus a greater probability that its species could inhabit a new environment. In terms of Site 3, the burn-control pair have 12 species in common, yet express 35.5% similarity. This is explained by the fact that the burn has 9 unique species, offering it more individuality when compared to the burn in Site 2. The burn-control of Site 1 exhibited an overlap of only two species, thus the control was more similar to the Haapiti sites with which more species are shared. The Beachcomber burn being so young and barren, shared no structural or vegetational characteristics with its control, only location. The two overlapping species, both ground spiders, must be able to tolerate intense heat with little or no cover to be able to live on the burn.

It is interesting to note that the two Haapiti burns, so similar in vegetative composition, do not pair primarily with each other. This demonstrates that similarity in location, climate, and vegetation does not necessarily grant faunal similarity. All these observations are speculation, no true conclusions can be

made without more replication. But it does pose some interesting questions including the idea of structure, not vegetation type, as a factor in determining faunal composition. The intermediate disturbance hypothesis may be employed to describe the possible trend of burn-control pairs initially moving towards similarity, and then regaining more individuality with time.

### Role of Habitat Heterogeneity and Ecological Groups

It seems that in terms of faunal composition, vegetational complexity associated with developing complex three-dimensional structure is important. With the addition of a single structural layer, species richness and abundance is increased. Thus, the converse should also hold true. The elimination of a single layer would leave faunal species without a structural habitat, whether it be for feeding or nesting, this elimination may be as detrimental as direct mortality from fire. The trends shown when comparing site species composition and richness with habitat complexity support the spatial heterogeneity hypothesis. The hypothesis states that on a local scale, the tropics contain more habitat subdivisions, or microhabitats, and this abundance of microhabitats allows taxa to partition each habitat more finely, allowing more species to coexist (Pianka 1966).

The macrofauna in the upper humus or litter layers are particularly susceptible to fires, as the insulating effects of the soil do not protect them. Furthermore, the litter layers have been known to be the main source of fuel in tropical fires (Uhl and Kauffman 1990). Most of these invertebrates play roles in nutrient cycling and decomposition, thus their presence is important in considering the regeneration of the burn site (Golley 1977). Because post-fire conditions often weather soil moisture and nutrients away, the absence of soil fauna could be a holdback to vegetative regrowth.

### *Functional and Taxonomic Groups*

Besides differences lying between the Site 1 burn and control pair, there is no obvious difference in species richness of the herbivore, detritivore, and scavenger groups in burn-control pairs. Though the numbers of individuals in each functional group is larger in the controls as compared to the burn sites. In all of the sites, the number of herbivorous species, excluding ant species, is depauperate. Possibly other herbivorous invertebrates are nocturnal, air-borne, or were not collected. Besides the control of Site 1, which included plant-hopper and plant-sucker species, ants were the predominant herbivorous species at all study sites. Ants themselves presented another problem in data collection. Since they are colonial species, the number of ants collected per quadrat was highly variable, resulting in a low confidence in the number of individuals representing the species itself as well as the numbers representing functional groups. Overall, conclusions cannot readily be drawn in terms of functional groups. Since night fauna, small invertebrates, and air-borne insects are not included in the study, it is difficult to make assessments or conclusions on trophic level changes. Furthermore, at the very least, more replication is needed to obtain the numbers needed to attain a certain level of statistical confidence.

In terms of difference in spider composition between burn and control pairs, some conclusions can be made. By grouping the spiders in guilds, it is easier to visualize the interspecific competition that occurs within a layer of vertical stratification. The obvious differences in spider composition are the following: 1) in Site 1, the number of ground spiders decreases with the alteration in ground landscape from shaded with litter deposition to barren with rock rubble, and 2) in Site 2, the number of web spiders decreases in the mid-strata along with the increased homogenous vegetational density. There are no differences to report between the Site 3 burn and control.

In the two Haapiti burns, the dense *D. linearis* provides a continuous and monotonous structure. Ground spiders living in the light-shielded litter layers and jumping spiders that inhabit the fern tops are found in the burns. But all the web spiders found were found in quadrats near erosion spots with shallower ferns. Other than microhabitats such as eroded topography lending less dense and irregular-heighted ferns, the *D. linearis* fields do not promote the colonization of web spiders. The greatest number and species of web spiders was encountered in the control of Site 3. The lower-mid stratification of the environment offered a rather complex three-dimensional structure with open air space to accommodate the presence of spider webs/snare. However, above this layer there is little

else, as the next layer is the tree canopy, which towers 10m or more above the ground.

In terms of vulnerability, the web spiders may fare worse in the aftermath of a fire than other spider groups. Immediately after the burn, web spiders will not be able to colonize since there will be no three dimensional structure with which to build webs on. Furthermore, if *D. linearis* continues to be the dominant plant species on fire scars, the web spiders will be offered an environment too dense to inhabit webs.

### **Conclusions**

Faunal succession follows floral succession i.e., given a set of vegetational conditions, floral succession provides habitat for a more or less distinct collection of invertebrate species. It is important to consider that fauna selects habitat on the basis of structure, which in essence could be the feeding site for one animal and a nesting site for another. In terms of the two Haapiti sites, if fire scars continue to be dominated by *Dichropteris linearis*, the environment will become less habitable for control species. The increase in light intensity above the ferns lacking a high tree canopy and the scant light penetration below the ferns harbors an entirely different structural and vegetational habitat for different group of faunal organisms.

Studies indicate that fire affects species composition and community structure. A simple change such as lessening the species composition may lead to the decline of the species directly affected or of one that is dependent on its presence for food, protection, or other interspecific interaction. The ecosystem is webbed with various degrees of direct and indirect interactions, which need to be studied to understand the effects of disturbance and the system's variable response.

To be able to make a more accurate assessment of faunal recolonization and succession, future studies should focus on one site and follow it through the course of time. Subsequent studies should practice further replication, and possibly study the system at night. Nocturnal collection and increased replication should portray a more accurate description of entire guilds participating in the system as well as determining relative species abundance. Sticky and pitfall traps can also be incorporated into the study in order to make general assessments of the faunal composition. Another possibility would be to continue this study and observe changes in species absence/presence through time in order to decipher the processes leading towards faunal turnover.

It is rare that conditions for fire all correlate at the same time without human influence. If human interaction can cause a change in the frequency of fires, it is also likely to affect species composition.

## Acknowledgements

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# Behavior and Distribution of the Bivalve Mollusk *Lima Fragilis*

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**ABSTRACT.** The bivalve *Lima fragilis* in Moorea, French Polynesia is a mollusk that has tentacles extending from its mantle and burrows under rocks. Few studies have been done on this species of *Lima* and this study was conducted to examine how predation might affect behavioral characteristics and habitat distribution of *L. fragilis*. This study contains four parts: (1) habitat distribution at Haapiti, Moorea, (2) day vs. night activity, (3) behavior in presence of a predator (*Octopus cyanea*), and (4) behavior in presence and absence of a rock. In addition, the affect of shortened tentacles on *L. fragilis* behavior was observed in parts 2, 3, and 4. The habitat distribution survey resulted in 4.5 *L. fragilis* per 100 m<sup>2</sup>, indicating low density and abundance. The day and night observations showed that *L. fragilis* were cryptic during the day and more active at night. Individual night activity indicated *L. fragilis* with shortened tentacles were more active in jumping than *L. fragilis* with normal tentacles. However, *L. fragilis* with normal tentacles were more active in different behavioral activities. Over a time period of 8 days, the presence of *O. cyanea* resulted in a mean movement of 10.49 seconds and mean immobility of 62.22 seconds of *L. fragilis*. In contrast, the absence of *O. cyanea* had a mean amount of movement of 27.12 and no movement for 35.65 seconds. A Pearson correlation matrix had a negative correlation between *O. cyanea* eating and *L. fragilis* with tentacles extended outward, indicating the tentacles of *L. fragilis* were not effective as a defense mechanism. The presence and absence of a rock was also found to influence the behavior of *L. fragilis*. In the presence of a rock *L. fragilis* with normal and shortened tentacles were significantly less active ( $p < 0.001$  and  $p \sim 0$ , respectively). Overall, *L. fragilis* with shortened tentacles were more active.

## Introduction

The bivalve mollusk *Lima fragilis* has several long, red and white tentacles that extend from its mantle. This species of *Lima* is approximately 23 mm and found on Moorea, French Polynesia burrowed under rocks in approximately 2-3 ft of water (Salvat and Rives, 1991; Silva, pers. obs.). Jefferies (1960) suggests that this habit of burrowing in substratum may have evolved from the order of Anisomyaria.

In addition, Gilmour (1967) found that locomotory forces of *Lima hians* aided in burrowing into crevices. These locomotory forces also enable Limidae to use water currents and rowing movements of their tentacles to swim (Gilmour 1967). Upon disturbance, *L. hians* were found to swim freely until burrowing itself again (Gilmour 1967). *L. fragilis* also exhibits similar locomotory behavior, but swims at a slower and more sustained pace (Gade 1981). This behavior suggests that swimming and burrowing act as escape responses from predators (Gilmour 1967; Gade 1981).

A potential predator of *Lima pellucida* was found to be *Octopus vulgaris*, who forages in crevices and under rocks (Mather 1991). *O. vulgaris* preferred to prey on *L. pellucida* for its inability to escape and swim away before captured and the minimal energy required to consume it (Mather 1991). However, Gilmour (1967) found that *L. hians* secreted distasteful mucus and autotomized their tentacles against potential predators. Another aversion from predation was found

by Mpitsos (1973), who discovered that *Lima scabra* has many eyes and dermal photoreceptors located on its mantle in order to maintain a strong sensory signal. Unfortunately, there is no current data available to provide sufficient evidence that *L. fragilis* share these same defense mechanisms.

Little research has been conducted on *Lima fragilis*. The focus of this study will examine how predation may affect behavioral characteristics and habitat distribution. This study contains four parts: (1) habitat distribution, (2) day vs. night activity, (3) behavior in presence of a predator (*Octopus cyanea*), and (4) behavior in presence and absence of a rock. In addition, the affect of shortened tentacles on *L. fragilis* behavior will be observed in parts 2, 3, and 4.

## Material and Methods

### Experiment #1: Habitat Distribution

This study was conducted in Haapiti (17°30'29"S; 149°52'29"W) in Moorea, French Polynesia (Figure 1). The site is situated along the mangrove beach of Haapiti.

Ten transects were set up perpendicular to the mangrove shoreline at roughly 20 m intervals. Each transect started at the shore and extended 100 m into the lagoon. Data was obtained by sampling 1m<sup>2</sup> quadrats on both sides of the transect every 10 m at 6:00 am and 6:00 pm. The number of *L. fragilis* and rocks were

counted within each quadrat. Depth of each quadrat was also recorded. Occasional strong winds and currents set transect line off by 1-2 degrees northwest.

*Experiment #2: Day and Night Activity*

*L. fragilis* were collected in Cook's Bay near the University of California at Berkeley's Richard B. Gump South Pacific Biological Research Station in Moorea, French Polynesia. *L. fragilis* were located under rocks in approximately 2-3 feet of water. Two 47 X 24 X 29 cm glass aquaria were set up with approximately 2 cm of sand, 2 rocks (approximately 15 cm in length), and continuously flowing seawater. Superglue was used to apply small identification tags to the outside shells of *L. fragilis*. Aquaria #1 (*L. fragilis* A-E and #1) and #2 (*L. fragilis* F-J) contained *L. fragilis* with normal and

shortened tentacle length, respectively. Tentacles were shortened to half the original length using dissecting scissors and trimmed every 3 days to maintain tentacle size.

Day observations were conducted from November 3, 1999 to November 10, 1999 from approximately 9:00 am to 10:00 am. Night observations were conducted from October 28, 1999 to November 8, 1999 from 8:00 pm to 9:00 pm. A 40-watt red light was used to observe behavior at night and faced away from each aquaria to reduce the amount of light exposure. The activities of *L. fragilis* for both day and night observations were determined by personal observations during 30-minute observational period of each aquaria. Table 1 summarizes *L. fragilis* behaviors during observational periods. A data sheet was used to record the amount of time spent at each behavior.

**TABLE 1.** *Lima fragilis* behaviors.

BEHAVIORS	DESCRIPTION
MOVING	Moving from one location to another in middle of aquaria
NOT MOVING	Stationary in middle of aquaria
FILTER FEED	Stationary in middle of aquaria exposing 4 filters
SIDE-MOVING	Moving along side of aquaria
SIDE-NOT MOVING	Stationary on side of aquaria
SIDE-FILTER FEED	Stationary on side of aquaria exposing 4 filters
CORNER-MOVING	Moving in corner aquaria
CORNER-NOT MOVING	Stationary in corner of aquaria
CORNER-FILTER FEED	Stationary in corner of aquaria exposing 4 filters
AT ROCK-MOVING	Moving within 0.5 cm of rock
AT ROCK-NOT MOVING	Stationary within 0.5 cm of rock
AT ROCK-FILTER FEED	Stationary within 0.5 cm of rock exposing 4 filters
BURROWED	Completely under rock
ON TANK	Stationary on side or corner of aquaria certain distance above bottom
JUMP	Upward movement across aquaria by clapping shell (swimming)
TENTACLES OUT	Tentacles completely extended outward
TENTACLES RETRACT	Tentacles receded inward

*Experiment #3: Behavior in Presence of Predator (O. cyanea)*

Four *O. cyanea* were collected at the University of California at Berkeley's Richard B. Gump South Pacific Biological Research Station in Moorea, French Polynesia. *O. cyanea* were placed into 4 separate 47 X 29 X 24 cm glass aquaria with approximately 2 cm of sand and continuously flowing seawater.

Each *O. cyanea* was fed 1 *L. fragilis* per day for 8 days at approximately 3:00 pm. *O. cyanea* - *L. fragilis* interactions were determined by personal observations during 10-minute observational period. A data sheet was used to record the behavior and interaction between *O. cyanea* and *L. fragilis* (See Table 1 for behaviors).

*Experiment #4: Behavior in Presence and Absence of a Rock*

*L. fragilis* were collected at the University of California at Berkeley's Richard B. Gump South Pacific Biological Research Station in Moorea, French Polynesia. One 47 X 29 X 24 cm glass aquarium with 1 rock (approximately 14 cm in length) was used to determine the activities of 10 *L. fragilis* with normal and shortened tentacles by personal observations. Tentacles were reduced by half the original length using dissecting scissors and trimmed every 3 days to maintain shortened length. Superglue was also used to apply small identification tags to the outside shells of *L. fragilis*.

These experiments were conducted from October 14, 1999 to November 10, 1999. *L.*

*fragilis* were individually placed on opposite side of the aquarium from the rock for 5-minute observational period. These experiments were repeated in the absence of the rock. *L. fragilis* behaviors were determined by personal observations. A data sheet was used to record the amount of time spent at each behavior in the presence and absence of a rock (See Table 1 for behaviors).

## Results

### Habitat Distribution

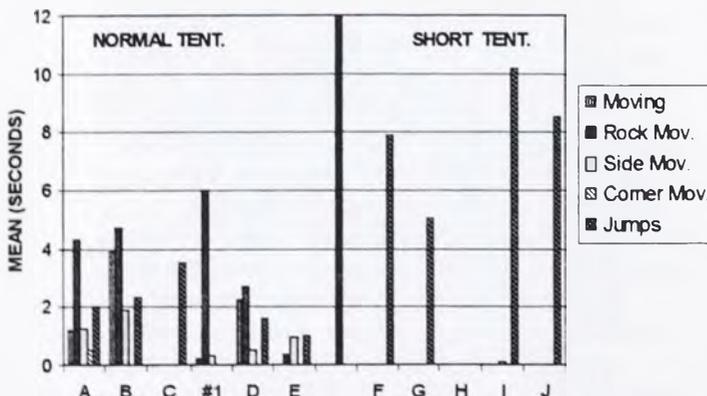
Haapiti transects resulted in 4.5 *L. fragilis* per 100 m<sup>2</sup> and 9 *L. fragilis* found out of 211 rocks turned over. Depths of *L. fragilis* found ranged from approximately .36 m to .77 m.

### Day vs. Night Activity

*L. fragilis* were not active during the day. Normal and shortened tentacles were found to be active at night (Figure 2). Two-sample t-tests were performed assuming unequal variances on each individual behavior (moving, at rock moving, side moving, corner moving, and jumps) on *L. fragilis* with normal and shortened tentacles. Overall, *L. fragilis* with normal tentacles were more active, excluding jumping behavior, at night than *L. fragilis* with shortened tentacles ( $p \sim 0$ ). However, *L. fragilis* with shortened tentacles jumped more than *L. fragilis* with normal tentacles ( $p < 0.046$ ).

Pearson correlation matrix was constructed for day and night activity. Day activity had strong positive correlations between at rock not moving and tentacle retraction ( $r = 0.533$ ) and at rock filter feeding and tentacle retraction ( $r = 0.536$ ).

Figure 2. Mean Time (seconds) of Individual Night Activity

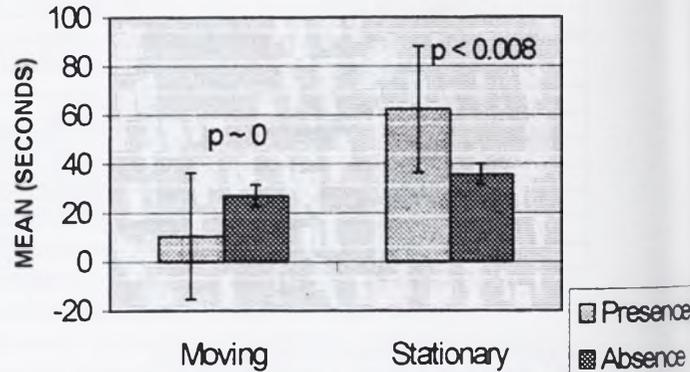


### Behavior in Presence of a Predator (*O. cyanea*)

*L. fragilis* behavior in the presence and absence of *O. cyanea* (Figure 3) was analyzed using paired sampled t-tests assuming unequal variances. When *O. cyanea* was present *L. fragilis* spent more time stationary (not moving and filter feeding) than moving ( $p \sim 0$ ). In the absence of *O. cyanea*, *L. fragilis* spent more time moving than in the presence of *O. cyanea* ( $p \sim 0$ ). When *O. cyanea* was present *L. fragilis* spent more time stationary than in the absence of *O. cyanea* ( $p < 0.008$ ). However, in the absence of *O. cyanea*, *L. fragilis* spent approximately the same amount of time stationary and moving ( $p < 0.055$ ).

Pearson correlation matrix was conducted to determine the correlation between *O. cyanea* eating and *L. fragilis* behaviors. A strong negative correlation was found between *O. cyanea* eating and tentacles out ( $r = -0.737$ ,  $r = -0.987$ ,  $r = -0.995$ , and  $r = -1.000$ ).

Figure 3. Mean (seconds) Activity of *L. fragilis* in Presence & Absence of *O. cyanea*

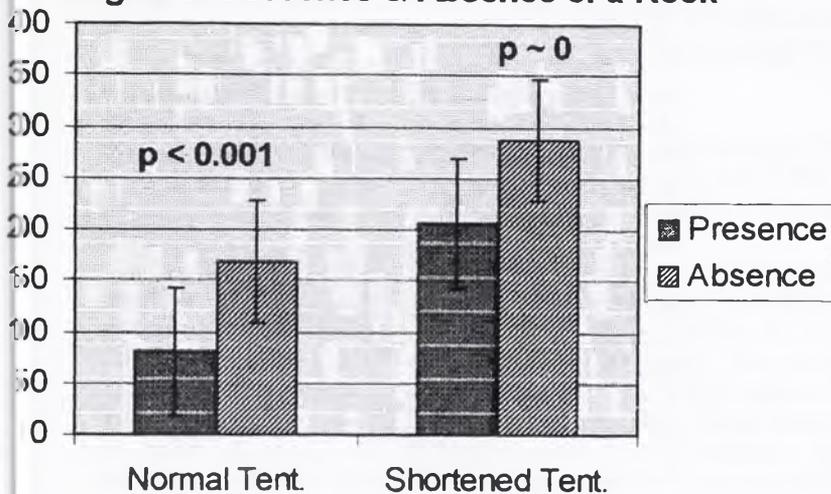


### Behavior in Presence and Absence of a Rock

Two-sample t-test was performed between all *L. fragilis* behavioral activities (excluding any behavior involving rock) in the presence and absence of a rock as well as *L. fragilis* with normal and shortened tentacles (Figure 4). *L. fragilis* with normal and shortened tentacles in the presence of a rock spent less time at behavioral activities than in the absence of the rock ( $p < 0.001$  and  $p \sim 0$ , respectively). However, overall *L. fragilis* with shortened tentacles spent more time at behavioral activities,

regardless of the presence or absence of the rock, than *L. fragilis* with normal tentacles ( $p < 0.055$ ).

**Figure 4. Mean (seconds) Activity of *L. fragilis* in Presence & Absence of a Rock**



## Discussion

The results from this study suggest that predation plays an important role in both habitat distribution and *Lima fragilis* behavior. The distribution of *L. fragilis* was low in density and abundance. These low numbers may be due to heavy predation on *L. fragilis* within their habitat. Possible predators may include octopus, carnivorous fish, crabs and sea stars.

*L. fragilis* were cryptic during daylight hours, usually remaining burrowed under rocks. When *L. fragilis* were not burrowed under rocks, they were found tightly nestled to a rock with their tentacles retracted. This suggests that *L. fragilis* use rocks for protection from possible predators that may forage during the day. Furthermore, *L. fragilis* were more active at night suggesting that the threat of possible predation must lessen.

*L. fragilis* were found to exhibit increased jumping behavior when their tentacles were shortened. This was found to be true only during nighttime hours. The increase in jumping behavior of *L. fragilis* with shortened tentacles may be due to the inability to generate rowing movements with their tentacles (Gilmour, 1967). In addition, jumping or swimming only required clapping of the shells together to create a driving force of water currents that lifted *L. fragilis*

upward (Gilmour, 1967). Whereas *L. fragilis* with normal tentacles were able to produce both clapping and rowing movements that enabled them to spend more time moving along the bottom of the aquarium. It is likely that swimming (jumping) can act as an escape reaction from possible predation. Further, shortened tentacles resulted in more limited types of movements which may make *L. fragilis* with shorter tentacles more susceptible to predation.

In the presence of *O. cyanea*, *L. fragilis* were less active and spent more time stationary. This suggests that *L. fragilis* sensed the presence of *O. cyanea* possibly due to the presence of eyes and dermal photoreceptors similar to *L. scabra*. Therefore, in order to reduce the chance of being eaten, *L. fragilis* decreased the amount of movement and became submissive. Although Gilmour (1967) found that *L. hians* could autotomize and make itself distasteful to predators, this same behavior was not apparent between *L. fragilis* and the predator *O. cyanea*. *L. fragilis* with tentacles out appeared to have no defensive mechanism against predation of *O. cyanea* and were consumed regardless if tentacles were out. It is even possible that the tentacles attracted *O. cyanea* to *L. fragilis*, thus promoting, rather than preventing predation.

In the presence of a rock *L. fragilis* were less active, whereas in the absence of a rock *L. fragilis* were more active, regardless of normal or shortened tentacles. *L. fragilis* may increase their activity in the absence of a rock in order to search for rocks to burrow under and gain protection. Thus, it is possible that *L. fragilis* can sense the presence of a rock due to the presence of eyes and dermal photoreceptors thereby decreasing its activity. In the presence of a rock *L. fragilis* with shortened tentacles were more active than *L. fragilis* with normal tentacles. The increase in activity of *L. fragilis* with shortened tentacles suggests that possible damage may have occurred to the eyes and photoreceptors, therefore, impairing the ability of *L. fragilis* with shortened tentacles to sense objects, such as rocks, in the surrounding environment. It is also possible that since *L. fragilis* with shortened tentacles has limited types of movement, it was less efficient at getting to the rock and spent more time moving.

## Conclusions

Predation was found to be an important factor in the distribution and behavioral activities

of *Lima fragilis*. It was demonstrated that *L. fragilis* is low in density and non-active during the day, possibly due to predation. There was more activity during the night suggesting that the chance of predation decreases at night. The clapping and rowing movements seem to enable *L. fragilis* to swim freely in order to escape potential predators. Evidence has been shown that *L. fragilis* has no apparent defense mechanism against the predation of *Octopus cyanea*, and will be consumed regardless of the tentacles. *L. fragilis* were also able to sense the presence of *O. cyanea* as well as rocks within their surrounding environment, indicating the possibility of eyes and dermal receptors similar to *Lima scabra*. Further studies of *L. fragilis* should focus on the anatomy and histology of the tentacles to show any defense adaptations as well as identifying possible sensory eyes or dermal photoreceptors.

## Acknowledgements

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# Banana Cultivation: The Agronomic Impact of the Insect Pest *Cosmopolites sordidus* in Moorea, French Polynesia

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**ABSTRACT.** *Cosmopolites sordidus* (Order: Coleoptera, Family: Curculionidae) is a major insect pest found across the globe in all regions of banana cultivation except for Egypt, Israel, and Hawaii, capable of deforming, stunting, or even preventing fruit growth and production. This damage is of great concern to Polynesians who regard bananas as an important traditional food crop.

This study contains two parts: 1) an interview and on-site survey of eight different banana growers, and 2) an insect survey intended to monitor the pest population using pit-fall traps and sticky traps comparing healthy and weevil affected trees at two sites under two different pest management regimes. The first site, in which no pesticides are applied, is an inter-cropped hillside plantation surrounded by a mixed forest near Cook's Bay. The second site, at which pesticides (Pyrethrine and Carbophuron) are applied, is a monoculture plantation at the Opunohu Valley Agricultural School. The insect traps showed that there was no significant difference in species abundance or species richness between healthy and affected trees within each site or between the two sites. Of the main banana varieties grown, the non-traditional hybrids are least affected by the pest, while the traditional varieties, notably the Maohi, Puruini, Hamoa, and Fe'i, are most affected. 75% of the interviewees reported a decline in productivity, 12.5% reported no change, and the remaining 12.5% reported an increase due to improved cultivation techniques. Five of the eight interviewees used pesticides and others only used cultural pest management methods such as crop rotation, paring and soaking shoots in salt water before planting. All interviewees sold some percentage of their crop (ranging from 20-100%) and all households had other forms of income, whether it is generated from a different agricultural product or employment in the public sector or private industry.

Key words: banana cultivation, pesticide, weevil, pest management

## Introduction

### History

Since the arrival and settlement of early Polynesians to the South Pacific islands approximately two thousand years ago, bananas have been regarded as an important traditional food crop of what is today known as French Polynesia (Purseglove, 1972). Thought to have originated in Southeast Asia, bananas were brought by the Polynesians to the South Pacific where they reached maximum importance in Tahiti (Purseglove, 1972). Many of these traditional varieties of banana, such as the cooking plantain, Fe'i or *Musa Troglodytarum*, are still cultivated by local growers and consumed by local inhabitants (Saquet, 1996). These traditional varieties are special and unique from those cultivars (i.e. the Gros Michel and Cavendish) commercially grown by United Brands, Castle and Cooke, and Delmonte (which control over 60% of global banana trade) (Bandou, 1994). Unfortunately, banana cultivation in French Polynesia is threatened by the damage caused by three main pests: nematodes, a fungus (*Cercosporriose*), and the insect pest, *Cosmopolites sordidus*. This study focuses solely on the impact of *Cosmopolites sordidus*.

### Biology of the Pest

The insect pest, *Cosmopolites sordidus* (Germ.), a weevil (Order: Coleoptera, Family: Curculionidae), attacks plants in the Musaceae family, most notably the banana. The black adult is approximately 10-12 mm long, with a long recurved sucking mouth part. The female adult, which can live up to 2 years and lay up to 100 eggs, drills a hole in surface of the banana corm where she deposits her eggs. Once the eggs hatch, the larvae eat tunnels through the corm and pseudo-trunk of the banana tree. The larval stage lasts up to 100 days. In effect, these tunnels serve as ports of entry for a wide range of opportunistic pathogens including other insects, bacteria, or fungi (Hammes, 1986). If the damage is extensive, it can cause the production of a deformed/dwarfed banana bunch or even prevent the banana tree from producing an inflorescence at all.

### Pest Impact

Agricultural insect pests have the potential to significantly alter a culture by changing the landscape, diet, and economy of a particular region. The insect pest, *Cosmopolites sordidus*, the banana weevil, is found across the globe in all regions of banana cultivation except for Egypt, Israel, and Hawaii (Hammes, 1986). This study focuses

primarily on banana growers. The objectives of this study were to describe physical and social phenomena regarding banana cultivation, including the agronomic status of the insect pest, *Cosmopolites sordidus*, and pest management methods used in Moorea, French Polynesia.

## Methods and Materials

### Study Sites

The study was conducted on Moorea, French Polynesia, a mid-plate volcanic island approximately 1.8 million years old, located in the South Pacific Ocean at 17° 30' S and 149° 50' W.

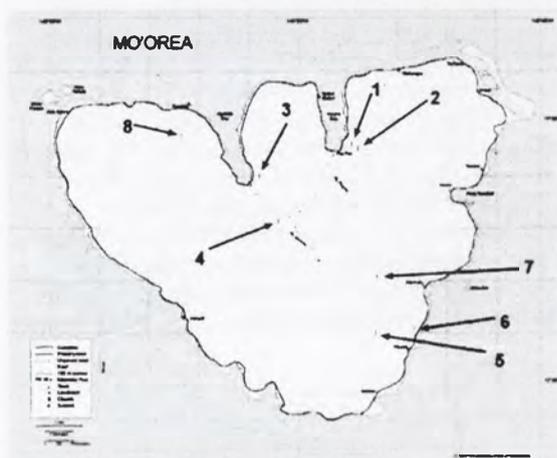


Figure 1. Map of Study Sites

### Interviews

With the help of a French/Tahitian translator, personal interviews and on-site surveys were conducted with banana cultivators from 12 October to 12 November 1999 at eight different sites across the island (Figure 1). Using a hand-held GPS unit, coordinates were determined for each of the sites (Table 1). Using the outline of an extensive questionnaire, physical, biological, and socio-economic information was collected from banana cultivators (Table 2).

Table 1. GPS Coordinates of Study Sites

Site #	Coordinates
1	17° 30' 25" S 149° 48' 55" W
2*	17° 30' 34" S 149° 48' 51" W
3	17° 31' 02" S 149° 50' 45" W
4*	17° 31' 56" S 149° 50' 29" W
5	17° 34' 05" S 149° 48' 22" W
6	17° 33' 46" S 149° 47' 36" W
7	17° 32' 54" S 149° 48' 26" W
8	17° 30' 19" S 149° 52' 21" W

\* Sites of Insect Survey

Table 2. Banana Grower Questionnaire

- 1) Name of owner
- 2) Locality (GPS and directions from Gump station)
- 3) Soil type and other geographic notes (i.e. slope, elevation, aspect)
- 4) Water availability ( irrigate or rain-fed?, by a stream?)
- 5) Surrounding vegetation
- 6) Notes on method of cultivation (i.e. monoculture plantation, mixed home garden, etc.)
- 7) Varieties Grown: Area devoted to each variety or Number of trees of each variety
- 8) Land History:
  - How long have you been growing bananas?
  - How have the number of varieties and types changed?
  - What is the change influenced by? (i.e. pests, prices, personal preference)
  - Productivity (measured in Kg. or bunches) (Have you sensed a change? when?)
- 9) Social/ Economic Implications:
  - Do you grow them for personal consumption or for sale?
  - % for personal consumption:
  - % sold:
    - \* where?
    - \* how often?
    - \* at what price?
    - \* other sources of income?
- 10) Do you have a pest problem? If so, affecting what varieties?
- 11) Symptoms (what does it attack), Disease, Pest (lifecycle, timing, etc.)?
- 12) For how long have you been affected by the pest problem?
- 13) Do you use any methods to try to control the pest problem? What are they?
- 14) Do you (and have you ever) used chemical pesticides?
  - Name of product
  - Frequency of use
  - Amount used

### Insect Surveys

An insect survey was conducted at two of the sampled sites. One site was the monoculture banana plantation of the Opunohu Agricultural School, located in the Opunohu Valley (Site #4 in Figure 1). At this site the pesticides Pyrethrin and Carbofuron were used to manage the presence of *Cosmopolites sordidus*. The second site was a polycultured hillside plantation of a private individual, Mr. Moana Maono in which no pesticides

were used, although *Cosmopolites sordidus* was present (Site #2 in Figure 1). Both sites were rain-fed and located near a running fresh water stream.

At each site, six trees were sampled. Three of the sampled trees were "Healthy" and the other three sampled trees were "Affected." In order to truly know if a tree is affected by *Cosmopolites sordidus*, the tree must be chopped down and the corm examined for damage caused by larvae. Since this process kills the tree, many banana growers are not willing to examine the tree until they have harvested the fruit. Therefore, by recommendation of a Tahitian entomologist outward features were used to define "Healthy" and "Affected" banana trees (Putoa, 1999). Features typical of vigorously growing trees, such as having a standard sized banana bunch and a thick pseudo-trunk, defined "Healthy" trees. "Affected" trees were defined as having compromised growth and malformed inflorescence, for example thin psuedo-trunks, short banana bunches, and small fruits.

Four uniform pit-fall traps, each with a mouth diameter of 8.0 cm and a volume capacity of approximately 250 mL, were placed 0.5 meters from the base of the pseudo-trunk, approximately equidistant from each other around each sampled tree. The pit-fall trap was laid so that the lip of the pit-fall trap was even with the surface of the substrate to allow insects to be caught. Each pit-fall trap was filled with 50 mL of soapy water to prevent insects from escaping once they had fallen into the trap. The pitfall traps were collected after a 24 hour period. Three 24 hour periods of pitfall traps were collected and analyzed.

Sticky traps were also set up at both pesticide and non-pesticide sites. Around the psuedo-trunk of each tree, one meter above ground level, a piece of 5.0 cm wide duct tape was wrapped around the circumference of the tree with the sticky side facing out and left for a 24 hour period. Due to unforeseen difficulties, only one full day of data on sticky traps was collected and analyzed.

The purpose of the insect survey using pit-fall and sticky traps was to determine the effect of pesticide use on insect populations, especially on the insect pest *Cosmopolites sordidus*.

## Results

### Part I: Interview Findings

All of the eight banana cultivators interviewed reported *Cosmopolites sordidus* a pest problem in their plantations and the majority of interviewees cited it as a major cause for decreases in overall fruit productivity (Figure 2). The farmers primarily grew "traditional" banana varieties

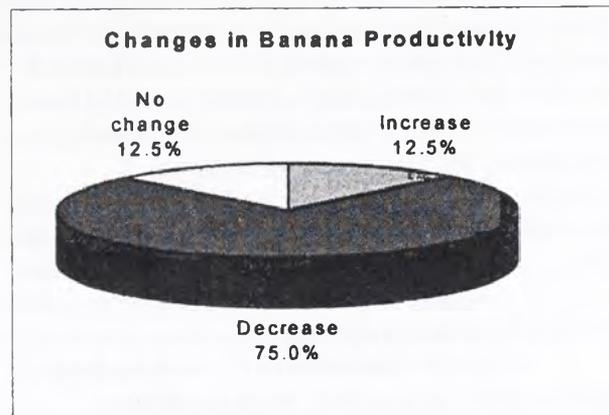


Figure 2. Changes in Banana Productivity

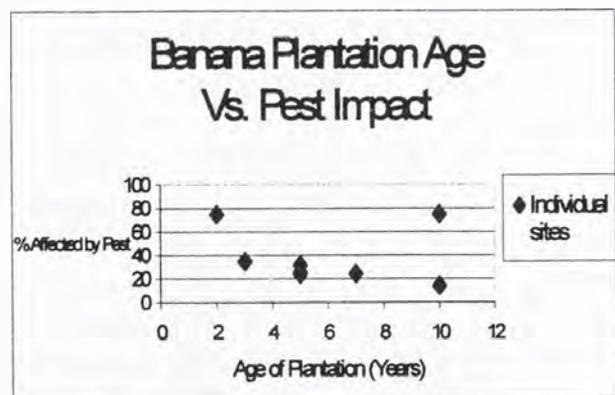


Figure 4. Plantation Age Vs. Pest Impact

(Table 3). Traditional banana varieties were more affected by *Cosmopolites sordidus* than the hybrid varieties (Figure 3). No significant relationship between plantation age and level of pest impact was found (Figure 4). Five of the eight banana growers interviewed used chemical products/pesticides such as used motor oil, Carbophuron, Pyrethrine, Phenamiphos, Isophenphos, and Lindane for pest management. Three of the eight growers did not use pesticides due to health and environmental concerns and/or lack of what they considered reliable pest management advice. Pest impact at sites that used pesticides was greater than sites that did not use pesticides (t-test: t-stat=2.33, p=0.03) (Figure 5).

Table 3. Banana Varieties Grown

Main variety	Sub-variety
Fei	
Hamoia	tei tei (tall)
Maohi	Hei, Pauratia, Tavara
Puruini	Fei, Rehu, Tahiti
Rima Rima	
Rio	
Yangambi	
Hybrids	

All of the interviewees sold some percentage of their banana crop ranging from 20% to 100%. All households had other sources of income, whether it was other agricultural crops or employment in the public sector or in private industry. All of the interviewees, except the agricultural school, maintained a percentage of their crop for personal/familial consumption ranging from 10% to 80%.

**Part II: Insect Survey Results**

Although specimens of *C. sordidus* were found in pitfall traps at both sites (site #2 non-pesticide site, and #4 pesticide site), the traps were

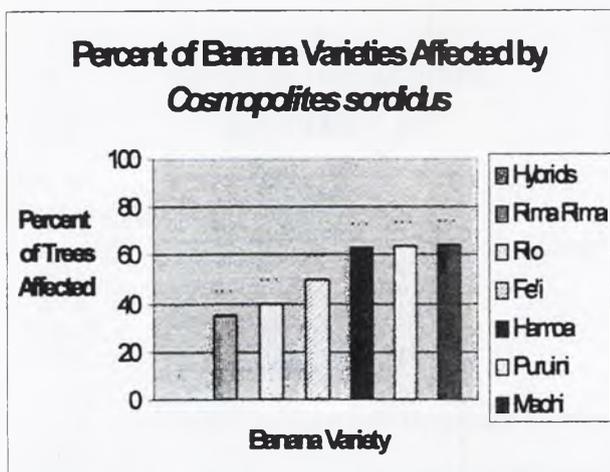


Figure 3. Banana Varieties Affected by *C. sordidus*

not adequate in reflecting the impact or prevalence of *C. sordidus* since only 3 specimens were captured. The difficulty experienced in trapping *C. sordidus* was consistent with monitoring difficulties documented by others (Jeger, 1996). However, the pitfall traps were analyzed for species richness and insect abundance. No significant difference was found in either species richness or insect abundance between the two sites (Figure 6 and Figure 7). No significant difference was found in either species richness or insect abundance between the healthy and affected trees within each site (Figs. 8, 9, 10, & 11).

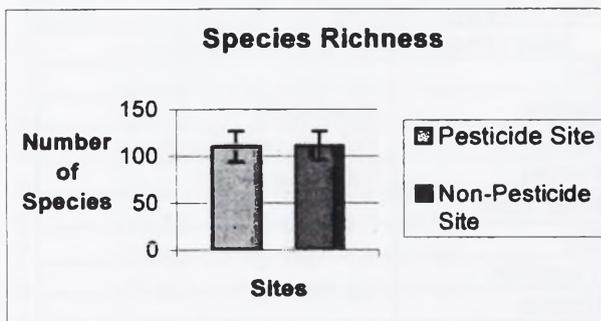


Figure 6. Species Richness

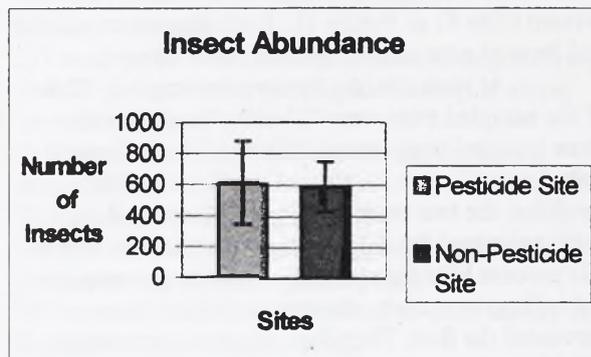


Figure 7. Insect Abundance

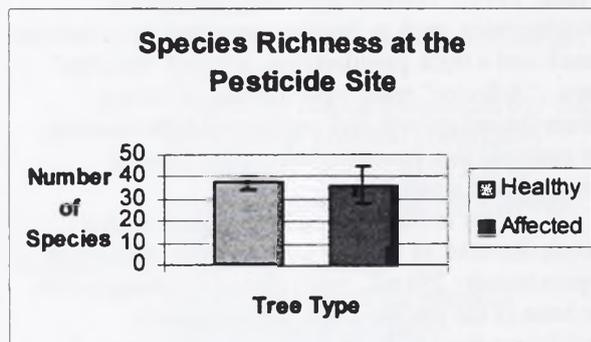


Figure 8. Species Richness at Pesticide Site

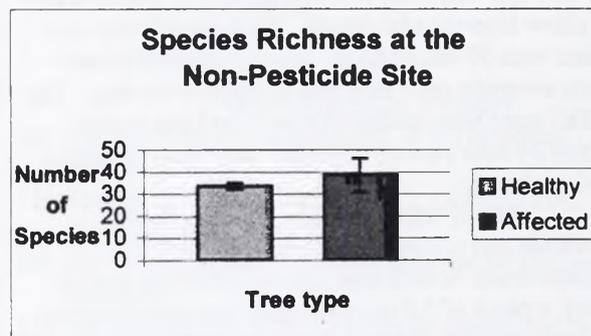


Figure 9. Species Richness at Non-Pesticide Site

**Discussion**

*Interview*

It is of significant concern that traditional varieties of banana are being more affected by *C. sordidus* than non-traditional hybrid varieties, although no variety has proven resistant to the insect pest. There was a lack of adequate information available to most of the growers regarding pest management methods. One of the growers was using Lindane, an illegal pesticide outlawed by the French government. Another grower reported applying used motor oil, a highly toxic substance, to control pests. Some of the growers interviewed expressed concern with pesticide use; others treated pesticide use as an unquestionable necessity.

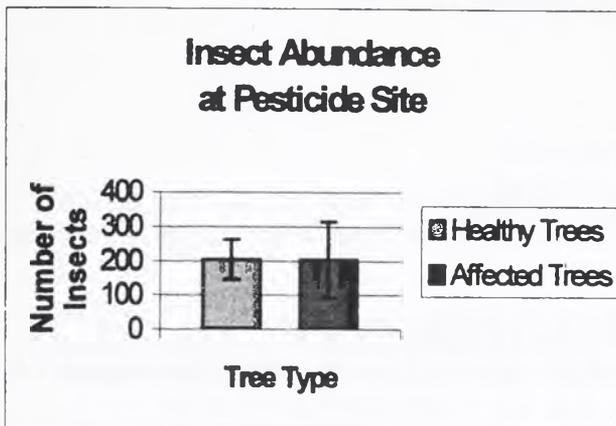


Figure 10. Insect Abundance at Pesticide Site

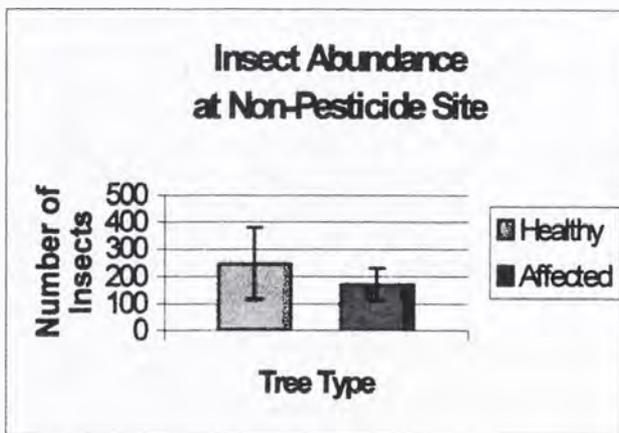


Figure 11. Insect Abundance at Non-Pesticide Site

I predict that there will be an increase in the use of pesticides that will lead *C. sordidus* to develop some level of pesticide resistance. This resistance is a possible explanation for the findings in Figure 5 which show that sites that use pesticides have a higher degree of pest impact than sites that do not use pesticides (Jeger 1996). A conservative alternative explanation for that finding is that the pest problem in those sites was so great that it facilitated the need for the growers to apply pesticides. However, there are alternative pest management techniques such as the use of biological control. Over 25 years ago, *Plaesus javanus* (Order: Coleoptera, Family: Histeridae) was introduced to French Polynesia by Harrison Smith and diffused by the Agriculture Service of Tahiti as a biological control agent against *C. sordidus* (Putoa 1999). It was considered successful, and another release and monitoring program should be instituted.

Another possible change in banana cultivation in Moorea is that growers will shift to planting varieties with greater resistance to the pest, i.e. non-traditional varieties. As traditional varieties become less abundant, their price will increase and

perhaps serve as a market incentive for a few to continue cultivating them to receive premium prices. Thus one sees how biological factors such as an insect pest problem can influence social/cultural/economic change.

It is a good economic strategy that the growers have other sources of income because, not only may employment in other sectors provide benefits such as health insurance, it makes them less affected by potential problems such as crop failure due to pest epidemics or other natural disasters.

#### Insect Survey

Although the pitfall and sticky traps did not catch adequate specimens of adult *C. sordidus* to monitor population size, the trapping of adults may still be useful in controlling pest populations. One method used in the 1950's to control pest populations was the use of allelochemical traps using freshly cut sections of pseudo-trunk placed on the surface of the soil to attract adults (Bandou 1994).

#### Conclusions and Recommendations

Banana cultivation in Moorea, French Polynesia is being seriously threatened by the presence of the insect pest, *Cosmopolites sordidus*. There is a serious need for an Agricultural Extension unit to be developed in Moorea in order to disseminate information about banana cultivation methods to reduce soil erosion, promote plant health and fruit productivity, and inform growers about effective pest management strategies as well as potential health hazards from agricultural chemicals. Low cost and low input cultural pest management strategies appropriate for helping resource poor farmers should be pursued as a top priority. Since the spread of *Cosmopolites sordidus* occurs primarily through infested suckers used for propagation, cleaning planting material by paring and/or hot/salt water treatment is recommended as an effective cultural control strategy against infestation by nematodes and *Cosmopolites sordidus* (Gold, 1998). Other cultural pest control methods and land management strategies such as crop rotation, clearing the land of infested material, and biological control must also be investigated.

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My deepest gratitude to my professors/instructors, class-mates, and friends (most of these roles were assumed by each and everyone) for scientific advice, a life-time worth of inspiration and food for thought packed into one beautiful semester. Special thanks to the Gump Station directors and staff; the CFPPA: Carole Corydon and Larry Teihoarii; the Lycee Agricole: Alexander Richard and Franny; entomologists: Rudolph Putoa, George Roderick, and

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# The Distribution and Predation of Tree Snails on Moorea, French Polynesia

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**ABSTRACT.** The tree snails, or arboreal gastropods, of Moorea have been the subjects of scientific study for over a century. A series of ill chosen introductions lead to the extinction, in the wild, of all Moorean species of the genus *Partula*. This study looks at the current status of the tree snail community and its chief threat *Euglandina rosea*.

The surviving populations of tree snails on Moorea consist of a handful of *Samoana attenuata*, a close relative of *Partula*, and widespread and relatively dense populations of micro-gastropods, *Elasmias peasianum*, *Liardetia normalis* and *Coneuplecta calculosa*. These micro-gastropods are distributed along an altitude gradient within the valleys of Moorea. The density of *Euglandina* on the island has dropped dramatically from the levels observed in the early nineties, so much so that one is hard pressed to find a single individual, even in ideal conditions. The question then arises, why the severe drop in the *Euglandina* population when there is plenty of prey to be consumed. The most obvious reason is that while there is plenty of food to maintain a reasonable population of *Euglandina* it would be impossible to maintain the density at the levels of the post-introduction population explosion. Even with this taken into account other factors must be contributing to the result in a population density this low. The shells of dead *Euglandina* collected are for the most part free of signs of predation by rats or birds. Disease and parasitism are possibly contributing but not major factors. Cannibalism, selection of members of their own species as prey items, seems to be occurring preferentially, due to the absence of any other animals within the optimal size class for prey. The fact that the micro-gastropods leave small, difficult to follow trails, and visit the ground infrequently makes the chances of a *Euglandina* tracking them into the trees unlikely.

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## Introduction

Oceanic islands provide an ideal natural laboratory for the study of evolution. Geographic isolation in conjunction with low competitive and predatory pressures allows for species to undergo rapid evolution and adaptive radiation. For these reasons, the tree snails of the island of Moorea have been the subjects of scientific study for over a century. Snails of the genus *Partula*, many species of which were endemic to the island, were studied for their unique banding patterns and chirality. (Murray 1993) The same characteristics that make islands ideal for evolutionary studies also make them vulnerable to invasion. A series of poorly thought out, deliberate introductions to the island's fragile ecosystem resulted in the destruction of this natural laboratory in the 1980s. (Civeyrel et al. 1996) The introduction of *Achatina fulica*, the giant African land snail, as a food crop, and the subsequent introduction of the predator snail, *Euglandina rosea*, as a biological control, lead to the extinction of *Partula* on Moorea. (Pearce-Kelly et. al. 1995) The surviving populations of tree snails on Moorea consist of a handful of *Samoana attenuata*, a close relative of *Partula*, and widespread and relatively dense populations of micro-gastropods, *Elasmias peasianum*, a 2-

5mm Tornatellinid snail, *Liardetia normalis* and *Coneuplecta calculosa*. 5-10mm diameter discoidal snails.

From preliminary observation, the density of *Euglandina* on the island had dropped dramatically from the levels observed in the early nineties, so much so that one was hard pressed to find a single individual, even in ideal conditions. (Coote 1999) The question then arose, why the severe drop in the *Euglandina* population when there was plenty of prey to be consumed. In this study multiple working hypotheses were proposed as reasons for the drop in *Euglandina* population density. The initial null hypothesis was that there was no drop in population density. The working hypotheses were as follows. 1) That there was not enough food, in the form of micro-gastropods to sustain a population of *Euglandina* and they starved. 2) That the *Euglandina* were being preyed upon by rats or birds. 3) The *Euglandina* were suffering from parasites or disease, micro-predation, which has to a small degree occurred in the Hawaiian population. (Hadfield et. al. 1993) 4) Widespread cannibalism, possibly as a result of 1, lead to a thinning of the ranks.

In order to test the first hypothesis, a sampling of micro-gastropod populations was

taken in order to determine average density, while at the same time expanding the study to look at their distribution and vegetation preference, which were previously undescribed. The null hypothesis for this portion of the study was that there would be a random distribution of the three species and that no altitude gradient or vegetation preference would be observed. The working hypotheses were as follows. 5) That the population density would be large enough to maintain a population larger than the observed population, but smaller than the population during the late 1980s and early 1990s. 6) That the species distribution would exhibit an altitude gradient with *E. peasianum* as the higher altitude component.

The final component to the study was the experimental component. In this portion live *E. rosea* were tested to see if they exhibited food choice. The null hypothesis was that they would exhibit no food choice. The working hypotheses were as follows. 7) The *Euglandina* would exhibit no preference for any of the micro-gastropods. 8) The adult *Euglandina* would exhibit preference for the juvenile *Euglandina* over the micro-gastropods or *Achatina fulica*.

#### Materials and Methods

For the sampling portion of the research data was taken from eleven locations on the island of Moorea, French Polynesia (17° 30' S, 149° 50' W). Three valleys, Opunohu, Afareaitu and Maatea, and one ridge top, between Vaiare and Pao Pao, were chosen to provide as wide a geographic range as possible while maintaining a reasonable degree of accessibility. Within these valleys, locations were chosen to fall within four distinct altitude ranges, greater than 300m, between 250m and 200m, between 150m and 100m and below 50m. At each of these locations, two or three, 5m x 5m plots were laid down in a haphazard manner. Multiple plots in each location were used in order to replicate the data for that location. The eleven locations as well as the number of plots for each location are noted on Fig. 1.

The plots were measured out using a 30m transect tape, a field notebook was used to assist with forming right angles. When available, flagging tape was used to mark the boundaries of the plot. When the flagging tape was not available plot edges were marked using fallen branches or articles of clothing. Within the plots, thorough searches of all vegetation were carried out, the species and vegetation type

found on was noted for each tree snail. In addition the leaf litter was searched for *Euglandina rosea*. All *Euglandina* shells within each plot were collected and returned to the station to be examined and measured.

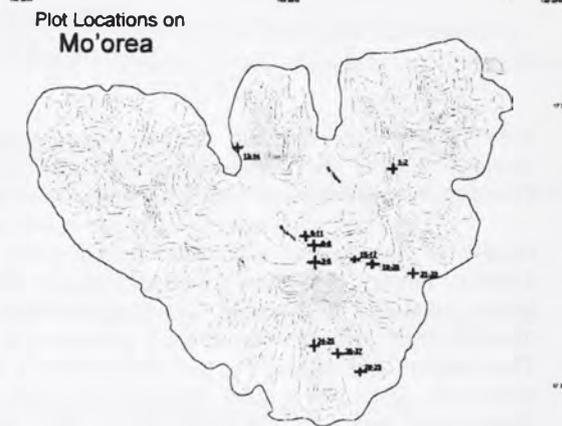


Figure 1. Plot Locations on Moorea

The *Euglandina* shells were examined for signs of predation, chipped lips, holes or scrapes, and measured along their longest dimension using a set of calipers, calibrated to the nearest millimeter.

The experimental portion of the research was carried out in the dry lab of the Gump Biological Field Station located on Cook's Bay, Moorea. (Fig. 1) Two Live *Euglandina rosea*, an adult of 44mm and a large juvenile 21mm, were used as test subjects. From this point on the adult will be referred to as *Euglandina* 1 or E1 and the juvenile as *Euglandina* 2 or E2. A large number of each of the arboreal micro-gastropod species as well as two *Achatina fulica* were also used. The snails were stored in a series of containers in the dry lab during the two weeks of trials. The *Achatina* and micro-gastropods were stored with food and the *Euglandina* were starved for a minimum of three days before beginning the trials.

For each trial a piece clean piece of .5cm thick plexiglass, measuring 60cm x 60cm, was placed on top of four 20cm high blocks. The blocks allowed the snail's path to be traced, using dry erase markers, without interfering with the snail or its slime trail. For the food choice experiments the *Euglandina* was placed on top of both trails, choice was determined by which trail the *Euglandina* followed at the Y junction. (Fig. 7) A large deviation, 30mm or more, from the trails was counted as a "No Track". 30mm

was chosen, as it is double the width of 15mm that *E. rosea*'s sensory lips cover. (Gerlach 1994 unpublished) Sides were alternated to cancel out possible left or right turn bias in the snail. In the equal width trials, cotton swabs were first covered in slime and then dragged across the plexiglass in the same Y pattern as in the previous trials. On the last day of experimentation the "final experiment" was performed, placing E1 and E2 in the same container to test for cannibalism.

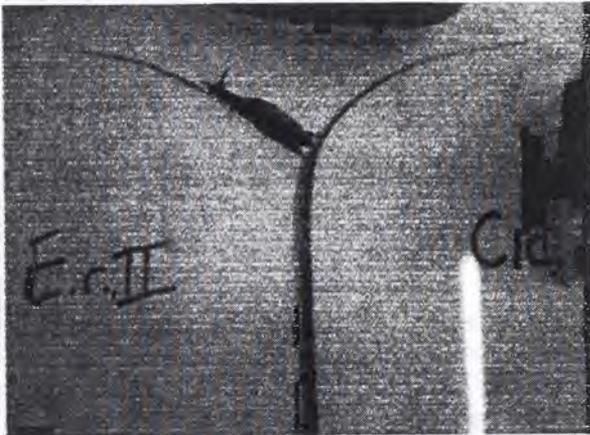


Figure 7. Snail Food Choice Apparatus

Table 1. Snails at each altitude

Altitude	Plot#	Number of Animals			
		<i>E. peasianum</i>	<i>C. callosa</i>	<i>L. normalis</i>	
>300m	1	45	4	7	
	2	23	7	0	
	3	36	0	5	
	4	35	10	4	
	5	18	0	3	
	mean		31.0	4.2	3.8
sd		11.5	4.38	2.59	
250-200m	6	21	20	18	
	7	14	22	16	
	8	10	18	12	
	15	23	18	17	
	16	0	17	13	
	17	7	14	16	
	24	20	24	18	
	25	3	19	19	
	mean		12.2	18.8	16.1
	sd		8.65	3.24	2.47
150-100m	9	16	18	25	
	10	6	24	10	
	11	0	15	12	
	18	0	0	0	
	19	12	20	28	
	20	0	12	13	
	28	4	25	22	
	27	10	19	24	
	mean		6.0	16.4	16.8
	sd		6.14	7.95	9.54
50-0m	12	0	0	28	
	13	0	3	21	
	14	0	0	10	
	21	0	9	19	
	22	0	0	0	
	23	0	10	21	
	28	0	15	30	
	29	0	15	15	
	mean		0.0	6.5	17.3
	sd		0.0	6.57	10.1

## Results

The data for the distribution portion of the study is summarized in Table 1 and illustrated by the graph in Figure 2. The data for the vegetation preference is summarized in Figure 3. Of the 956 *Euglandina* shells collected 32 showed some damage and 18 were less than 25mm in length. These quantities are represented graphically in Figures 4 and 5 respectively. The shells found in all of the plots appeared to exhibit a clumped distribution. This distribution was mapped for some of the plots. The distributions for two such plots are illustrated in Figures 6 and 7. The results of the *Euglandina* food choice between microgastropods experiments are illustrated in Figures 8 and 9 and the data collected from the *E. peasianum* vs. *A. fulica* vs. *E. rosea* following experiments are graphed in figures 10 and 11. No statistical analysis was performed for the food trials, as there were not enough test subjects to yield significant data. The result of the final experiment was that E1 consumed E2.

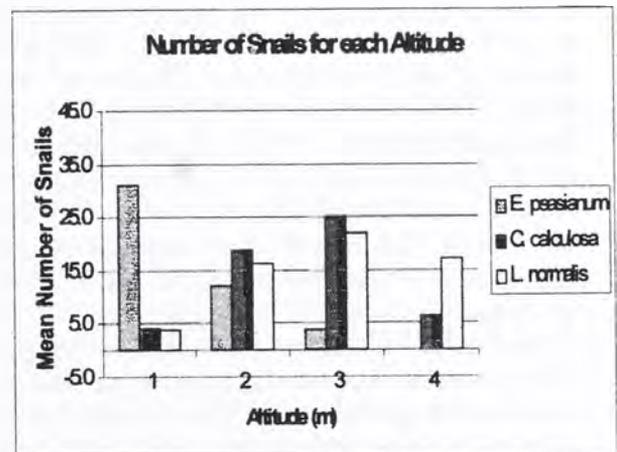


Figure 2. Number of Snails for each altitude

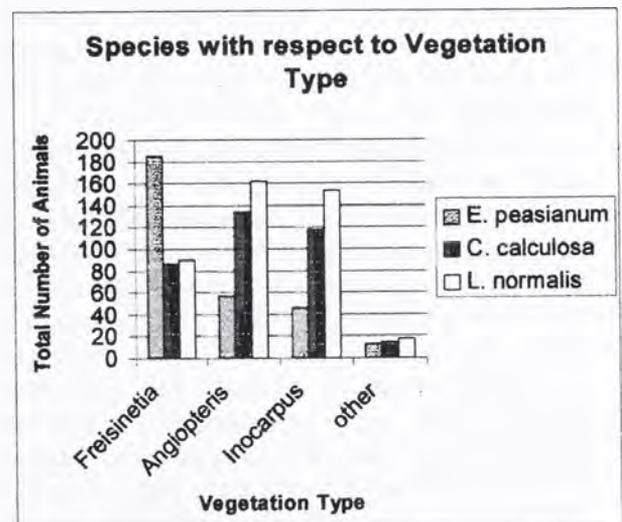


Figure 3. Species with respect to vegetation type

## Discussion

The results of the distribution data when analyzed using a one way ANOVA for each altitude yield F values greater than 1. The F values are 23.16, 2.807, 4.655 and 12.35 for the >300m, 250m-200m, 150m-100m and 50m-0m respectively. There were 14 degrees of freedom for the >300m set, 23 degrees for the middle two altitudes and 22 for the 50m-0m set. The F value for the 250m-200m set of 2.807 is not significantly greater than 1, i.e. the p value is not significant at the 5% level, and thus no significant difference exists between the numbers of the three species at this altitude. The F values of the other 3 sets show that there is significant data to reject the null hypothesis. The hypothesis that there is an altitude gradient is supported. Furthermore the graph in Fig. 2 clearly shows that the high altitude is dominated by *E. peasianum*. The graph, supported by the low F value then shows a range of overlap with no dominant species at 250m-200m, followed by *C. calculosa* and *L. normalis* sharing dominance at 150m-100m and finally *L. normalis* dominating the lowest altitude. The second part of the distributional study, food preference, is illustrated in figure 3. The graph of figure 3 would seem to show that *E. peasianum* prefers *Freisineta* and that *C. calculosa* and *L. normalis* show equal preference for *Angiopteris* and *Inocarpus*. The study does not take into account the greater presence of *Freisineta* at higher altitudes, and thus one cannot determine whether or not *E. peasianum*, when given equal access would have a preference for the other plants. The same can be said for the other two snails and their over all preference. The study however does show that *C. calculosa* and *L. normalis* have no clear preference for *Angiopteris* or *Inocarpus*, but they do prefer them to other vegetation.

The total number of snails counted, 1079, divided by the number of plots, 29, divided by the number of m<sup>2</sup> per plot, 25, yields the average population density of 1.49 snails per m<sup>2</sup>. This population of micro-gastropods, as predicted, should be large enough to maintain a visible population of *Euglandina*, but no where near large enough to maintain the population levels at the time of invasion. This is considering the fact that the population density estimates for *Partula*, an animal more than 30 times larger than the micro-gastropods are at least as high as 1.5 snails/m<sup>2</sup>. Thus the null hypothesis was in part rejected, there was a high

enough density of food that starvation alone was an unlikely answer to the near absence of *Euglandina* on Moorea.

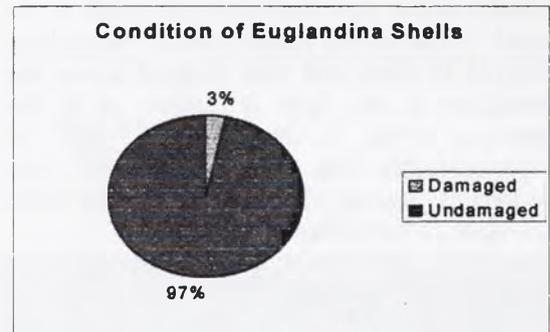


Figure 4. Shell condition

The next question that needs to be addressed is that of predation by rats or birds. From the 29 plots, 956 shells were collected and examined for damage that would indicate signs of predation, holes, chips etc. Of these shells less than 3% of them showed any sign of macro predation. (Fig 4) It seems therefore unlikely that macro predation has played a major role in the near wipe out of the *Euglandina* population.

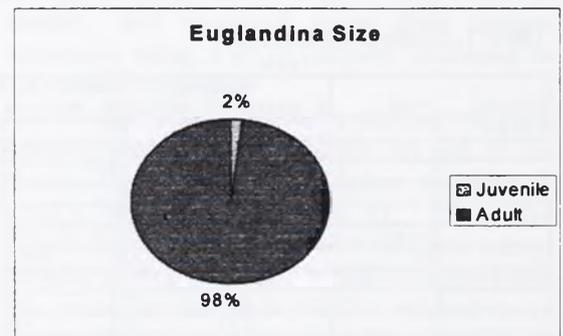


Figure 5. *Euglandina* size

Hypothesis three, that the *Euglandina* were falling victim to disease or parasites was also investigated using the collected shells as evidence. Although no sign limited signs of predation were observed on the shells, a strange clumped distribution of shells was observed during collection. (Fig. 6) It is proposed that this clumping may be a sign of healthy individuals tracking a diseased individual and upon coming in contact with that individual dying of the disease. Apart from this theory there is no concrete evidence from the study to support or refute the possible contribution of micro-predation.

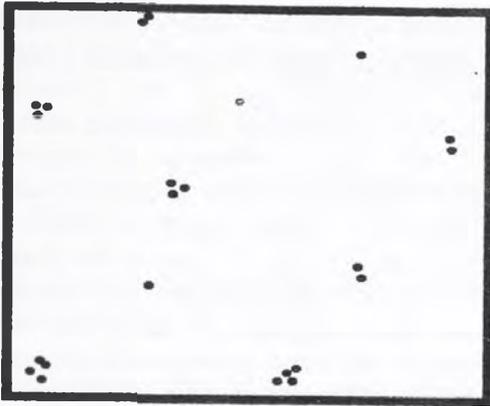


Figure 6. Distribution within plot

The clumping observed in figure 6 could also be used to support the hypothesis that cannibalism played a role in the population drop. Much as was described above, one snail could track another snail, one of those would end up being cannibalized. While that snail is digesting another snail could follow the same trail and eat that one, or possibly be eaten. This process could continue until four or five snails have been consumed, at which time the surviving snail would set off to find another victim. It is not proposed that it is impossible for this clumping to occur randomly, it is simply improbable. If not due to the factors above it is more likely the clumping could be artificially created by water flow or that more shells are found in places where they are less exposed to erosion, although neither of these was observed as an obvious cause.

Very few juvenile shells, shells under 25 mm were found in the plots, 18 total of 956 shells. Originally it was thought that this data along with the evidence from the fact that no juvenile shell was found in a clump might lead to further proof of cannibalism. The low numbers of juvenile shells, are most likely due to the fact that *Euglandina* do not begin to fully calcify their shells until they reach approximately 20mm in length, thus making juvenile shells far more susceptible to erosion. This merely means that the low number of juvenile shells does not provide significant evidence for cannibalism, it in no way detracts from the other evidence.

In the ten weeks spent on Moorea only two live *Euglandina* were found, thus the food choice experiments had to be pseudo-replicated and no significant data could be derived. The data is however strongly suggestive of certain theories and is supported by similar findings in larger studies. Neither of the *Euglandina* showed any obvious preference for one species of micro-gastropod over another. (Figs. 8, 9)

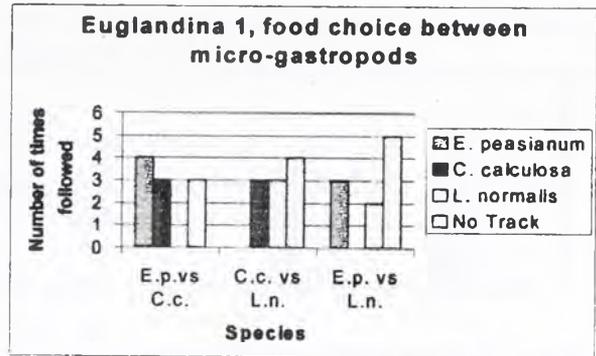


Figure 8. E1 food choice

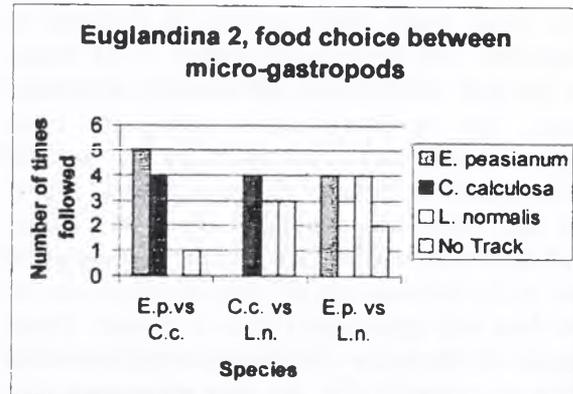


Figure 9. E2 food choice

E2 did however prove to have less No Track data than E1. This finding lead to the question that if the size of the snail matters in tracking, then possibly it is the size of the trail, which can be directly correlated to the size of the organism, that is important to the *Euglandina*, not the species of organism leaving the trail. Thus a second set of experiments were designed, in which the following preference was judged first using the organism's natural trail, and then using a cotton swab coated in slime to leave the trails, thus giving each trail equal width. In the first round of experiments E1 showed clear preference for E2 with a trail width of 6-10mm, little preference for the *A. fulica* (35mm) or the *E. peasianum* (2-3mm), and a large number of No Tracks. E2 showed a large number of No Tracks and a little greater preference for *E. peasianum* than did E1, smaller snail likes smaller trails. (Fig. 10)

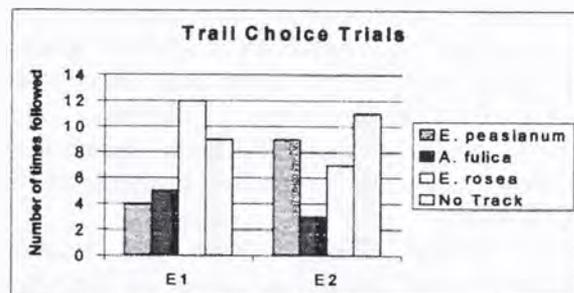


Figure 10. Species trail choice

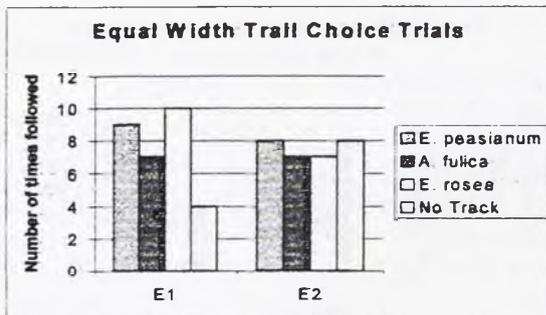


Figure 11. Equal width trail following

The equal width trials resulted in findings as expected. The tracking percentage of E1 rosea, as the trail widths were all uniform at around 7mm. The number of tracks per species once again does not seem to support any food choice with regards to species. E2 as expected, due to the trail width being slightly larger than ideal, had more No Tracks than E1, but fewer than it had in the previous set of trials in which two of the three trail types were 10mm or greater. Upon return to Berkeley examination of pertinent literature revealed that the data suggesting that trail width, and not species type is the major factor in *E. rosea*'s trail following behavior, and moreover that 10mm, just slightly more than the cotton swabs and E2's trail widths is the optimal tracking width for an adult *Euglandina* (Cook, 1985). Thus it can be stated that the hypothesis that E1 would prefer E2 over the other options is supported, more for the fact that it's trail happens to be of optimal width than of cannibalistic intent. Never the less this finding does make cannibalism a likely contributing factor to the low population numbers and the clumped distribution of shells.

### Conclusion

The final product of all the research can be summed up as follows. A small population of *Euglandina* persists on the island of Moorea, French Polynesia. This population is significantly smaller than it was in the early 1990s. This population decline can largely be explained by the drop in available food, as the population explosion drove their primary food source extinct. A populations of arboreal micro-gastropods exist with a fairly high density of 1.49 snails/m<sup>2</sup> in the valleys of Moorea. This density should be high enough to maintain a visible population of *Euglandina*. (Gerlach, 1994 unpublished)

Within these valleys the micro-gastropods are distributed along an altitude gradient with *E. peasianum* dominating at higher

altitudes, no dominance occurring at the 250m-200m altitude range, *C. calculosa* and *L. normalis* co-dominating at the 150m-100m altitude, and *L. normalis* dominating near sea level. No clear evaluation of vegetation preference among the micro-gastropods can be made, save the evident equal preference for *Inocarpus* and *Angiopteris* among the discoidal snails and the over all preference of *Freisineta*, *Inocarpus* and *Angiopteris* above all other vegetation for the micro-gastropods in general.

Collection and analysis of the shells of dead *Euglandina* failed to suggest that predation by rats or birds has played a major role in the low *E. rosea* population density.

It did however suggest through the strange clumped distribution of shells, that micro-predation, disease or parasitism, or macro-predation, in the form of cannibalism, were likely contributors.

The food choice experiments suggest that the *Euglandina rosea* preferentially track and thus eat other *Euglandina rosea* due to the fact that their trails are within the optimal tracking width. Whereas none of the other species of gastropod left on Moorea fall within the 10mm trail width range.

The arboreal micro-gastropod populations may higher than if *Euglandina* was preferentially tracking them. It is quite likely that what few *Euglandina* exist do not venture up into the trees much as they are likely feeding on terrestrial micro-gastropods and other *Euglandina* before following the few small trails up into the trees.

The status of this biological system on Moorea should be continually monitored as it could one day be as useful a tool to explaining the long-term effects of island invasion as it once was a tool for studies of evolution.

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hikes and smiles, all in all an exhilarating experience. Thank you my friends.

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# Reproductive Ecology Of *Metrosideros Collina* (Myrtaceae) Of Moorea, French Polynesia

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**ABSTRACT.** The plant *Metrosideros collina*, was studied to determine recruitment of seedlings in native populations. The first part of this research involved transects through different *Metrosideros* populations on the island of Moorea, French Polynesia in order to obtain data on the number of individuals in different size classes. The three populations that were surveyed all showed extremely low numbers of *Metrosideros* seedlings and juveniles in the understory.

The second part of this study examined four possible reasons for this low recruitment in *Metrosideros collina* populations. Conducting visitation studies of the *Metrosideros* flowers tested the first hypothesis, loss of pollinator. The honeybee was found to be a common visitor of the flowers and pollen removed from the anthers matched pollen found on the honeybee. The second hypothesis, which assumed that *Metrosideros* seeds were not viable, was quickly disproved by germination studies. The third hypothesis, allelopathy from *Dicranopteris linearis*, was investigated by applying leachate from live foliage, dead foliage and roots/rhizomes of *Dicranopteris* to *Metrosideros* seeds. This study did not prove statistically significant. The fourth hypothesis, which tested seedling shade intolerance in the dense *Dicranopteris*, was proved to be the most likely cause of low seedling recruitment in *Metrosideros* populations. Five different light treatments showed the highest germination occurred in filtered light. Light meter readings showed minimal light penetration through *Dicranopteris* cover. Young *Metrosideros* plants were found in areas of low *Dicranopteris* cover.

This study showed that in many mature *Metrosideros* populations there are limited seedlings and juveniles in the understory. These shade intolerant seedlings possibly require a large-scale disturbance to germinate and form a successive or new population.

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## Introduction

*Metrosideros collina* (Myrtaceae), puarata in Tahitian, is a native plant of Moorea, French Polynesia. *Metrosideros* is a genus that is found throughout the Pacific Islands, with a latitudinal range of more than 60 degrees (Carpenter 1976). *Metrosideros polymorpha*, which is considered to be a closely related species (Mueller-Dombois and Fosberg 1998) although no genetic analysis have been done, is the dominant canopy forming tree in Hawaiian rain forests (Stemmermann 1983). The Moorean *Metrosideros collina* does not grow to such heights, but does have a great deal of ecological as well as morphological plasticity. *Metrosideros collina* on Moorea has an elevational distribution from about 100 meters above sea level to the tops of many ridges and mountains including Mount Rotui at 898 meters. It appears to thrive on these sunny exposed sites. The plant grows as a tree in protected areas and has a more bushy form on exposed ridges. The leaves vary in shape and texture from round to ovate and pubescent to glabrous. The red bottlebrush flowers are similar to a *Eucalyptus* flower and arranged in an inflorescence. The fruit is a small dehiscent capsule with tiny (2-3 mm.) airborne seeds.

Island ecosystems are known to be more susceptible than mainlands to species decline and

extinction (D'Antonio and Dudley 1995). Often, island communities have a small percent of native species remaining. This makes these species precious assets because of their link to the past and importance to native ecosystems. For these reasons, it was worrisome when preliminary inspection into native *Metrosideros collina* forest revealed no young plants in the understory. There were no conspicuous seedlings or juveniles. The mature overstory plants did not appear to be recruiting which meant there were no plants waiting to become members of the successive population. Without any apparent regeneration, the future of these *Metrosideros* stands seemed unsure and the place of *Metrosideros* in many Moorean ecosystems might be threatened.

This paper describes research done with the intent to gain more information on the native populations of *Metrosideros collina* in Moorea. The first objective of this research was to further explore the observed lack of young *Metrosideros* by examining the demographic structure of *Metrosideros* in some of its native environments on Moorea. This would answer the question of whether or not native *Metrosideros collina* populations are recruiting.

The second part of this study examined possible reasons why *Metrosideros collina* might not be recruiting. I examined four possible hypotheses.



**Figure 1.** Topographic map of Moorea, French Polynesia. Map shows sites of observation and data collection of *Metrosideros collina*.

The first hypothesis is that *Metrosideros* has lost its pollinator. *Metrosideros* is generally thought to be a flower type that is pollinated by birds (Carpenter 1976). However, many native bird species on Moorea have gone extinct because of the introduction of predatory and competitive species, loss of habitat and predation by humans (Lobban and Scheffer 1997). It is possible that the original pollinator has gone extinct or declined and that successful pollination is no longer occurring.

The second hypothesis for why there is no recruitment is that the seeds of *Metrosideros* are not viable. The seeds of other *Metrosideros* species are known to have low fertility. Only 20% of the seeds of *Metrosideros polymorpha* of Hawaii are thought to contain embryos (Burton 1982). It is possible that there has been some ecological change or stress that has led the fruits to not produce embryos and hence have infertile seeds.

The third hypothesis is that allelopathy from the fern *Dicranopteris linearis* is inhibiting germination of *Metrosideros* seeds. *Dicranopteris* is found as the major understory component of *Metrosideros* forests or shrublands in Moorea. *Metrosideros collina* was never found to be growing without a *Dicranopteris* understory. *Dicranopteris linearis* (Gleicheniaceae) is a native climbing fern found throughout Polynesia (Russel et al. 1998). It forms dense thickets sometimes greater than two meters high in the understory. It is shade intolerant and

often found as a pioneer species in recently disturbed sites (Walker and Boneta 1995). These fern thickets may have deleterious effects on its associated species by producing allelopathic chemicals. These chemicals could inhibit the germination as well as growth of *Metrosideros* and be the reason for limited recruitment in the understory.

The last hypothesis for the low recruitment in *Metrosideros* stands is that the seeds are unable to germinate in the low levels of sunlight found beneath the dense *Dicranopteris* which is always associated with *Metrosideros*. If *Metrosideros collina* seeds are shade intolerant, like its associate species in Hawaii, then the seeds might not be receiving adequate light to grow and germinate beneath the *Dicranopteris*. This could explain the lack of recruitment in *Metrosideros* populations

The purpose of this study, then, was twofold: first to examine the population structure of *Metrosideros collina* to determine whether or not *Metrosideros* was recruiting, and second to address possible reasons why the population appeared to have no young plants and how this might effect the future of *Metrosideros collina* in Moorea.

#### Materials and Methods

This study was done between the dates of September 28, 1999 and November 20, 1999 in Moorea, French Polynesia. The study involved both laboratory and fieldwork. All lab work was done at

Gump Field Station in Cook's Bay, Moorea. The five field sites were chosen because of the presence of *Metrosideros collina* (Figure 1). At all five sites, type specimens of *Metrosideros collina* were collected and are now located in the University and Jepson Herbarium to be used as voucher and reference specimens. Work was done at the University and Jepson Herbarium to try and confirm the species was in fact *Metrosideros collina*. The Moorean specimens were compared with *Metrosideros* species from all over the Pacific. The high morphological variability found just amongst the Moorean plants made it difficult to positively identify the plant as *Metrosideros collina*. Historically, this has been the name of the Moorean species and it seemed very similar to the *Metrosideros collina* in the collection. It also appeared to be similar to the *Metrosideros polymorpha* of Hawaii. Until further information is obtained, this paper assumes the species found in Moorea is *Metrosideros collina*.

#### Population Structure Study

*Site 1.* Lower Belvedere. This site was located above the lookout spot, the Belvedere, in the Opunohu Valley of Moorea (17° 32' 34''S, 147° 49' 34''W). This population of *Metrosideros* was located on the ridge just south of the parking lot. The distinct population was ca. 140 individuals located on the top of the ridge and along a west-facing mountain slope. The overstory consisted mainly of *Metrosideros* trees as well as some *Hibiscus* and *Acacia*. The understory was dominated by a dense coverage of the fern *Dicranopteris linearis*, which varies from a meter to almost two meters in height. There was also *Stachys* and *Lantana* in the understory. At this site one belt transect was run along the top part of the ridge as well as another parallel transect along the hillside. Both transects were selected because of accessibility, which was limited in some areas by treefalls and heavy underbrush. The transects were five-meter-wide belts starting at the roadcut above the parking lot. The ridge transect ran along the flat part of the *Metrosideros* population above the parking lot. The hillside transect was three meters downslope of the main trail leading to Three Coconuts Pass. For each *Metrosideros* individual encountered within both transects, the diameter one meter above the base of the plant was measured (in inches, due to available diameter tape). Because there is no way of determining the age of the *Metrosideros*, diameter was used as a rough estimate of age (Gerrish and Mueller-Dombois 1984). The diameter was taken a meter above ground level because in many cases the thick underbrush made it much more difficult to get any measurements at the base of the tree. This information was useful to determine the number of plants in particular diameter size classes. If

the plant was smaller than a one meter in height, the plant was put in the smallest size class with the diameter taken at the base of the young plant and recorded separately. A thorough attempt to find all *Metrosideros* within the transect was made. At times it was difficult to search through the tangled mat of *Dicranopteris* for seedlings in the ground below, but every effort was made. Along with diameter, the presence of fruit and flowers on the sampled plants was noted.

*Site 2.* Upper Belvedere. This site was also located above the Belvedere lookout, but further up the trail towards Three Coconuts Pass (17° 32' 36''S, 147° 49' 31''W). This was treated as a distinct population of *Metrosideros* because of its physical separation from the first population by about 20 meters as well as a noticeable change of environment. The *Metrosideros* in this population had a great deal more epiphytic growth, and were larger trees that grew more densely. Once again there was a very thick *Dicranopteris* understory. This population of *Metrosideros* had ca. 78 individuals. The population was almost exclusively on the east side of the trail. The transect began three meters from the east side of the Three Coconut Trail and once again was five meters wide. The transect started at the large mango tree in the clearing along the trail and ran for 40 meters. Again the diameter and presence or absence of flowers and fruits was noted.

*Site 3.* Three Coconut Pass. This site was along the upper ridge at the termination of Three Coconuts Trail (17° 32' 56''S, 149° 50' 25''W). A population of ca. sixty *Metrosideros* stretch along this narrow ridge on either side of the trail. This plant community was dominated by a *Metrosideros* overstory as well as an understory of *Dicranopteris* and some *Lantana*. Measurements of diameter and fruiting/flowering were taken for all trees within about a meter and a half on either side of the trail. This sampling method was chosen with safety in mind because of a sharp drop-off on either sides of the trail, dangerously obscured by heavy *Dicranopteris* growth.

*Site 4.* Mount Rotui. This population of *Metrosideros* stretched all along the ridge of Mount Rotui starting about 150 meters above the end of the *Cassurina* grove and continued to the top of Rotui. No measurements were taken because of the danger of the drop-offs on either side of the trail, but observations were made.

*Site 5.* Haapiti Fire. This site (17° 33' 44''S; 149° 51' 58''W) was discovered at the end of the research term. It was an eight-year-old burn located behind the church in Haapiti. The burn site had heavy *Dicranopteris* growth in most areas with some larger *Acacia* trees as well as shrubby *Metrosideros*. No transects were done because of time constraints as well

as the high variability and size of the site. However observations were made as well as sampling of a population of younger *Metrosideros* that was found. Once again diameter (this time at ground level because many of the plants were not even a meter high), flowering/fruitletting as well as height of surrounding *Dicranopteris* was recorded.

#### *Pollination Studies*

In order to determine if *Metrosideros* had a successful pollinator, visitation studies of *Metrosideros* flowers were performed. These studies were done at the Lower Belvedere Site. Areas where I could observe a substantial number of *Metrosideros* flowers simultaneously were watched for fifteen-minute intervals. For every insect or bird that visited the flower, I estimated the total time at the plant, and how many flowers were visited. This was done eight different times over three days in early October. These studies were done when the sun was high and many insects appeared to be out. Further observations were made of pollinators on Rotui, at the Haapiti site, and at Three Coconuts, but no data was collected.

Anthers were collected from *Metrosideros* flowers to ensure that the flowers were producing pollen, and the pollen grains were examined under the microscope. A honeybee that was observed visiting various flowers was collected. Pollen was removed from the lower leg of the bee with tape and observed under a microscope.

#### *Seed Viability Study*

Seeds were randomly collected from the partially dehiscent fruits of various trees at the Lower Belvedere Site and Three Coconuts Pass Site. I conducted germination studies to ensure that the seeds were viable. The seeds were very small (about 3 mm); so to save time most studies did not involve actual counting of seeds. The seeds (about 50) were placed in two petri dishes (total about 100 seeds) between two paper towels and put in a north-facing window of the dry lab at the Gump Station. The petri dishes were watered every day until germination. Germination was considered to be when the radicle was clearly emerging from the seed coat. Because this study was only to see if the seeds would germinate under lab conditions, no percent germination was done at this time. The plants that germinated in this experiment were then transplanted into soil from the Lower Belvedere site and put in the north-facing window of the dry lab at Gump Station. I watered and monitored their growth for five weeks after the transplanting.

Three half-meter square plots were created at the Lower Belvedere site in the third week of the nine field weeks in Moorea. The three sites were picked for accessibility along trails and for different types of

overstory cover. At each plot there was at least a one meter high growth of *Dicranopteris*, which was cleared away along with the major rhizomes and roots. There was generally nothing else growing under the fern canopy. The soil was turned and tilled in order to have bare mineral soil. Seeds from fruits of nearby trees were sowed into each of these plots (about 1000 seeds in each plot). Plot One was in full sun with no overstory trees. Plot Two was in the shade with overstory trees, which let filtered sunlight reach the cleared area. Plot Three was in partial shade as well as on more of a slope. All three plots were monitored weekly to see if any seedlings ever grew in them.

#### *Allelopathy Study*

*Metrosideros* seeds were collected from opened fruit at the Lower Belvedere site, as was live *Dicranopteris* foliage, dead *Dicranopteris* foliage and *Dicranopteris* roots. This material was taken to the Gump Lab.

About 25 seeds were put between paper towels in each of 20 different petri dishes. These dishes were separated into four treatment groups with five replicates in each treatment. The first treatment was the control and was watered every day with tap water. The other three treatments were seeds watered with the supernatant after grinding up live foliage, dead foliage and roots/rhizomes with water. The roots/rhizomes and dead and live foliage were soaked in a bowl of water over night. The live and dead foliage were separately ground in the blender with 0.5 liter of water (from the soaking) and 0.5 liters of foliage. The roots were first ground up in the coffee grinder and then 0.25 liters of ground roots and 0.25 liters of water (from the soaking) were blended. The supernatant from all three of these solutions was extracted and placed in the refrigerator along with a cup of water for the control. Every day the petri dishes were watered with the specific treatment. The petri dishes were in the window of the dry lab and their positions were rotated daily. Every day the petri dishes were examined to see if any *Metrosideros* seedlings had germinated. This data was recorded.

After 25 days of observation the experiment was terminated. The total number of seeds in each dish along with the number that had germinated was recorded. An average of the five petri dishes (for each of the four treatments) was recorded. A one way analysis of variance with a Bonferroni correction was conducted to test the significance of differences in responses of *Metrosideros* seeds to different allelopathy treatments.

#### *Light Tolerance Study*

*Metrosideros* seeds were exposed to five different light treatments, in and around the Gump station lab, in

order to determine at what levels the seeds germinate the fastest and have the highest percent germination. Seeds were placed in between two paper towels in a petri dish and watered every day. Because of the small size of the seeds, varying numbers of seeds were placed within each petri dish but an average of about 150 seeds per dish was attained (the number of petri dishes in each treatment was not even either because of accidents during watering and counting). The first treatment was direct sunlight. Three petri dishes with *Metrosideros* seeds were placed directly outside the Gump wet lab, and received full sun for a good part of the day. All treatments were measured with a light meter on a sunny day at noon, and the full sun site received ca. 1400 fc. The next treatment was four petri dishes in the north-facing window of the Gump Lab, which received filtered sunlight throughout the day (about 300+ fc on a sunny day at noon). The third treatment, which received indirect light throughout the day, was three dishes located on the counter in the lab away from any windows (ca. 30 fc). The fourth light level was shade under a counter in the Gump Lab. Here again there were four petri dishes, which received about 10 fc of light during midday. The last treatment was four dishes in complete darkness in a drawer in the Gump lab.

After four weeks of observation, the experiment was terminated. The number of seeds in each petri dish was counted, as was the number of germinations in each dish. The percent germination for each dish was calculated, as was an average amongst the dishes in each treatment. These five mean values were then individually compared in T- tests assuming unequal variance.

Light level readings were also taken from the Lower Belvedere Site. Above and below *Dicranopteris* cover, measurements were taken in full sun at midday.

#### Other Data Collected

Seeds and capsules from fruits were collected at the Lower Belvedere Site. The number of seeds in ten different capsules was counted, and an average was calculated. Drawings were made of the fruit and inflorescence/infructescence.

Information about how *Metrosideros* seeds responded to fire was collected. A 2-inch layer of soil from the Belvedere was placed on a baking sheet lined with foil. *Metrosideros* seeds were sprinkled on top of this and another layer of soil was placed upon this. Dead *Dicranopteris* foliage was laid on top of the soil in a pile. The foliage was then lit on fire. It burned for about four minutes at a high temperature of 425° F as measured with an oven thermometer. I then removed seeds from the fire, noting whether they came from the middle of the sheet-which burned the most completely or along the edges. As many seeds as

possible were removed, though it was very difficult to find them amongst the ash and dirt. I divided the seeds into high-fire and low-fire groups and divided these into eight petri dishes, four of each. The seeds were put between paper towels, put in the sun of a north lab window, and watered every day. After three weeks I recorded percent germination of the seeds.

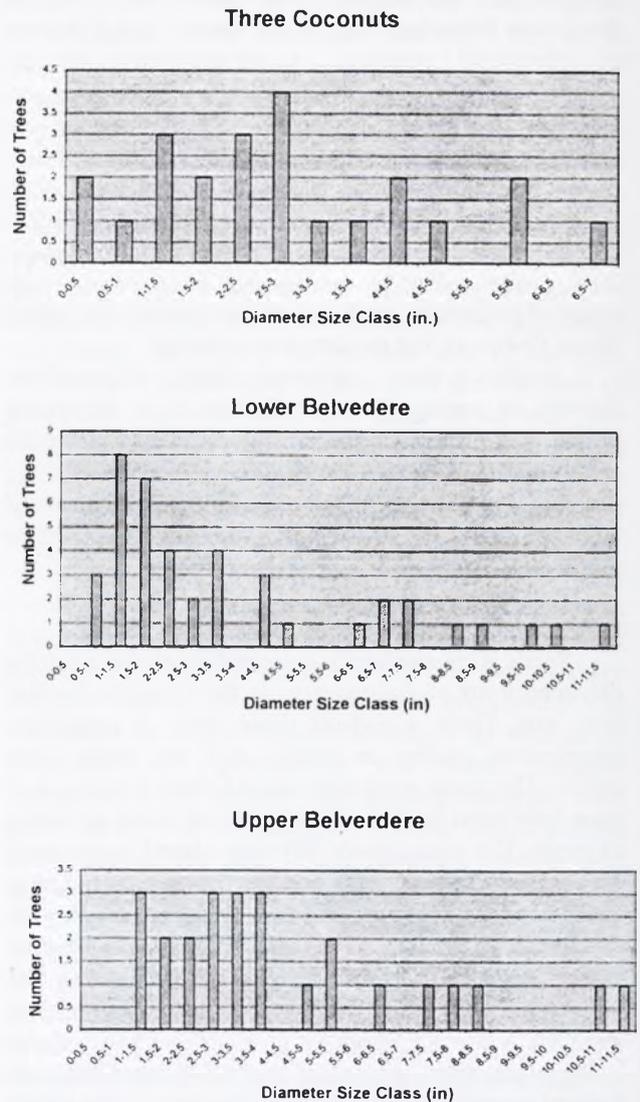


Figure 2. The number of *Metrosideros collina* per half-inch diameter class at three sites in Moorea, French Polynesia. These graphs show the lack of plants in the smaller diameter size classes-suggesting a lack of seedling recruitment.

## Results

### Population Structure

The diameters of *Metrosideros collina* at the Upper Belvedere, Lower Belvedere and Three Coconuts Pass sites all showed a distribution of diameters that was lacking young plants (Figure 2). The seedling and juvenile size classes are very underrepresented in all of the populations. Figure 2 shows the diameter distribution of sampled plants at the Three Coconuts site. Most of these plants have a diameter one-meter above the ground of one to three inches. These plants were mostly shrub-like and extensively branched. The two plants in the 0.5 inch diameter size class were found on the edge of a clearing at the top of Three Coconuts. The Lower Belvedere and Upper Belvedere graphs both show the limited numbers of smaller size class plants. At the Lower and Upper Belvedere Sites, no seedlings or juveniles were found in the underbrush. At the Upper Belvedere, no plants with an inch diameter a meter off the ground were found. At these two sites, an especially thorough search was conducted.

Observations were made on the climb up Mount Rotui. Once again there was a thick understory of *Dicranopteris* with a more shrubby *Metrosideros*. Although the ability to do a thorough search was hindered due to the danger involved, as much observation and searching as possible was done, and no seedlings or juvenile plants were seen. There did, however, seem to be a change in the physical appearance of the plants. Higher up on the ridge, there were fewer of the normal glabrous *Metrosideros* plants and more pubescent types. These pubescent types had much rounder leaves that were closer together on the stem. These plants also were not flowering nearly as much as the glabrous *Metrosideros*, which could be found growing adjacent to the pubescent forms.

The Haapiti Fire Site was discovered later on in the project and there was limited time for data to be taken. The site had burned eight years ago. There appeared to have been *Metrosideros* at the site before the fire. Many of these plants seem to have burned, but have since that time stump sprouted from the remaining root mass. These plants seem to be healthy and are fruiting and flowering. Most of the site had very heavy *Dicranopteris* growth, ranging from 1 to 2 meters in height. However, there was a particular area of interest that was sampled because of the low *Dicranopteris* cover. The soil here was poor and rocky. The *Dicranopteris* seemed to be between 0.2 and 0.3 meters tall; and within that area were young, red-colored, *Metrosideros*. Some smaller plants seemed as though they had sprouted from an existing root mass since the fire, but there was a population of about seven plants that had obviously seeded in recently. They

ranged in diameter at the base from .05 to .30 inches and had heights of less than a half a meter.

### Pollination Study

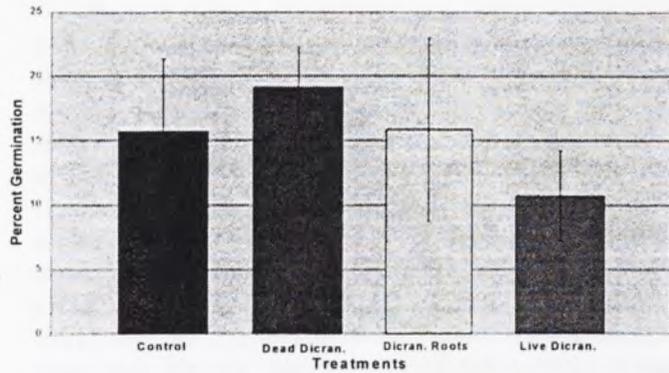
The pollinator visitation study showed that many insects as well as birds are visiting *Metrosideros* flowers. The major visitor appears to be the honeybee. In the timed visitation study the honeybee (same or different individuals) had the most flower visits per fifteen-minute period (19.8+ 8.0). Other minor pollinators appeared to be the bird, *Zosteropsis lateralis* (white eyes), a wasp; and possibly different Lepidoptera. These had less than 2% of the flower visits during the timed periods. At all five sites mentioned, honeybees were seen on and around *Metrosideros* flowers.

Flowers that were collected in the field and brought into the lab proved to be producing pollen. The pollen was collected from the anthers of the flowers and matched up with pollen found on the tape strip that removed material off the legs of the honeybee. The flowers were also producing nectar, which was especially noted during sunny days. The nectar is very sweet to the taste. In field observations the honeybee was seen collecting nectar at the bottom of the cup as well as pollen from the stamens.

### Seed Viability.

The *Metrosideros* seeds proved not only to be viable, but also to germinate quickly, sometimes within five days of watering and exposure to sun. The seeds are a winged fruit with slight variations in morphology. The plants that germinated in this experiment and that were transplanted to soil, did not grow well after the transplant. The largest plants that grew in the soil containers in the lab were later identified as weeds that had been in the soil. None of the *Metrosideros* that were transplanted put out their first leaves in the total of seven weeks of observed growing.

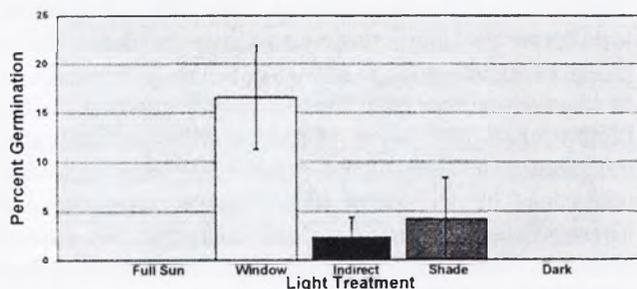
The plots that were created at Belvedere also demonstrated how slowly *Metrosideros* grows. Throughout the seven weeks that the plots were monitored seedlings started to grow in these plots. Many of these were fast growing weeds that had been in the soil or had seeded in since the creation of the plot. Small plants that appeared to have the same morphology as *Metrosideros* germinants seen in the lab could not be positively identified as *Metrosideros*. There appeared to be no major difference in results between Plot One, Plot Two and Plot Three. The invasability of *Dicranopteris* was also seen in this experiment as the fern sent out new fronds and rhizomes into the plot. It seemed as though the cleared plots would not remain without *Dicranopteris* cover for long.



**Figure 3.** Allelopathic effects of the fern *Dicranopteris linearis* on *Metrosideros collina* seed germination. The different treatments are leachates from *Dicranopteris* that were applied to the seeds daily. There was no statistical significance between percent germination of the different treatments at the 0.05 level ( $P = 0.115$ ).

### Allelopathy

The differences that were seen between percent germination of *Metrosideros* seeds in the allelopathy experiments were not statistically significant at the 0.05 level (d. f. =3,  $f=2.4$ ,  $p=0.115$ ) in a one way analysis of variance (Figure 3). The control had a 15.7% germination as well as the treatment that involved the supernatant from the roots and rhizomes of *Dicranopteris* (15.8%). The experiment that involved the treatment with live *Dicranopteris* foliage had a germination rate of 10.7%. The paper towels in the five petri dishes in this experiment were stained a dark brown from the supernatant. It seemed as though some of the seeds in this experiment were rotting. The paper towels in the roots experiment also were stained a darker color but to a much lesser extent than the live foliage treatment. The dead *Dicranopteris* treatment had the highest germination at 19.1%.



**Figure 3.** Allelopathic effects of the fern *Dicranopteris linearis* on *Metrosideros collina* seed germination. The different treatments were applied to the seeds daily. There was no statistical significance between percent germination of the different treatments at the 0.05 level ( $p=0.115$ ).

### Light Levels

The percent germination of *Metrosideros* at different light levels is shown in Figure 4. The highest germination was seen in the seeds in the filtered light of the window with an average of 16.6% germination. This resulting percent germination was statistically significant in comparison with the percent germination of all other light treatments. No germination occurred in the direct sunlight experiment. These petri dishes dried out quickly and got very high amounts of light. There was also no germination in those seeds that were in the dark. Although germination in the indirect (2.4%) and shade treatments (4.3%) were significantly less than germination in the window treatment ( $p=0.0045$  and  $p=0.010$  respectively), they were not significantly different from each other ( $p=0.245$ ). The percent germination of the indirect light treatment was not significantly different from the zero percent germination of the full sun and dark ( $p=0.114$ ).

Light meter readings were taken at all of the light treatment areas and the average irradiance on a sunny day at 12:00 noon were mentioned in the material and method section. Light meter readings taken below *Dicranopteris* canopy cover on a sunny day varied between heights of *Dicranopteris* growth. Readings were all below 60fc and mostly close to zero. The average of 10 random readings below *Dicranopteris* canopy at the Belvedere was  $13.7 + 18.9$ fc.



**Figure 5.** The inflorescence and infructescence of *Metrosideros collina* of Moorea, French Polynesia.

### Other Data Collected

Drawings of *Metrosideros collina* inflorescence and infructescence are shown in Figure 5. The calculated mean number of seeds in a *Metrosideros* capsule was  $323.0 + 94.6$ . In the germination study of *Metrosideros* seeds that had been exposed to fire, only one of the 119 seeds removed from the ashes, germinated. This seed was from the low fire area. The

seed coats of *Metrosideros* appear to be thin and are probably not very resistant to fire and high temperatures.

## Discussion

It is clear from the sampling done at the Belvedere and Three Coconut sites as well as observations at Haapiti and Rotui, that there is a general lack of young *Metrosideros collina* plants. The size class below one inch in diameter, a meter above ground level, is greatly lacking in representatives. Considering how slowly these plants grow as seen in the germination experiments and as reported in other studies (6-10cm per year of *Metrosideros polymorpha* by Hatfield et al. 1996) this is a large gap. Further, this distribution of size classes is contrary to what is usually expected in a healthy plant population (Gerrish and Mueller-Dombois 1980). Generally there are a great deal of seedlings and juveniles in the understory, only a small fraction of whom succeed the current population by making it to the overstory. Without young plants, once the current population senesces, there will be limited regeneration of the species in that area. In a study done on *Metrosideros* communities in Hawaii, the number of individuals per size class was described as an inverted J- shaped curve, which is associated with the population structure of a species that is maintaining its presence within a community (Gerrish and Mueller-Dombois, 1980). The lack of recruitment seen in *Metrosideros* populations of Moorea was a cause of concern, which fueled the search for possible answers. Of the four hypotheses that were proposed, the first three, loss of pollinator, inviable seeds and allelopathy did not prove to be valid.

It seems quite apparent from visitation observations that the honeybee is pollinating *Metrosideros* flowers. The flowers are producing pollen that can be transferred from one flower to the next as the bees visit multiple flowers and plants. Pollen found on the leg of the honey bee was identified as the same pollen produced by the *Metrosideros* flowers. The original pollinator of *Metrosideros* was not the honeybee, who was introduced to the island earlier this century. Birds were probably the first pollinators. The flower is considered to be a "bird flower" (Carpenter 1976) because of its red color and sweet nectar reward. However, because it is non-tubular and shallow, insects are free to use the nectar and pollen and cause pollination. It was suggested by Carpenter(1976) that island species, such as *Metrosideros*, are relatively generalized because of the release from competition and the need to thrive under changing conditions. This might explain why *Metrosideros* flowers, even when faced with extinction of certain pollinators, are still able to be pollinated by other species. The hypothesis that the flowers are not

being pollinated does not seem to explain the reason that there are so few young *Metrosideros* plants, and can be rejected.

The germination experiments with *Metrosideros collina* quickly proved that a certain percentage of the seeds are viable. Although *Metrosideros* plants grow slowly, the seeds do not appear to have problems germinating under lab conditions. It has been noted in other experiments done on *Metrosideros* that they have a high number of infertile seeds or seeds without embryos (Burton 1982; Drake 1993). Previous experiments (Burton 1982) reported that less than 20% of *Metrosideros polymorpha* seeds of Hawaii contained embryos, while other experiments suggest that only 9.6% of *M. polymorpha* contained embryos (Drake 1998). The shade intolerance as well as allelopathy experiments both had plants germinating in the window of the Gump lab with germination percents of 16% and 15%, respectively. Assuming these are ideal conditions for germination, this could suggest that 15-16% percent of *Metrosideros collina* seeds are fertile. Whether or not there is a low percentage of fertile seeds, my data suggests that *Metrosideros* plants have a very high amount of seed rain. Seed production fluctuates seasonally, but seeds are produced year-round (Drake 1998). *Metrosideros collina* capsules collected contained over 320 seeds on average. If there are >15 capsules in an infructescence (personal observation) and a range of from 10 to hundreds of infructescences on a plant (personal observation); it seems apparent that a great deal of these small seeds are being dispersed into the environment. In a *Metrosideros polymorpha* dominated canopy in Hawaii, the total annual seed rain was 56,755 seeds/m<sup>2</sup> (Drake 1998). Seed viability and dispersal do not appear to be limiting *Metrosideros* regeneration in Moorea.

The allelopathy experiments did not support the idea that *Dicranopteris* is inhibiting the growth of *Metrosideros* by allelochemicals. There are often very few other plants found in the understory of *Dicranopteris* cover. However, this could be due to other reasons such as light or water competition, and not explained by allelopathy (Stemmermann 1983). Although there was no statistical significance at the 95% confidence interval in the allelopathy tests, there were differences between the germination percentages of the different treatments. This could possibly be explained by the fact that the different leachates that were prescribed were causing differences in the amount of light absorption possible. The live foliage (10% germination) and root/rhizome (15% germination) treatments both stained the tissues a darker color, which could have inhibited the amount of sun the seeds received and hence retarded the break in dormancy of the seeds. The live foliage treatment also appeared to

cause some seeds to rot, which would lower the percent germination. It was interesting that the highest germination was in those plants with the dead *Dicranopteris* foliage. This could very well be due to chance, but it might be interesting to study further. The bioassay that was done to test for allelochemicals, might not have been sensitive enough. It is possible that the *Dicranopteris* does not inhibit germination, but it inhibits growth. It was known (Rizvi and Rizvi 1992) that often times the radicle length is affected by allelochemicals. In my experiment, I did not actually take any measurements, but upon inspection under the microscope, this did not appear to be the case. I assume, because of the lack of evidence to support the hypothesis, that allelopathy is not a factor in the lack of *Metrosideros* recruitment.

The last hypothesis that was tested seems to be the most likely cause for the limited amount of young *Metrosideros* plants. This research showed that *Metrosideros collina* seeds need relatively high levels of light in which to germinate successfully. Light at the forest floor may not be optimal for the germination of *Metrosideros collina*. Light is an important stimulus for seed germination of many small-seeded, woody, tropical species (Drake 1993).

The light experiments showed that the highest germination was in a window that received about 300 fc of light on a sunny day. Everywhere *Metrosideros* was found, there was a heavy growth of *Dicranopteris* (usually above a meter in height). Light meter readings show that beneath this *Dicranopteris* there is generally close to zero fc of light. This would be similar to conditions such as that found in the dark treatment in the lab, where there was 0% germination. The 1.5 meter deep thickets formed by ferns in the Gleicheniaea family (of which *Dicranopteris* is a member) have been known to reduce photosynthetically active radiation at the ground surface by as much as 12 fold (Walker 1994). If *Metrosideros* seedlings are shade intolerant, very few can probably germinate under these conditions. The shade and indirect light treatments, with 4% and 2% germination, respectively, give an idea of the low recruitment that would happen under these conditions.

It is interesting that there was no germination in the full sun treatment. Possibly the seeds that were in petri dishes in full sunlight were exposed above a certain threshold of light tolerance. In experiments by Burton (1982), *Metrosideros* germination showed a generally positive response to increasing light levels, but the data had a high amount of scatter, and leveled off and declined at higher irradiances. It has been observed that *Metrosideros polymorpha* seeds' optimum growth is at about 50% full irradiance (Burton and Mueller-Dombois 1984). It is also possible that the high irradiances could have led to

temperatures above the tolerance limits for *Metrosideros* germination. The seeds were between two white paper towels, which reflected a lot of light and dried out quickly.

Finding young plants at the Haapiti fire site was another piece of evidence suggesting that *Metrosideros* seeds are shade intolerant and have a low levels of germination under *Dicranopteris* growth. The Haapiti fire site was mostly covered with *Dicranopteris* growth about a meter in height and above. However, the one area where the *Dicranopteris* was not growing nearly as thickly, or to such heights, was the only place that a population of young *Metrosideros* plants was found. The two younger *Metrosideros* found at the Three Coconuts pass site, were just on the outside edge of a clearing which had possibly expanded or contracted in recent times. The young plants found in Haapiti were only found in this area of low *Dicranopteris*. The seeds were apparently able to germinate and grow with the high amount of sunlight that reached the ground through the sparse *Dicranopteris*.

It is apparent that the low amount of sunlight that *Metrosideros* seeds are receiving through the heavy underbrush is a factor inhibiting their germination and possibly growth beneath mature *Metrosideros* populations. It has been suggested that *Metrosideros* cannot maintain itself in mature rainforest because its seedlings cannot grow in the dense forest shade (Mueller-Dombois et al. 1980). These data suggest that *Metrosideros collina* seeds are shade-intolerant.

*Metrosideros polymorpha* of Hawaii is considered a shade-intolerant plant (Friend 1980) and is generally the first plant to colonize barren lava deposits (Hatfield et al 1996; Gerrish and Mueller-Dombois 1980). I suggest that *Metrosideros collina* is similar to its Hawaiian relative, in that it is also a disturbance-dependant plant. *M. Collina* may not be successful in, nor depend upon, regeneration and seeding into its own stands as long as *Dicranopteris linearis* is an associate in the community. The shade-intolerant seedlings seemingly cannot grow in that environment. Instead *Metrosideros collina*, with its tiny, wind-dispersed seeds, can be among the first to colonize new areas of disturbance in Moorea.

If the plant is dependent upon disturbance, it is probably large-scale natural disasters that would be the most ideal for colonization and establishment. Small-scale disturbances such as a tree fall gap, might not be as successful as an agent of regeneration so long as *Dicranopteris* still grows in the understory. This idea is contrary to a study done in Hawaii, which proposed that *Metrosideros polymorpha* maintains itself by "gap phase replacement," invading areas after a large tree fall (Burton and Mueller-Dombois 1984). In Moorea it seems that the sun-loving *Dicranopteris* would quickly invade these areas; this was exemplified by my cleared

plots at the Belvedere, which will probably soon be covered by *Dicranopteris*.

The large-scale disturbances that might be necessary for the continued existence of *Metrosideros*, have probably been created historically by landslides. As the island of Moorea erodes away into the sea, large areas of bare mineral soil are created. It is in these areas that *Metrosideros* seeds will get the sun they need to germinate and grow. This is probably why many *Metrosideros* populations are located along the high ridges of Moorea –this is where landslides have occurred.

Since the arrival of Polynesians on the island, there has probably been an increase in fires (Mueller-Dombois and Fosberg 1998). These can also create large areas of disturbance in which *Metrosideros* seeds can germinate and grow. Yes, it is very likely that *Dicranopteris* will also invade these areas of disturbance, but there may be some areas that can be considered “safe sites” (Harper 1997). In these areas, conditions are perfect for the growth of *Metrosideros*, but possibly not for the growth of *Dicranopteris*. This might be due to edaphic or topographic variations, or possibly just due to chance. The *Metrosideros* found growing at the Haapiti sight could be seen as an example of this.

The last question that needs to be asked is whether or not there should be concern for the continued survival of the native tree *Metrosideros collina* in Moorea. I feel that it is a very wise idea to monitor the growth of both *Metrosideros* and *Dicranopteris*. It would be important to know if there are any major changes in the distribution or range of either of these plants. It would also be interesting, although possibly dangerous, to monitor areas of recent disturbance to see if there are any *Metrosideros*.

Theoretically, both *Dicranopteris* and *Metrosideros* are native plants and have coexisted on Moorea for millennia. If there are no major changes in the disturbance regime, alterations in climate or introduced competitors, then it seems that both species should continue to cohabit Moorea. Besides careful monitoring, there does not appear to be any immediate need for concerted conservation efforts.

This study raises a great number of other questions about the role of *Metrosideros collina* in Moorean forests. It is important to look at other possible reasons for the low recruitment in *Metrosideros* populations. Other factors such as competition for water and nutrients might be important. Do the seeds have a hard time even reaching the ground and adequate moisture

because of the thick dry fern litter? Since *Metrosideros* is always found growing with *Dicranopteris*, is there some nutrient or mineral provided by *Dicranopteris* that *Metrosideros* needs? It might be interesting to look a little more carefully at the effects that allelopathy might have on *Metrosideros* growth. As mentioned, a very important study would examine areas of recent disturbance to look for young *Metrosideros* plants. It would also be interesting to know if the ranges of either *Metrosideros* or *Dicranopteris* have changed in recent history. Lastly, *Metrosideros* are known to grow as epiphytes in Hawaii, and it would be interesting to know if they do the same in Moorea.

### Conclusion

The purpose of this study was to explore possible reasons for the low seedling recruitment observed in *Metrosideros collina* populations of Moorea, French Polynesia. The data seem to show that it is the dense growth of *Dicranopteris*, a fern that is always found in association with *Metrosideros*, which inhibits the germination of seedlings. *Metrosideros* is a shade-intolerant plant and needs high levels of light to grow. It is not receiving this light in the *Dicranopteris* understory. For this reason, it was proposed that *Metrosideros collina* is disturbance-dependent, relying on natural disasters to create large areas of bare mineral soil in which it can grow. If this is the case, then the *Metrosideros collina* populations in Moorea do not seem to be in danger of extinction, but future monitoring is suggested.

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# The feeding ecology and effects of flooding on the tropical freshwater shrimp, *Caridina weberi* (Atyidae)

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**ABSTRACT.** *Caridina weberi* food preferences, effects on the rate of decomposition, and changes in microhabitat abundance were studied in the Opunohu River, Moorea, French Polynesia. *Caridina* is a small shredder that is most abundant in upstream reaches of the river. In a feeding experiment, shrimp consumed more *Hibiscus* leaves with microbes than without microbes ( $P < 0.0001$ ), and did not appear to eat aquatic moss. Although they did eat leaves, shrimp were found to have no effect on the rate of decomposition. Decomposition rates were estimated from an experiment in pools where representative samples of leaves from the streambed were placed in stream cages with and without shrimp. In this system the rate of decomposition is more influenced by water flow than by shrimp. Following a flash flood, the total abundance of shrimp at each of three study sites did not change. However, the relative abundance of shrimp within microhabitats at each of the sites changed significantly at two downstream sites ( $P < 0.10$ ), but not at the upstream site. The increased water volume and velocity at downstream sites during the flood may have caused the shrimp to move between microhabitats.

## Introduction

Tropical streams are characterized by small drainages, substrata composed of cobbles, boulders and bedrock, water with low mineral content, warm temperatures, and a constant input of riparian vegetation (Maciolek and Ford 1987). Unlike temperate streams that receive a major flux of nutrients and energy at one distinct point during the year, typically in autumn when deciduous trees drop their leaves, tropical streams receive a continuous influx of nutrients and energy from the forest. This allochthonous input from the forest is important in the upper reaches of a stream where canopy cover is complete and primary productivity is almost zero (Vannote et al. 1980). The input of leaves provides the basis for a detritivorous food web rather than one based on photosynthesis.

The allochthonous input from the forest is well studied in temperate streams, but this has received very little attention in tropical streams (Stout 1980, Dudgeon 1982, Pearson et al. 1989, Khandwala and Mishler 1997). Macroinvertebrates, especially insect shredders, are known to play a large role in decomposition in temperate streams (Wallace et al. 1982). However, it is relatively unknown what effect macroinvertebrates have on the rate of decomposition in tropical streams. Shredders are less diverse on tropical oceanic islands, and have negligible biomass (Resh et al. 1990). The few studies that have been

done on the effects of macroinvertebrates on decomposition have given mixed results. Covich et al. (1999) found a positive effect on decomposition, while Rosemond et al. (1998) found no effect. It has been argued that in tropical watersheds, warmer temperatures and mechanical damage play a more important role than macroinvertebrates in decomposition (Winterbourn et al. 1981).

Mechanical damage of leaves may be caused by floods, which are common in tropical streams. Water tables are especially low on oceanic islands, causing a rapid response in both frequency and magnitude of flood surges following a rainstorm (Maciolek and Ford 1987). A rapid change in the water level, either an increase or decrease, can have important implications for stream biota (Covich et al. 1996). Events such as hurricanes may wash organisms downstream as well as change the stream course and add more leaf input than usual (Covich et al. 1991). Although the effects of such large events on macroinvertebrates have been documented, no studies have been published on the effects of more frequent flash floods on the distributions of macroinvertebrates.

This study investigates whether macroinvertebrates affect decomposition in a tropical stream as well as the effects of flash floods on the distributions of macroinvertebrates. It focuses on *Caridina weberi*, a shredder (Resh et al. 1990, Feldman 1996). Specifically, this study addresses the

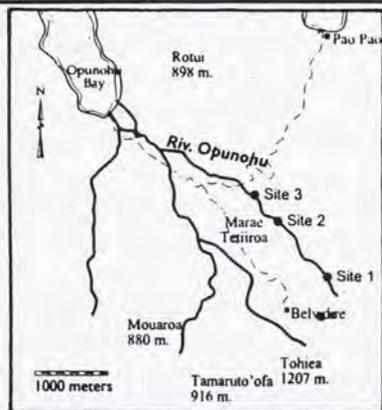
following questions: (1) What type of food does *Caridina weberi* prefer? (2) Does this shrimp affect the rate of decomposition in the stream? (3) Lastly, what effect does flooding have on the microhabitat distribution of this shrimp?

## Materials and Methods

### Study sites

This study was carried out in the upper Opunohu River (17° 31' S, 149° 51' W) on Moorea, French Polynesia from 9 October through 16 November 1999. The stream has three species of shrimp, along with several groups of snails and insects (Resh et al. 1990). *Caridina weberi* (Atyidae) is the most abundant species of shrimp (80 %) in the upper reaches of the stream (Feldman 1996). Other species of shrimp include *Macrobrachium* spp (Palaemonidae), a grazer, shredder and predator, common at low and mid-elevation reaches, and *Atyoida pillipes* (Atyidae), a filter feeder most common at mid-elevation reaches (Feldman 1996).

The three major sites (Figure 1) selected were all along a second-order stream in the higher elevation reaches of the Opunohu watershed, with site 1 at the most upstream location. Similar localities to these sites have been characterized in more detail by Feldman (1996) and Resh et al. (1990). The closed canopy surrounding the stream at all sites was dominated by *Inocarpus fagigerus* (Fabaceae) and *Hibiscus tiliaceus* (Malvaceae), with the under story dominated by *Angiopteris evecta* (Marratiaceae).



**Figure 1.** Map of Opunohu Valley showing sites. Sites 1A, 1B, and 1C are located between sites 1 and 2 with site 1A closest to site 1.

During the dry season, there was no water flow in the streambed from approximately 40 m downstream of site 1 to 10 m above site 2. However, the stream channel filled up after the first flash flood on 3 November, marking the beginning of the wet season. The water level in this previously dry reach fluctuated

greatly, rising after each rainstorm, and then receding again. Flowing water remained near the bottom of site 1 and top of site 2, but dried up completely in the very middle of these two sites over the days following a storm. Three sample sites (labeled 1A, 1B, and 1C) were set up following this first flood to track shrimp colonization into the previously uninhabitable areas.

### Food choice assessment

Pilot studies with a Y-maze to determine food choice failed quickly. The shrimp did not eat, or even come into physical contact with either of the different food choices at the end of each arm of the Y-maze, making it impossible to determine preference. Instead, small plastic cups (33 cL) were used to determine the average amount of each food item shrimp eat, since actual preference was impossible to quantify. The preferred food choice, indicated by greatest average amount ingested, lends insight to the effects of shrimp on decomposition in the stream. *Caridina* were collected above site 1 and kept individually in cups in the lab for a week to starve them and clear their digestive tracts. I changed the water in the cups every day to ensure enough oxygen remained in the water for the shrimp to survive. I placed one shrimp in each cup with a food choice and then compared the weight lost to that of a control cup with the food choice and no shrimp.

I used three different food choices corresponding to the food sources found in the river: aquatic moss and *Hibiscus* leaves with and without microbes. Leaves without microbes represented recent input from the forest, while those with microbes had more aquatic derived energy. *Hibiscus* leaves were chosen because they were more common in the river than those of any other tree species (personal observation), and in past studies, shrimp preferred *Hibiscus* leaves to *Inocarpus* leaves (Khandwala and Mishler 1997). Each treatment had ten replicates. The *Hibiscus* leaves were all collected from the stream and cut into 5 cm disks. Half of the leaves were dried at 40°C for a week to kill the microbes and then soaked in water overnight to provide a comparison for the two different leaf treatments. I used 2 g (wet weight) of aquatic moss that was rinsed in the river and then squeezed to remove excess water. Wet weights, with excess water removed by a towel, were used so as not to kill the moss or the microbial layer on the treatment of leaves with microbes. After a week, I removed the shrimp and weighed the leaves and moss again. I used a t-test to compare the moss treatment with shrimp to the control without shrimp and a 2-way ANOVA to compare mass lost between the two leaf treatments with shrimp and no shrimp and to examine the interaction between the two treatments.

### *Effect of shrimp on decomposition*

To determine how shrimp affect decomposition, I set up a cage experiment in the river. I put cages at each of the three high elevation sites as described above, because decomposition rates are higher upstream (Khandwala and Mishler 1997). A high rate of decomposition would make it possible to see any differences in decomposition rates over the short period the cages would be in the river.

The cages were 20 cm x 10 cm x 10 cm boxes, built out of two kinds of mesh. Plastic green mesh (1 cm<sup>2</sup> mesh) provided support, and window screening (1 mm mesh) prevented the contents from escaping. The cages were stitched together with fishing line, leaving an opening to insert the shrimp and leaves in the field.

Each replicate contained two cages: a control with a leaf pack and no shrimp, and a leaf pack plus *Caridina*. Newly fallen leaves were collected from under trees between sites 1 and 2 on 11 Oct, and allowed to sit in the stream to accumulate a microbial coating before being placed into the cages. This ensured that all leaves were near the same state of decomposition at the start of the experiment. The leaf packs consisted of approximately 15 g of *Hibiscus*, 4 g of *Inocarpus*, and 2g of *Angiopteris*, totaling 21 g (wet weight) of leaf material. Again, wet weight was used because drying the leaves would have killed the microbial layer. The proportion of the leaves in each leaf pack was similar to the proportion of these leaves in the stream.

On 16 October, three replicates were placed into pools in the river at each of the three sites, for a total of 18 cages. Pools were chosen to minimize the flow through the cages that might carry away material or dislodge the entire cage. The cages were tied to roots near the river, and weighed down with a rock. Every cage received one randomly selected leaf pack, and the cages with shrimp received four *Caridina*, collected above site 1.

The cages were checked after a week to make sure no shrimp had escaped. Unfortunately, at least one *Caridina* was missing from all but one cage. New shrimp were placed in those cages that did not have four shrimp, and all cages were sewed up more tightly.

Although I had intended to leave the cages in the river for a month, on 3 November, a huge flash flood raised the water level by at least 0.5 m. This increase in the water level coupled with greatly increased water velocity washed eight cages away, leaving five complete replicates intact, three from site 1 and two from site 3. I removed the surviving cages for fear

they would be swept away in a future flood. An identical experiment was also set up with *Macrobrachium* as the treatment shrimp, but no data are reported because seven of the nine treatments were lost. After rinsing sediment off the leaves and removing excess water, final wet weight was obtained. I used a paired t-test to analyze the difference in decomposition rates between the control and *Caridina* treatment.

### *Sampling methodology*

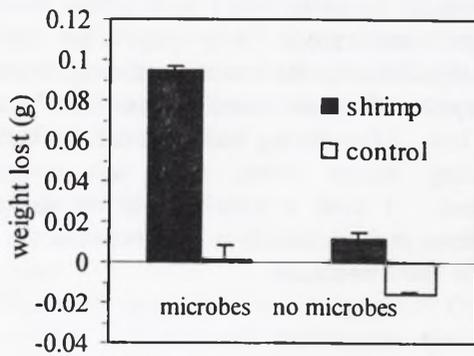
I sampled relative abundance and microhabitat preference at each of the three sites on 10 October (during the dry season), several days after the flash flood on 3 November, and two weeks after the flood. I examined four microhabitats: riffles, runs, pools, and leaf packs. A riffle is defined as an area with fast, non-laminar flow, a run as an area with laminar flow and intermediate velocity, and a pool as an area with deeper water and very slow velocity (Cuplin 1986). Leaf packs were any accumulation of leaves against rocks, branches or logs. These were found in both riffles and pools.

At each microhabitat, I used a 15 cm diameter aquarium net with 1 mm mesh to collect the shrimp. I scooped it 15 times over the surface of rocks and 10 times under rocks while turning them over. Leaf packs were scooped into a bucket and sorted through to look for shrimp. Four microhabitats were sampled at each of the 3 sites, although due to the geomorphology and flow at the sites, they did not all contain 4 pools or runs at every sampling date. I also sampled at three new sites (1A, 1B, and 1C) in between sites 1 and 2, where water did not flow until after the first flash flood. I used  $\chi^2$  tests to compare the distribution of shrimp among the microhabitats at each site before and after the flood. More than four microhabitats were sampled before the flood, so replicates were randomly selected to equalize the proportions of sites sampled across time periods.

## **Results**

### *Food choice assessment*

*Caridina* ate *Hibiscus* leaves both with and without microbes (Figure 2). Not only was this evident through weight lost, but was also visually apparent: leaves with microbes and shrimp were almost transparent at the end of the experiment, while leaves without microbes showed some damage due to the shrimp. Of most interest is that the shrimp ate tenfold more leaves with microbes than leaves



**Figure 2.** Results of cup experiment. Weight lost is the difference between the initial and final wet weights of the leaves. Error bars show one standard error.

without microbes (Figure 2, Table 1). The slight reductions in sample size were due to misidentification of several shrimp as *Atyoida*, and loss of a few shrimp during daily water changes.

The shrimp did not eat the moss ( $t = 2.179$ ,  $P = 0.175$ ,  $df = 9$ ). The presence of rocks in the moss and pieces of moss that fell out of the cups as the water was changed confounded these results. However, small pieces of moss accumulated on the bottom of cups with shrimp, and the moss remained intact in cups without shrimp. This indicates that the shrimp had some effect on the moss, even if they did not ingest a significant portion of it.

#### Effect of shrimp on decomposition

Both the shrimp treatment and the control lost approximately 15 % of their leaf packs, indicating that decomposition did occur in the cages. However, there was no influence of *Caridina* on the rate of decomposition ( $t = 2.77$ ,  $P = 0.565$ ,  $df = 4$ ).

#### Shrimp distribution before and after the flood

I caught a total of 628 shrimp at the major sites over three sampling dates, averaging 96 at site 1, 74 at site 2, and 36 at site 3. The abundance of *Caridina* at each site did not change after the flood (paired  $t$ -test:  $t = 4.403$ ,  $P = 0.474$ ,  $df = 2$ ). However, the flood did have some effects on the distribution of the shrimp among the various microhabitats at each site. Immediately following the flood, the distribution

**Table 1.** Summary of 2-way ANOVA for weight loss of hibiscus leaves during feeding experiment.  $N = 10$  for each of the leaf controls, and  $n = 7$  for each of the shrimp treatments.

Source of Variation	df	F	P
<i>Caridina</i>	1	53.261	0.0001
Microbes	1	35.043	0.0001
Interaction ( <i>Caridina</i> x microbes)	1	15.072	0.0005
Error	31		

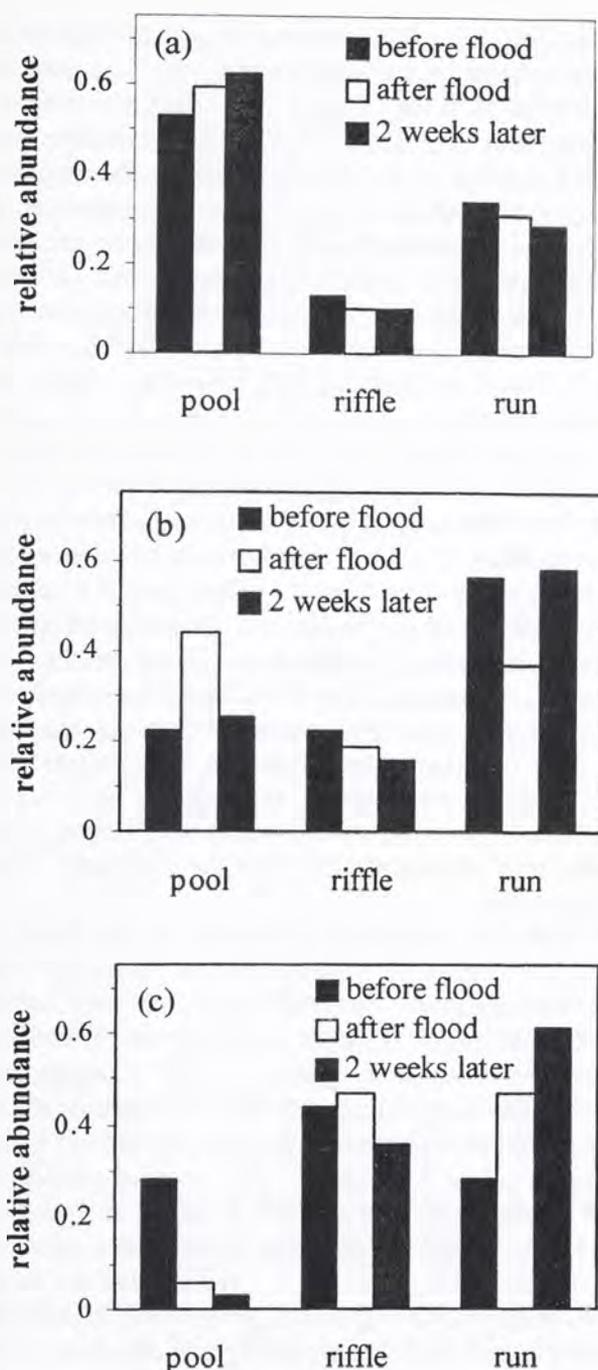
changed at sites 1 and 2, but not at site 3 (Table 2, Figure 3). At site 2, there were more shrimp in pools and less in runs (Figure 3b). At site 3, fewer shrimp were found in pools and more were found in riffles and runs (Figure 3c). Two weeks after the first large flood, the distribution of shrimp changed only at site 2 (Table 2). At this site, the shrimp returned to near their pre-flood state with no difference in distribution from the initial sample date (Figure 3b,  $\chi^2 = 0.675$ ,  $P = .714$ ,  $df = 2$ ). The proportion of shrimp found in each microhabitat is different from that reported by Feldman (1996), but he sampled along the entire length of the river. The physical changes in the river at locations downstream from my sampling area may explain these differences.

I did not include the leaf packs in the  $\chi^2$  analyses, because they had completely disappeared after the flood. Clearly the shrimp previously found in leaf packs were forced to move to a new microhabitat. When leaf packs were included in the analyses, site 1 had a significant change from before the flood to immediately following the flood ( $\chi^2 = 26.52$ ,  $P < 0.0001$ ,  $df = 3$ ), and site 2 became much more significant ( $\chi^2 = 16.15$ ,  $P = 0.001$ ,  $df = 3$ ).

A few shrimp were found after the flood in areas that had previously been dry (Table 3). Site 1A may have had water in its upper half, but not in the lower half, so the shrimp in this area either spread out after the flood or were washed downstream because of the flood. Site 1B dried up several times between sampling periods. Although only two shrimp were found at site 1C immediately after the flood, the lower extent of the site was marked by a large waterfall (1.5 m) that appeared after the flood and

**Table 2.**  $\chi^2$  results detailing effects of flash flooding on the distribution of shrimp within microhabitats. Significance results indicate that the shrimp changed their distribution among the three microhabitats: riffles, runs, and pools. In all cases, there were 2 df.

	Before the flood to immediately after the flood		Immediately after the flood to two weeks after the flood	
	$\chi^2$	P	$\chi^2$	P
Site 1	5.992	0.050	1.335	0.513
Site 2	5.785	0.055	7.416	0.025
Site 3	0.712	0.701	0.175	0.916



**Figure 3.** Microhabitat distribution at three sampling dates: before the flood, immediately after the flood, and two weeks after the flood. (a) Site 1; (b) Site 2; (c) Site 3.

**Table 3.** Total number of *Caridina* found at sites in between Sites 1 and 2 listed from upstream to downstream. Sites 1B and 1C were dry before the flood, and at least part of Site 1A was dry before the flood.

Location	Immediately following the flood	Two weeks after the flood
Site 1A	32	39
Site 1B	1	0
Site 1C	2	0

dropped into a pool filled with shrimp. No shrimp were caught at this site during the second sampling period, but one was observed just above where I stopped sampling.

## Discussion

### *Feeding biology of Caridina weberi*

Although it has been previously shown that *Caridina* prefer *Hibiscus* leaves to *Inocarpus* leaves (Khandwala and Mishler 1997), no one has ever looked at whether *Caridina* eat other food sources in the stream. The cup experiment strongly suggests these shrimp prefer to eat microbes (Figure 2), and they ingest actual leaf material only in the process of scraping the microbial layer off leaves. Since macroinvertebrates will choose the most nutrient rich microbial fauna (Dudgeon 1982), and the microbial layer is more nutritious than recently senesced leaves, this result is not particularly surprising. It does suggest that shrimp play at least some role in decomposition in the stream, having either a positive or negative impact on the rate, since they are shredding leaf material (Feldman 1996). They could increase the decomposition rate by increasing surface area for microbes to colonize through shredding action, or decrease the rate by ingesting microbes without breaking down the leaf material.

It did not appear that the shrimp ate aquatic moss, even though they were often found in places where moss covered rocks lined the edge of the stream. Although *Caridina* may be able to shred up small pieces of moss (personal observation), leaves probably contribute a greater portion of their diets. A more sensitive experiment would have to be run to conclude with any certainty that shrimp do ingest moss—taking care to remove all pebbles and not losing pieces in daily water changes.

Algal and diatom films were the only food choices present in upper elevation reaches of stream that were not examined. Given the scraping mouth parts of *Caridina*, it is possible that these shrimp do scrape films off rocks.

Putting aside the relative amounts of each food source the shrimp ate, it seems likely that these shrimp are opportunists as they were able to ingest or shred at least some material of all choices presented. This would enable them to switch feeding modes if dominant food sources change, following a flood that washes away all leaf packs, for example. An atyid shrimp in Puerto Rico, *Xiphocaris*, switches back and forth between scraping and filtering depending on the flow of the water (Covich, et al 1991, A. P. Covich, personal communication). Water flow was not considered as a variable in any previous experiments

and *Caridina* were not observed filter feeding (Feldman 1996), but perhaps this should be considered in the future.

#### *Decomposition in the high elevation reaches of the Opunohu River*

This cage experiment examining decomposition rates resulted in only 15 % mass lost as compared to 38-50 % mass lost in another study of the same system (Khandwala and Mishler 1997). Perhaps the duration of the most recent experiment, two weeks instead of a month, was too short to get comparable rates of decomposition. Another explanation for the lower rate of decomposition in this experiment is that the leaves were already leached before being placed in the cages. Leaching contributes to an initial weight loss; the elimination of this step can make decomposition rates lower than expected (Pearson et al. 1989).

*Caridina* did not have any effect on the rate of decomposition, despite previous expectations (Feldman 1996, Khandwala and Mishler 1997) that predicted their role as shredders in the stream would contribute to decomposition. Other factors such as water flow, stream temperature, time of year, and shrimp density may be more important than *Caridina* in breaking down leaves.

During floods, most leaf packs were washed downstream or lodged on branches far out of the water. This places them out of reach of the shrimp or requires that shrimp either climb out of the water or move downstream to eat leaf packs. Frequent flushing of the stream during the rainy season would remove new leaves that fall into the water before the shrimp have a chance to shred them. During the dry season when leaves have more time to accumulate into leaf packs and water flow is decreased, perhaps shrimp effect the rate of decomposition. Increased water flow during the wet season also physically shreds the leaves as they are washed downstream, smashing them repeatedly against branches and rocks. In the cages, the leaves were pressed against the walls during the flood, overshadowing any effects of the shrimp over the first two weeks of the experiment.

High stream temperature in the tropics greatly increases the rate of microbial activity over that in temperate streams (Dudgeon 1982). Although shredding activity increases surface area available to microbes, shrimp eating the microbes may either balance out the advantages of shredding or slow down decomposition. Finally, even if *Caridina* do shred leaves, their densities may be too low to have an effect on the rate of decomposition.

Despite all the explanations for *Caridina* having no effect on decomposition in the river, a huge degree

of uncertainty exists. Further cage experiments or larger stream enclosures would be necessary to determine if these shrimp can effect the rate of decomposition. The success of future experiments would depend on taking into account the frequent flash floods that occur during the rainy season. A study that compared the effect of shrimp on the rates of decomposition before and after the rainy season could be enlightening. It is also still unknown if *Macrobrachium* or *Melanoides tuberculata*, a small snail found in leaf packs, have any effect on decomposition.

#### *The effects of flash flooding on stream biota*

The abundance of shrimp at each site did not change after the flood, implying they did not get washed away downstream. They may be highly adapted to hang on in cracks, crevices, and under rocks during the frequent flash floods of the wet season. In contrast, Hurricane Hugo caused severe flooding in Puerto Rican streams that significantly reduced the abundance of shrimp in upstream and small downstream pools (Covich et al. 1991). Perhaps a more severe flood would have caused some changes in the abundance of shrimp, washing them downstream.

*Caridina* responded differently to the flood at each site (Figure 3). These different responses may be attributed to the differences in streambed geomorphology. The most upstream site (1) had the least amount of water going through it during the flood. The lessened severity of the flood meant that most of the pools remained pools, so the shrimp had a place to hide. Water height also returned quickly to the pre-flood state. At site 2, pools disappeared during the flood, and the water level did not return to normal as quickly as it did at site 1. Once the water level did return to near normal, the shrimp returned to their original distribution among microhabitats. The water level at site 3 never returned all the way to pre-flood state, providing an explanation for why the shrimp did not return to their previous distribution. The pools at site 3 were deep, but had only small rocks at the bottom instead of cobbles like in the upstream sites. This lack of hiding places in pools would make runs a more favorable place to escape the fast moving water of a flood, because they could hide under cobbles.

Between sites 1 and 2, where the stream channel was previously dry, some shrimp did move into the new areas. It is difficult to tell if they arrived by moving upstream or downstream. Since more shrimp were found downstream of site 1 than upstream of site 2, it seems likely that the shrimp were washed downstream. On the other hand, an eel observed at

site 1C was almost certainly was moving upriver. No eels were ever observed at site 1, but several were seen at site 2.

The section of the stream that is completely impassable during the dry season has several implications for the reproduction, dispersal and abundance of the shrimp in the area above this area. *Caridina* are thought to have larvae that develop in the estuary of the river and then swim upstream as they mature (Resh et al. 1992). Although Resh et al. (1992) suggest the shrimp have multiple reproductions per year, the shrimp would have to time their reproduction at site 1 to coincide with the time of year when larvae could be washed to the ocean. The shrimp at site 1 also had to arrive there during or immediately after a flood since the middle section dries out very quickly. Once a shrimp reaches the most upstream sites, a difficult endeavor, the area is relatively free from predation. The lack of predators at site 1 may explain why the abundance of shrimp was higher at this site than at the other sites.

## Conclusions

*Caridina weberi* ate more leaves with microbes than those without, implying they eat the more microbes than leaves. These shrimp do not effect decomposition in the stream, at least on the scale that was measured. These shrimp are well adapted to frequent flooding events, which do not cause much change in their microhabitat distributions.

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# Aggregation behavior of the nudibranch *Risbecia imperialis* using chemical cues in Cook's Bay, Moorea, French Polynesia

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**ABSTRACT.** Usually found in pairs, the nudibranch *Risbecia imperialis* in Cook's Bay, Moorea, French Polynesia exhibited a low population density. This study tested whether or not *R. imperialis* uses chemical cues to find other members of its species via a chemical Y-maze and trail following techniques. Results showed that *R. imperialis* can sense waterborne chemicals emitted by members of its species. The ability to follow each other's trails is also evident. A chemical detection of *R. tryoni* by *R. imperialis* was also examined using the same methods as above. No significant data supported the detection of *R. tryoni* waterborne chemicals by *R. imperialis*; however, trails left by *R. tryoni* were followed by *R. imperialis*. Evidence indicates that trails laid by *R. imperialis* and *R. tryoni* are not species specific, yet *R. imperialis* trails are unidirectional and persist up to 4 hours in still water. Communication of *R. imperialis* via chemical cues is evident for a distance up to 30cm. Further studies need to be examined to confirm nudibranch use of chemicals for aggregation purposes.

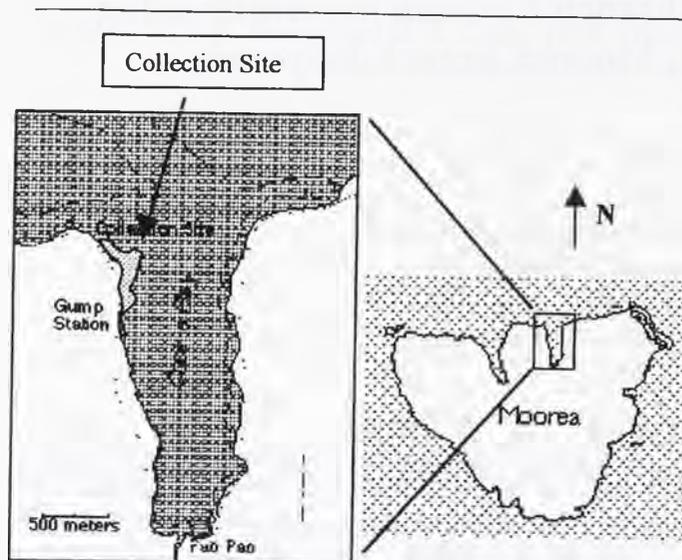
## Introduction

Nudibranchs have been well documented and described for over a century. Studies depict their distribution, anatomy and even their responses to chemical cues emitted by prey and predators, but little is reported about their interactions within their subclass. Although the ecology of nudibranchs has attracted the interest of many researchers and photographers, there is sparse literature about the uses of its chemosensory system for aggregation (Croll 1983; Karuso 1987; Murphy and Hadfield 1997). Some claim that chemoreception might be used to detect other nudibranchs using waterborne pheromones and/or trail following (Todd 1981), but evidence has yet to be recorded. Most trail-following studies in molluscs have focused on a variety of terrestrial and marine gastropods (Cook 1993) other than nudibranchs. The importance here lies in understanding more thoroughly the interactions between nudibranchs using their chemosensory system so as to interpret their community organization.

*R. imperialis* seems to have a very low density in the western part of Cook's Bay, Moorea, French Polynesia, relative to other nudibranchs found in that area. Only fifteen individuals were found between September 26-November 1, whereas over

5 *Glossodoris cincta* individuals were found in one day. Another nudibranch, *R. tryoni*, resides in the same area and is also rarely found. Only four members of *R. tryoni* were located.

Nudibranchs of the *Risbecia* genus is frequently found in pairs (Debelius 1996). Reasons for the aggregation of nudibranchs suggest they group for reproductive purposes, lack of food resources, a reduction in temperature, and/or some physiological change (Kohn 1961; Todd 1981). This aggregation behavior, also observed in Moorea, is coupled with a unique head-to-tail following behavior. Similar behaviors exist within *Phestilla* species, and evidence supports a stable bond between pairs, especially in adults (Harris 1973). Given the low-density of the population and aggregation behavior of *Risbecia imperialis*, the purpose of this study was to test whether *R. imperialis* responds to waterborne chemicals and trails laid from individuals intraspecifically and interspecifically with *R. tryoni* or if their aggregation behavior is random. Other functional properties of trail following were also examined, including directionality and persistence of trails.



**Figure 1.** Location of collection site in Cook's Bay, Moorea, French Polynesia.

### Materials and Methods

All nudibranchs used for this study were collected on the fringing reef east of the Gump Station in Cook's Bay, also known as Point Nuurua (Figure 1). They were found on a variety of substrates including sand, coral rubble, live coral and encrusting algae in depths ranging from 1-7 meters. A total of 15 *R. imperialis* and 4 *R. tryoni* individuals were collected, of which 10 *R. imperialis* and 2 *R. tryoni* were found in pairs.

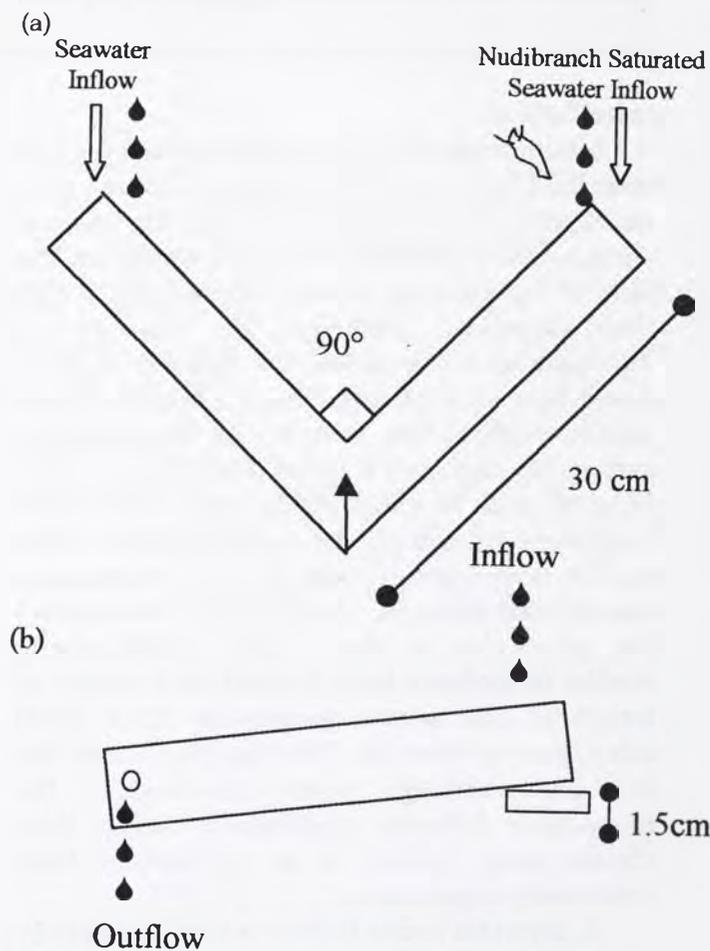
### Waterborne Chemicals

During the study period, all individuals were housed in the same tank with continuously flowing seawater directly from the collection site. To test the sensitivity of *Risbecia imperialis* individuals to waterborne chemicals emitted by other members of its species and of *R. tryoni*, I first isolated all of the individuals in 300mL of seawater for a 24-hour period to ensure chemical saturation of the water. Subsequently, the water was used as a testing variable in a chemical Y-maze. The Y-maze was shaped like a right-angled "V," but still functioned like an Y-maze having two paths for the test organism to choose between. Each arm, 30cm long and 6.5cm wide, had an inflow of either seawater from the collection site or chemical-saturated water from an individual nudibranch, plus an outflow hole (Figure 2a,b). Inflows alternated between legs

after each trial to discount maze biases. The legs were raised 1.5cm allowing water to freely exit the maze through the outflow holes (Figure 2b). Water flows were constant and continuous in both legs during each trial. All individuals were placed in the Y-maze with its tail in the corner of the "V" and its head facing the parallel corner. I noted when an individual chose a path if it traveled 3/4 or more of a leg's distance.

### Trail Experiments

For all trail-related experiments, a plexiglass-covered tank acted as an arena for nudibranchs to crawl in and for their trails to be traced. The trails were traced on top of the plexiglass cover based on the assumption that wherever a nudibranch crawls, a trail is left behind. In addition, observations indicated that nudibranchs prefer to crawl on the edge and sides of tanks; therefore,



**Figure 2.** Chemical Y-maze set-up. (a) Top view. (b) Side view. (↑) Represents nudibranch orientation at beginning of trial.

once a nudibranch's entire body resided on an edge or side of the arena during a trial, it was removed. The trails were traced and measured to determine the distances of the trail laid by the first nudibranch and the overlap trail produced by the second nudibranch.

#### *Intraspecific*

One *R. imperialis* individual was placed in the arena and left to crawl until removed. A second *R. imperialis* individual was placed head-first at the origin of the first individual's trail and left to crawl until removed. This completed one trial. Between each trial, the arena was thoroughly scrubbed and flushed with seawater for 1 minute. Ten trials were conducted.

#### *Interspecific*

This experiment was conducted using the same method as above except a *R. tryoni* individual always laid the initial trail until removed.

#### *Control*

For the control, the same above method applies except the arena was thoroughly scrubbed and flushed with seawater for 1 minute every time a nudibranch was removed, not between each trial. The control was run to eliminate any other variables such as the properties of the tank that might bias the experiment.

#### *Trail Direction*

To test if trails left by *R. imperialis* are unidirectional, the same trail following method was used, but the second nudibranch's head was not placed on the origin of the first trail. Instead, the second nudibranch was placed at the end of the first trail, facing the direction opposite to which the trail had been laid.

#### *Trail persistence*

After a nudibranch laid a trail and was taken out of the arena, the trail was left in stagnant water for a given time interval. After the time had elapsed, a second nudibranch was placed to sense the trail, using the same above method. The time intervals tested were 15 minutes, 30 minutes, hour intervals between one and six inclusively, and 8 hours. Three trials were conducted for each time interval.

## Results

#### *Waterborne chemicals*

In 15 intraspecific trials, *R. imperialis* chose the arm with chemical cues 11 times. A chi-squared analysis revealed a 90% significance ( $\chi^2=3.266$ ,  $0.05 < P < 0.10$ ). For interspecific trials, only 2 *R. imperialis* individuals chose the arm with *R. tryoni*-saturated water out of 8 trials. These results were not statistically significant ( $\chi^2=2$ ,  $0.15 < P < 0.20$ ).

#### *Trails Experiments*

Examining all of the trials revealed all trail lengths varied considerably. Trails laid by the first nudibranch varied between 6.5cm and 28cm. Trail overlap distances ranged from 0cm to 26cm. To standardize all trials, the distance of trail overlap was divided by the total distance of the first nudibranch's trail. However, standardizing the data using this method seemed problematic if trail distances caused error in the experiment and in the analysis. For example, chemicals in longer trails could have dissipated before the second nudibranch entered the arena. To test trail biases, all trials were combined and divided arbitrarily into two categories of short and long trails. Any trial beginning with a trail less than 12cm was classified as short and more than 12cm was considered long. The variances of the overlap trail distances and the distances of trails laid first were equally proportional between short and long trail trials (short:  $n=17$ ,  $\text{overlapVar}=9.399$ ,  $\text{var}=2.715$ ; long:  $n=23$ ,  $\text{overlapVar}=42.299$ ,  $\text{var}=14.889$ ). Since there appeared to be no biases between trail distances, using the above method to standardize the trailing data seems valid and is comparable.

#### *Intra- and Interspecific*

*R. imperialis* followed trails completely in 7 out of 10 intraspecific trials and 4 out of the 10 interspecific trials. Using the standardized number, intra- and interspecific trailing experiment means were compared to the control mean in a T-test assuming unequal variances. Both experiments exhibited statistically significant results (intra:  $t=4.674$ ,  $P=0.0001$ ; inter:  $t=3.286$ ,  $P=0.0023$ ).

### Trail Direction

In the trail-direction experiment, it appeared as though *R. imperialis* did not prefer to follow a trail if placed on the end of the first trail laid. In 4 out of 10 trials, the nudibranch turned 180°, paused, then continued to crawl around the arena's edge. In other trials, the travel direction of the second nudibranch was random. The standardized values of this experiment closely resemble the values of the control, whereby a comparison of these experiments using a T-test would not reflect an accurate measure of significance ( $t=0.465$ ,  $P=0.324$ ). Since in the intraspecific study the forward direction of trails was already established, a comparison between the intraspecific and trail-direction experiments would give a more accurate representation of significance. A T-test comparing their means assuming unequal variances showed a significant difference between the two experiments ( $t=-4.968$ ,  $P=0.0002$ ).

### Trail Persistence

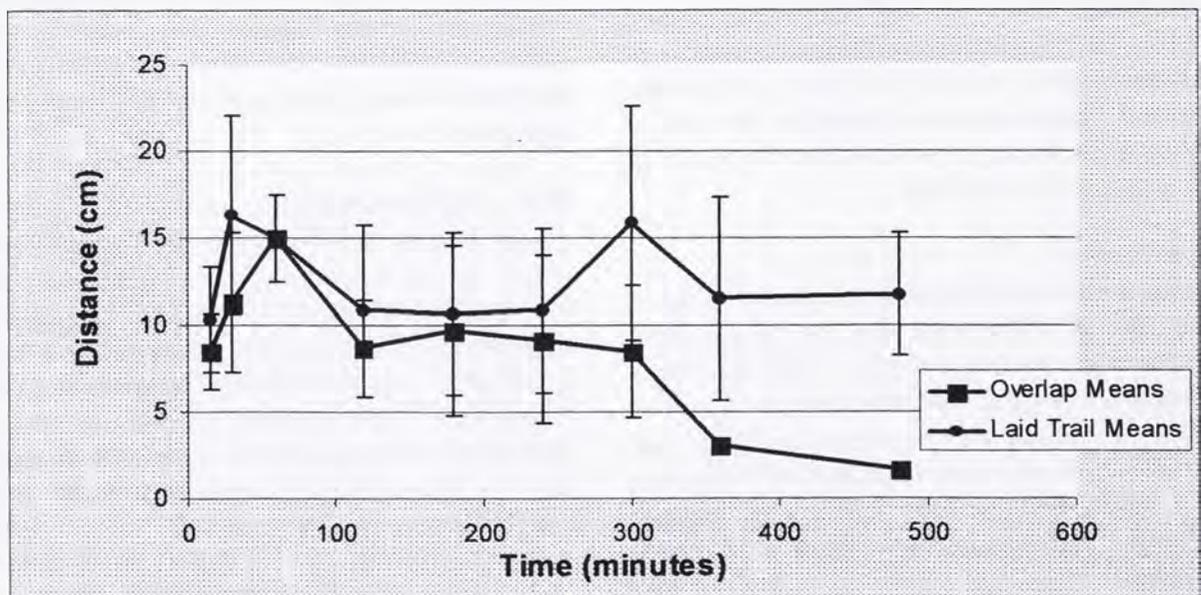
Examining the means of the overlap distances and the distances of the first trail laid within each time-interval trial, the two means correlate from the 15-minute trial through the 4-hour trial. At 5 hours, the correlation between the means begin to separate, and by 6 hours, there is no correlation between the distances (Figure 3).

### Discussion

Results of the Y-maze provide evidence of sensitivity of the *R. imperialis* species to chemicals released in the water by intraspecific individuals. This supports questions raised about nudibranch use of chemicals as attractants (Karuso 1987). However, this experiment is only significant at 90% due to a low  $n$ . Perhaps an increase in trials would make this claim more evident.

There is not enough evidence to support a response of *R. imperialis* to *R. tryoni* using waterborne chemicals, and only 8 trials were conducted. Suggestions for any replication of this experiment include to increase the number of trials and to conduct a simultaneous Y-maze experiment giving *R. imperialis* two choice variables: water from its species, and water from *R. tryoni*.

It is evident that *R. imperialis* follows trails left both by members of its species and by *R. tryoni*, indicating that trails are not species-specific. There may be many reasons for this phenomenon. One reason may be the utilization of tactile more than chemical cues. *R. imperialis* and *R. tryoni* have similar body types, with approximately the same lengths and widths, and therefore lay down similar size mucus trails. Or perhaps their trails are chemically similar and do not need to be distinguished.



**Figure 3.** Trail persistence in stagnant water. Lines represent mean distances of 3 trials for each time interval. One standard deviation is shown above and below each mean.

The fact that trails laid by *R. imperialis* and *R. tryoni* are not species-specific does not come as a surprise. During my 9-week stay, I observed only 5 other genera in the collection site, none of which had similar body types to *Risbecia*, and all of which thus laid trails of different sizes. If *R. imperialis* follows trails using tactile sensory mechanisms, it has a 50% chance of finding a partner if it chooses to follow a trail that it can detect. If trail following is mostly due to chemical sensing, then the chance of *R. imperialis* finding a partner remains at 50% only if trails left by nudibranchs of other species are chemically distinguishable. Whether or not trails are chemically distinguishable between other species not included in this study is unknown.

Data supports the hypothesis that trails are unidirectional. Some researchers claim that the direction of a trail can be detected by other gastropods due to a chemical polarization of the left and right sides (Bretz and Dimock 1983; Chelazzi 1990; Cook 1993). If trails are sensed using chemical cues, a chemical gradient may tell a nudibranch the direction of a trail where the higher chemical concentration would be closer to the nudibranch still laying the trail.

In still water, evidence indicates that trails persist up to 4 hours. Between 4-5 hours, the overlap trail is considerably shorter. By 6 hours there is no longer detection of a trail. Previous research exhibited behavioral relevance in terrestrial trails to last between 10-20 minutes after exposure to substances that could potentially weather trails in nature (Cook 1993). I suspect marine trails to have a shorter persistence in the wild where there are currents, though I have no evidence yet to support this claim. To further test trail persistence, a current should be incorporated in the experimental apparatus to model the effects of the natural environment. With results from such an experiment, a comparison between terrestrial

and marine trails could be more accurately analyzed.

Combining all of the data described, there is evidence strongly suggesting that nudibranchs use chemicals released in the water and on trails as modes of communication. Whether or not these ways of communicating are for aggregation purposes is not completely clear. Directionality of trails and their persistence hints towards trail-following for the purpose of aggregation. Continued intraspecific research on different species should be conducted in order to describe aggregation behavior more thoroughly. Also, more interspecific studies need to be examined, especially between genera living in the same community. This would help to support theories of terrestrial ecologists concerning allelochemicals and marine organisms (Whittaker and Feeny 1971). These studies will help to further advance behavioral ecology studies of nudibranchs, community organization, and the adaptations of species.

### Conclusions

*R. imperialis* can sense waterborne chemical cues emitted intraspecifically and follows trails made both intraspecifically and by *R. tryoni*. Also their trails, persisting up to 4 hours in stagnant water, are only followed intraspecifically in a forward direction. Reasons for this phenomenon are not known. All of the data collected reflect possible modes of detecting other nudibranchs in their environment for aggregation purposes (i.e. mating, food finding).

### Acknowledgments

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## Landbirds of Moorea encountered within five habitat categories

- 1) Hibiscus Forests
- 2) Inocarpus Forests
- 3) Coconut Plantations
- 4) Pine Plantations
- 5) Home Gardens

### *Gallus Gallus* Jungle Fowl

**Range:** Introduced centuries ago by early Polynesians, some individuals have returned to the feral state, forming a stable population.

**Identification:** This is the only large terrestrial bird in the islands of Polynesia. Smaller than the domestic variety, the jungle cock is richly colored. The hen is generally brown.

**Habitat:** The wild fowl lives in the lowlands, where it inhabits the secondary forests. It is seen foraging on the ground in home gardens, coconut plantations, *Inocarpus* and *Hibiscus* forests.

**Breeding and diet:** Nests on the ground and feeds on invertebrates, seeds, and fruits.

### *Circus Approximans* Swamp Harrier

**Range:** Introduced to Moorea in 1885 to prey upon rats. It is present today in most of the Society Islands.

**Identification:** Length 50-53cm. A slender-looking bird of prey with a long narrow tail and slender feet. The coloration of the plumage varies greatly between individuals, but the adults often have a light rump and a brown or gray belly. The young have a dull uniform coloration. They often soar, with their wings held in a V shape.

They whistle in flight, usually when displaying. The Swamp Harrier is the only bird of prey in the Society Islands. It is common and easily located in flight in the skies over the valleys.

**Habitat:** It establishes its nest on the ground in a cleared area. Hunts in all kinds of habitats: swampy areas, secondary valley forests, pine plantations, and deforested areas. Rare or absent above 1500 meters. Seen soaring above the Gump station, coastal coconut plantations, and home gardens. Seen roosting in pine plantations.

**Breeding and diet:** Its nesting habitats are not well known in Polynesia. The clutch is known to be about seven eggs. Eats mostly rats and small birds.

### *Geopelia strata* Zebra Dove

**Range:** Successfully introduced to Tahiti in 1950, the Dove is now present in Moorea and the Windward Islands.

**Habitat:** Very common, thrives in an urban setting and in the gardens and clearings of the coast and the inland valleys. Establishes a large nest in a tree or low bush. Seen commonly at the Gump Station, home gardens, and Coconut plantations.

**Breeding and diet:** Breeds all year long and has a clutch of two eggs. Eats scraps, seed, and small invertebrates.

### *Ptilinopus purpuratus frater* Gray-green Fruit Dove

**Range:** Endemic to Moorea

**Habitat:** This tree-dwelling forest bird is fairly common in wooded habitats below 1000 meters. Rarely noted these days in the gardens of coastal areas, it lives mostly in the valleys of the island interiors, where it constructs a large nest in trees or bushes. Seen commonly above the Gump Station near Black Rock, and in Hibiscus forests and abandoned coconut plantations.

**Breeding and Diet:** The nesting period lasts all year. Raises one young. Eats the smaller varieties of ripened fruit.

*Halycon venerata youngi*

Tahitian Kingfisher

**Range:** Endemic to Moorea

**Habitat:** The Kingfisher is sometimes found in gardens or parks, but lives mostly in the lowland secondary forests, but in this survey it was found only in the *Inocarpus* forests. It is absent from higher altitude forests. It digs a hole in softwood trees to form its nest.

**Breeding and Diet:** Nests from September to February. Raises one to three young. Eats mostly insects.

*Pycnonotus cafer*

Red-bellied Bulbul

**Range:** Originally from Asia, the Bulbul was introduced to many of the South Pacific Island chains (Fiji, Tonga, Samoa). It became established on Tahiti by the ends of the 1970s. It is now abundant throughout Moorea.

**Habitat:** The Bulbul likes inhabited environments, in garden areas of the coast, and the cleared areas of the valleys. It has been noted further inland, at heights of up to 1500 meters. As it has so recently been introduced, its range is not likely to have stabilized, but it already occupies an important place in the avifauna of Moorea. It was found abundantly at the Gump Station, home gardens, coconut plantations, and pine plantations.

**Breeding and Diet:** In the islands of Fiji, where it has been well studied, the Red-bellied Bulbul nests from October to February. It has a clutch of two or three eggs in a nest of twigs, grasses and other materials, built in the crotch of a tree. It eats fruits and insects.

*Zosterops lateralis*

Silver Eye

**Range:** Originating in Tasmania, the Silver Eye was introduced to Tahiti in 1939. The species has been remarkably successful, and is now present on all the Society Islands.

**Habitat:** Present in all the wooded regions, gardens, fields, and forests up to high latitudes. The Silver Eye is gregarious, and often flies in flocks of up to a hundred birds. It is the only specie to live in all habitats, from the coast to the highest summits. It was seen in all habitats sampled. Establishes a small nest in a tree or shrub.

**Breeding and Diet:** In Tasmania, the clutch is from two to four eggs, and the nesting period extends from August to February and December. Eats principally insects and fruits.

*Ramphocelus dimidiatus*

Crimson-backed Tanager

**Range:** Originally found in Central and South America. Introduced to Tahiti just before 1940.

**Habitat:** Is present in some of the home gardens along the coast but possibly lives in other locations. Builds a large cup shaped nest in a bush. It was seen foraging in home gardens and roosting in banana plantations.

**Breeding and Diet:** In the Americas, the Tanager has a clutch of two eggs, but there is little information available on the Moorean populations. Eats fruit, seeds, and insects.

*Emblema temporalis*

Fire-tailed Waxbill

**Range:** Originally from Australia, this Waxbill was introduced to Tahiti at the end of the last century. It is present today in Tahiti, Moorea and the Marquesas.

**Habitat:** Commonly seen as it moves about the tree cover along the coast. Encountered as well along the ridges at medium elevation. Though a tree dweller, it feeds mostly on the ground under trees. The nest is an enclosed dome of grass. It was commonly seen at the Gump station, coconut, and pine plantations.

**Breeding and Diet:** Has a clutch of between four and eight eggs, though the details of the breeding process in Moorea are not well known. Eats seeds and insects.

### *Columba livia*

#### **Rock Dove**

**Range:** Introduced to Polynesia.

**Habitat:** Abundant along the coast in inhabited areas such as parking lots, shopping centers, and home gardens.

**Breeding and Diet:** Feeds on the ground. Seen foraging on a wide variety of food: waste, seeds, fruit, insects, etc.

### *Estrilda astrild*

#### **Common Waxbill**

**Range:** Originally from Africa, and introduced to Polynesia at the beginning of this century. Present in Moorea and Tahiti.

**Habitat:** Encountered mostly in flocks of 15 to 30. Lives along the coast and in the interior up to 750 meters. Lives in open areas, plantations and gardens where the soil is covered in grass. Established a large nest in the trees, comprised of an enclosed room accessed by a tunnel.

**Breeding and Diet:** A clutch of four to eight eggs. Nests all year long. Eats primarily seeds, and sometimes insects.

### *Lonchura castaneothorax*

#### **Chestnut-breasted Mannikin**

**Range:** Originally from New Guinea and Australia. Introduced into Polynesia at the end of the 19<sup>th</sup> century. Present in Moorea and most of the Society and Marquesas Islands.

**Habitat:** Abundant along the coast and in the interior up to 800 meters. Lives in open areas, fallow land, and plantations. The Mannikin is gregarious, traveling in flocks. The nest is a round structure made of grass and constructed in trees and shrubs.

**Breeding and Diet:** Not well known in Polynesia. Elsewhere the clutch is from four to six eggs, and it can nest at any time during the year. Feeds mostly on seeds.

### *Acridotheres tristis*

#### **Indian Mynah**

**Range:** Common in many parts of Asia, the Mynah was introduced to Polynesia at the beginning of the 20<sup>th</sup> century. Present in Moorea and most of the Windwards, as well as the Marquesas and Tuamotu.

**Habitat:** Abundant along the coast and inland up to 700 meters. Lives in town, gardens, plantations, and forests where the cover is not too dense. Feeds on the ground. The nest is an enormous mass of plant and other material, set on a building or in the crook of a tree. Most abundant bird seen in this survey.

**Breeding and Diet:** Nests throughout the austral summer. The clutch is from three to six eggs. The Mynah can eat almost any kind of food: waste, seeds, fruit, insects, etc.

# A Checklist of the Flora of the Gump Station Moorea, French Polynesia

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This checklist is listed alphabetically by family name and by genus and species within each family. Whenever possible, the Polynesian common names are included followed by English and French common names. Alternate Latin binomials have been provided and are either out of date or misspelled, and thus synonymous, or have been misapplied in earlier literature. Each entry contains a short description of the plant in question. All of the plants on this list are to be found on the University of California at Berkeley Richard B. Gump South Pacific Biological Research Station property on the island of Moorea, French Polynesia, and are either naturalized or planted. This list contains all plants observed and identified on site, however voucher specimens have not been made for the majority of plants on this list. By no means should this list be considered complete, and all additions and corrections are encouraged.

## DICOTS

### Acanthaceae

*Thunbergia fragrans*

White flowered climbing vine, petals fused, 5 lobed, tube incurved, stamens 4, leaves hastate, opposite

### Anacardiaceae

*Mangifera indica*

Vipopa'a, Tumi Vi, Vi

Mango, Manguier

Large tree, leaves lanceolate, margins undulate, flowers many in terminal panicles, fruit a drupe, turning red and yellow as it ripens

### Apiaceae (Umbelliferae)

*Centella asiatica*

Gotu Kola

(*Hydrocotyle a.*)

Low leafy weed, very broadly cordate to reniform, flower with minute petals, fruit orbicular. Plant a recent introduction, important herb in Western and Eastern forms of herbal medicine, not to mention Polynesian medicine.

### Apocynaceae

*Allamanda cathartica*

Golden Trumpet, Monette Jaune

(*A. c. var. hendersonii*, *A. hendersonii*, *A. schottii* & *A. oenotherifolia* [both poss. vars. of *A. c.*])

Low shrub-like vine (or vice-versa), commonly grown for its large, yellow, tubular flowers. Leaves oblanceolate, shiny glabrous, stamens hidden by small hairs at base of throat. Maroon flowers formed by another local variety.

*Catharanthus roseus*

Madagascar Periwinkle,

(*Vinca rosea*, *Lochnera rosea*)

Pervenche de Madagascar

Short herb, flowers 5-lobed, varying in color, white, pink, or red often with a yellow center, leaves obovate, undulate, opposite

*Nerium oleander*

Tarona

Oleander, Rose-Laurel, Laurier-Rose

(*N. indicum*, *N. odorum*)

Large shrub with narrowly lanceolate leaves and showy flowers ranging from scarlet to white, calyx 5 lobed, leaves whorled

*Plumeria rubra*

Tipani, Tipanie

Frangipani, Plumeria, Frangipanier

(*P. acuminata*)

- Large shrub or tree, flowers white or red with a yellow center, or variations thereof, flowers fragrant and sweet, 5 petals, 5 stamens, leaves oblanceolate, deciduous
- Tabernaemontana coronaria*      Tiare Moorea, Potii Moorea      Crepe Jasmine, Jasmine Café,  
East Indian Rose Bay
- (*T. divaricata*, *Nerium divaricatum*, *Ervatamia divaricata*, *Ervatamia c.*)
- Shrub with gardenia-like flowers, petals doubled, white with yellow center, fragrant, elliptic to oblanceolate leaves glabrous, margins undulate
- Asteraceae (Compositae)**
- Emilia fosbergii*  
Short, weedy discoid composite, corollas red to bright pink, head cylindric, leaves alternate, clasping basally, variably lobed and dentate
- Synedrella nodiflora*      Nodeweed  
(*Verbesina n.*)  
Low weed with radiate heads, rays yellow, heads only a few mm in size, heads sessile, leaves ovate with a winged petiole
- Tridax procumbens*      Coat-Buttons  
Short composite with solitary radiate heads on long peduncles, ray florets white, disc florets yellow to tan, leaves 3-lobed, mostly basal with short, stiff hairs
- Vernonia cinerea*      Little Ironweed  
(*Conyza cinerea*)  
Purple flowers with white chaff, heads discoid, narrowly cylindric, leaves alternate, simple, plant usually less than 50 cm tall
- Wedelia trilobata*  
(*Silphium trilobatum*, *Wollastonia t.*)  
Spreading ground-cover, recent introduction. Heads radiate, broad, yellow ray and disc florets, leaves mostly glossy, dark green, opposite, clasping basally
- Caricaceae**
- Carica papaya*      I'ita      Papaya, Papayer  
Small tree, leaves alternate, clustered apically, variously and deeply lobed, staminate flowers numerous, pendulous, pistillate flowers 1-3 on short peduncles, fruit yellow-orange when ripe, sweet, with numerous seeds
- Casuarinaceae**
- Casuarina equisetifolia*      Aito, Toa      She-Oak, Ironwood, Beefwood,  
(*Casaarina littorea*)      Horsetail Tree, Arbre de Fer  
Tall tree closely resembling a pine, needles are actually photosynthetic stems with highly reduced leaves, similar to *Equisetum*, common Horsetail, also produces cone-like floral structures, heartwood is very dense and resists rotting
- Combretaceae**
- Terminalia catappa*      Autara, Autara'a Popa'a,      Badamier, Tropical Almond, Myrobalan  
Auari'i-roa, Taraire  
(*T. glabrata*, misspelled *T. cattapa* by Welsh, 1998)  
Large tree with whorled branches, fruit a fleshy, winged, elliptic drupe, falls off tree when green, leaves broadly obovate, turning red, flowers small, green-white, 5-lobed, no petals
- Convolvulaceae**
- Ipomoea obscura*  
(*Convolvulus obscurus*, *I. koloaensis*)  
Small clambering vine preferring rocky slopes, fences, or low ground-cover as a substrate, leaves small, cordate, apex acuminate, corolla composed of 5 fused petals, cream colored with a maroon-purple throat, stamens 5
- Merremia peltata*      Pohue  
(*Convolvulus peltatus*, *Ipomoea p.*, *M. nymphaeifolia*)  
Aggressive liana, leaves peltate, broad, ovate to cordate, flowers white, petals fused, corolla campanulate, plant found in the highest canopies, often not producing leaves or flowers in the understory
- Merremia umbellata ssp. orientalis*      Volubilis  
(*Convolvulus umbellatus*)  
Yellow-flowered climbing vine, flowers in dense umbellate clusters, leaves usually basally truncate, narrowly deltate, common roadside, often found with *Wedelia trilobata*
- Euphorbiaceae**
- Aleurites moluccana*      Tahii tiari, Ti'a'iri,      Candlenut, Bancoulier

- (*Jatropha m.*, *A. triloba*) Tutui, Tahiri  
 Small to medium tree, leaves 3-5 lobed, resembling Sycamore, with stellate hairs on juvenile leaves, flowers many, terminal, small, petals white on both staminate and pistillate flowers, fruit walnut-like, waxy and apparently flammable
- Codiaeum variegatum* Croton  
 (*Croton v.*)  
 Ornamental shrub with much variation, leaves oblanceolate to narrowly elliptic, variously marked in white, yellow, red, and green, inflorescences long racemes, calyx green-white, many varieties cultivated
- Euphorbia prostrata* Prostrate Spurge  
 (*Chamaesyce p.*)  
 Prostrate herb, common to lawns, leaves opposite, elliptic, cyathia densely packed on short branches, staminate flowers 4
- Manihot esculenta* Maniote Manioc, Manihot, Maniote,  
 (*M. ultimima*, *Jatropha manihot*) Cassava, Tapioca  
 Common food crop, also naturalized in spots, many cultivars with varying levels of edibility, many contain hydrocyanic acid which can be extracted, but sweet varieties are preferred. Large herb to shrub, petioles long, often tinged red, leaves deeply palmately 3-7 lobed, leaf veins also tinged red at times, flowers terminal, pistillate flowers borne basally, staminate flowers apically, green-white to orange
- Fabaceae (Leguminosae)
- Mimosoideae
- Inga feuillei* Pakai, Pacay Ice-Cream Bean, Pacayer  
 (*I. edulis*, *I. ynga*, *Mimosa ynga*)  
 Medium to large tree, leaves even-pinnate, rachis (petiole) conspicuously winged, leaflets lanceolate, basally rounded, flowers axillary, racemes of small salverform flowers, white-pink, fruit a large, green pod with shiny black seeds surrounded by a sweet, cottony, edible liner.
- Leucaena leucocephala* Acacia Acacia  
 (*L. glauca*, *Mimosa l.*, *M. glauca*)  
 Large tree, native to tropical America. Essentially a weed, this tree can be found growing in wet valleys and dry scarps forming dense, almost monotypic forests. Leaves with 3-8 pairs of pinnae, each with at least 7 pairs of leaflets, flowers white, 1-2 peduncles per leaf, pods very flat, glabrous
- Mimosa pudica* Pohe h'avare, Pope Haavare Sensitive Plant, Sensitive Pudique  
 (*M. p. var unijuga*)  
 Prickly prostrate creeper, stems at times purple-red, leaves 2-pinnate, sensitive and to touch, closing upon contact, flowers in pink globose heads, stamens 4
- Caesalpinoideae
- Senna surattensis*  
 (*Cassia s.*)  
 Shrub to small tree, leaflets 6-10 pairs pinnately arranged, ovate-elliptic, racemes many flowered, petals bright yellow, pods up to 10 cm long, grown ornamentally but possibly indigenous
- Papilionoideae
- Alysicarpus vaginalis* Alyce Clover, Alysicarpus  
 (*A. nummularifolius*, *Hedysarum vaginale*)  
 Mat-like prostrate plant common on lawns and disturbed areas, spreading via stolons, leaves stipulate, stipule lanceolate and persistent, corolla typically papilionaceous, up to 6 mm long, red to purple, recently introduced
- Crotalaria pallida*  
 (*C. striata*, *C. mucronata*, *C. saltinata*)  
 Erect subshrub with pubescent stems, leaves with 3 leaflets, difficult to distinguish whether pinnate or palmate, each leaflet ovate to oblanceolate, margin white, terminal racemes many flowered corolla up to 14 mm long, keel strongly curved, corolla yellow with red-orange veins, stamens 10, introduced weed
- Desmodium incanum* Spanish Clover  
 (*D. racemosum*, *D. canum*, *Hedysarum racemosum*)  
 Prostrate to erect subshrub, leaves with 3 leaflets (pinnate), leaflets with white pallor above, corolla up to 7 cm long, red to purple, stamens 10, pod pubescent, sticky, 3-4 cm long, one margin entire, the other undulate
- Vigna marina* Pipi Tatahi, Pipi, Tutu Farao Beach Pea, Haricot du Bord du Mer  
 (*Phaseolus marinus*, *Dolichos luteus*, *V. lutea*)  
 Sea-side vine, trifoliolate, sparsely pubescent, leaflets orbicular to obovate, apex rounded, racemes up to

15 cm long, corolla yellow, banner wide, keel slightly incurved, style bearded, used medicinally for fevers and various other ailments

Lamiaceae (Labiatae) (including Verbenaceae)

*Clerodendron thompsoniae*  
(*C. thomsonae*)

Bag-Flower, Bleeding-Heart Vine,  
Coeur de Marie

Shrub-like vine (or vice-versa), leaves opposite, elliptic, acuminate, flowers borne in many flowered cymes, corolla red to magenta, stamens and style long exserted, grown ornamentally, close relative of the beautiful Pagoda flower (*C. paniculatum*)

*Lantana camara*

Tatara moa

Lantana

Weedy herb with dense hair and sharp prickles, leaves ovate, when crushed have a fetid minty odor, flowers borne in a flat head-like spike, corolla salverform, limb spreading, irregular though typical of many flowers of the family, opening yellow and turning pink-red with age, usually making a rainbow of colors on one flower head, grown ornamentally in temperate climes, stamens 4, fruit a shiny purple-black drupe

*Ocimum basilicum*

Miri, Miri Tahiti

Sweet Basil, Common Basil,  
Basilic Commun

Short herb, grown ornamentally and for culinary use, leaves ovate, serrate, with highly fragrant oil glands, opposite and decussate, glabrous, stems 4-sided, flowers borne in racemes, bilabiate, white

*Stachytarpheta urticifolia*

Blue Rat's-Tail

(*S. jamaicensis*, *Verbena* j., *Cymbus urticaefolius*)

Common herbaceous weed, stem somewhat woody at times, leaves opposite, ovate to elliptic, acute, upper surface rugose, margin dentate, petiole winged, inflorescence a long spike of embedded flowers, corolla purple, salverform, stamens 2, fruit a nutlet

Lauraceae

*Persea americana*

Avota

Avocado, Avocatier

(*Laurus persea*, *Persea gratissima*)

Medium to large trees, grown for its fruit used in cooking and for extracting avocado oil used in the cosmetics industry, leaves oblanceolate to elliptic, entire, pinnately veined, flowers borne terminally on branches in dense clusters, perianth yellow-green, roughly 5 mm long, fertile stamens 9, fruit green, pear-shaped with one large seed

Lecythidaceae

*Barringtonia asiatica*

Hotu, Hutu, Tira-Hutu, Tua

Fish-Poison Tree

(*Mammea a.*, *B. speciosa*)

Medium to large trees, leaves obovate, sessile, becoming striped with red-purple away from veins with age, alternate, clustered near branch tips, flowers terminal, petals 4, white, stamens many, maroon, filaments up to 15 cm long, fruit 4-sided, sepals and style persistent, developed fruit (fruit that has fallen from the tree and browned) contains high amounts of saponins harmless to humans but is ichthyotoxic (traditionally used to stun and collect fish).

Malvaceae

*Gossypium barbadense*

Vavai

Cotton, Sea Island Cotton

(*G. peruvianum*, *G. brasiliense*, *G. vitifolium*)

The species on the Gump property may indeed be *Gossypium hirsutum* (aka. *G. taitense*, *G. religiosum*) however the distinction between *G. barbadense* and *G. hirsutum* is slight, although *G. barbadense* is known to have been introduced from America and *G. hirsutum* has been collected in Tahiti as far back as Banks and Solander on the first voyage of Captain James Cook.

Shrub, 1-2 meters tall, leaves mostly glabrous, palmately 3-lobed, corolla yellow to pink, fruit usually 4-valved with large amounts of white lint emerging upon opening which is used for production of textiles

*Hibiscus rosa-sinensis*

Aoute, Aute, Aute-Maohi

Hibiscus, Rose of China, Jamaica Flower,  
Chinese Hibiscus, Shoebblack Plant

Common ornamental shrub, leaves ovate to lanceolate, minorly stellate-hairy, margin dentate to serrate, flowers solitary, petals 5, stamens twisted and fused into a well exserted staminal column, corolla usually bright red, at times pink, purple, orange, yellow, or white, petals used commercially in teas, for dyes, and in traditional medicine

*Hibiscus tiliaceus* ssp. *hastatus*

Purau, Burao, Fau, Hau, Faurau Maire

(*H. hastatus*, *H. tricuspis*, *Paritium t.*)

Abundant tree, found from the ocean up to the highest points on Moorea, trunks of soft white wood, leaves up to 30 cm long, cordate with acuminate apices, sepals 5, petals 5, yellow to yellow-orange with dark maroon-purple basally, the yellow fading to pink-red with age, stamens fused into staminal column, can be observed growing in a mangrove-like fashion, the wood is used for carving and the plant also has traditional medicinal value mostly topically for sores and cuts

- Malvaoviscus arboreus* Wax Mallow, Firecracker Hibiscus,  
(*M. mollis*, *Malvaoviscus a.*) Sleeping Hibiscus  
Low shrubs with alternate leaves, tomentose, leaves ovate, simple to 5-lobed, flowers borne on pendulous peduncles, never fully opening, corolla bright red, stamens fused into staminal column, slightly exerted
- Thespesia populnea* Miro, Amae Portia-Tree, Bois de Rose-Oceania  
(*Hibiscus populneus*)  
Short trees, leaves with stipules, leaves ovate-cordate to deltoid, glabrous, flowers solitary, white to yellow with maroon center, stamens fused into staminal column, fruit a capsule with multiple seeds and yellow sap used medicinally for centipede stings and other skin ailments, purportedly a symbol of peace to Tahitians
- Moraceae**
- Artocarpus altilis* Uru, Uru Maohi, Breadfruit, Arbor a Pain  
Maioire, Uru Anahonaho  
(*Sitodium altile*, *A. communis*, *A. incisus*)  
Widely grown tree with edible fruit which tastes almost, but not quite, entirely unlike bread, branches heavily marked with leaf and stipule scars, leaves commonly 60 cm long, ovate in outline, deeply pinnately lobed, leaves thick, staminate and pistillate flowers borne in spikes, fruit large, roughly spherical with a patterned surface, emitting large amounts of latex upon being picked. The fruit is usually prepared by baking it and removing the seeds but can also be sweetened and made into a jam-like desert spread
- Ficus elastica* Indian Rubber Tree  
Giant banyan with adventitious prop-roots and buttresses, leaves up to 45 cm long, oblong-elliptic, glossy, stipules pink, forming figs in axillary, sessile clusters
- Myrtaceae**
- Psidium guajava* Tuava, Tumu Tuava, Tuvava Guava, Goyavier  
(*P. pyriferum*, *P. pomiferum*, *P. pumilum*, *P. angustifolium*)  
Shrub to small tree with edible fruit used commonly in making juice, partly woody, young stems rectangular, leaves up to 20 cm long, elliptic, veins impressed from above, leaves irregularly yellow-green, flowers white with many stamens, fruit globose, yellow with pink or yellow flesh, native to the Pacific, grows like a weed in exposed areas, used medicinally by the Polynesians as an astringent and styptic
- Syzigium cumini* Pistache, Pistachier, Pistas,  
(*Eugenia c.*, *Myrtus c.*, *E. jambolana*, *S. jambolanum*) Jamelonier, Jamelonguier  
Large tree, glabrous leaves and stems, leaves lanceolate, flowers with 4 white petals borne in cymes with generally at least 3 flowers, stamens many, pink, fruit ovoid, purple to black
- Nyctaginaceae**
- Bougainvillea glabra* Bougainvillea  
Low shrub, glabrous, weakly spinose, leaves elliptic with acuminate tip, flowers partially concealed by conspicuous, showy bracts usually colored red to magenta, sometimes white, common ornamental plant
- Bougainvillea spectabilis* Tiare vareau Bougainvillea  
Shrub, tomentose, stem with curved spines, flowers partially to completely concealed by papery bracts much like *B. glabra* with similar color variation
- Onagraceae**
- Ludwigia octovalvis* Raau papaa Primrose-Willow  
(*Oenothera o.*, *Jussiaea erecta*, *J. suffruticosa*)  
Herbaceous perennial, leaves alternate, leaves narrowly lanceolate, flowers solitary, petals 4, yellow, notched at the tip, 4 lanceolate sepals alternate petals, stamens 8, surrounding stigma, fruit an 8-ribbed capsule
- Oxalidaceae**
- Oxalis corniculata* Patoa avaava, Patoa ahia Wood Sorrel  
(*Oxalis repens*)  
Perennial creeper, leaves palmately trifoliolate, blades obcordate, flower petals 5, oblanceolate and yellow, stamens 10, 5 long, 5 short, 5 styles, fruit pubescent, 5-lobed, cylindrical with acute tip
- Passifloraceae**
- Passiflora foetida* Pua Manini, Puka Heahea Love-in-a-Mist, Running Pop,  
Wild Water-Lemon  
Densely hairy vine with fetid odor (hence the name), tendrils coiled, leaves alternate, 3-lobed, margins wavy, flowers solitary, sepals 5, white internally, surrounded by pinnately branching bracts, petals 5, white, stamens 5, corona white with purple basally, stigmas 3, fruit a globose red-orange berry surrounded by persistent bracts
- Passiflora quadrangularis* Para Pautini Giant Granadilla

Liana with rectangular stems, tendrils long, leaves glabrous, ovate to elliptic, entire, petals white with pink markings, corona with purple bands, stamens 5, stigmas 3, fruit a green berry up to 30 cm long

Rosaceae

*Rosa* sp. (cultivated hybrid) Red Rose  
Cultivated red rose, flowers up to 5 cm in diameter, petals deep red

Rubiaceae

*Gardenia taitensis* Tiare Tahiti, Tiare, Tiare Maohi Tahitian Gardenia, Tiare  
Shrub, glabrous, leaves glossy, leaves obovate to oblanceolate, flowers white darkening with age, petals 7 or 8, sometimes 6, calyx 3-4 unequal lobes, stamens equal in number to petals formed, fruit rare, flower highly fragrant, worn decoratively behind the ear of men and women alike, also used in lei making, medicine, perfumery, and has various culinary applications

*Morinda citrifolia* Nono, Noni Noni  
Small tree or shrub, leaves opposite, glabrous, up to 45 cm long, elliptic, stems quadrangular, flowers with a sweet scent borne in clusters directly on the developing conglomerate fruit, fruit globose to irregular, green, dense with white flesh with a putrid, acidic taste, used in the production of medicines such as the highly marketed Noni juice available from healthfood stores and multi-level marketing companies worldwide, the uses ranging from diabetes to arthritis to you name it

*Mussaenda philippica* Mussaenda, Ashanti Blood  
Ornamental shrub, leaves pubescent, ovate to elliptic, opposite, sepals enlarged and pure white, corolla orange, petals 5, stamens yellow, similar to *M. erythrophylla* in seemingly every way except coloration

MONOCOTS

Agavaceae

*Cordyline fruticosa* Auti, Ti Ti Plant, Tree of Kings  
(*C. terminalis*, *C. australis*, *Convallaria* f., *Asparagus terminalis*, *Dracaena australis*, *Taetsia* f.)  
Shrub to small tree, usually planted ornamentally, leaves lanceolate, up to 70 cm long, variously colored with green, yellow, white, red, pink and purple, panicle up to 1 meter long, flowers sessile, perianth parts 6, pink to white, fruit a deep red globose berry

Amaryllidaceae

*Crinum asiaticum* Eri Eri Lily  
Ornamental shrub, leaves up to 1 meter long, basal and overlapping, flowers white, borne in an umbel, fragrant, up to 30 per umbel, stamens red, long

*Hymenocallis littoralis* Spider Lily, Lis Blanc  
(*Pancratium littorale*, *H. caribaea*)  
Cultivated ornamental, native to South America, leaves up to 120 cm long, broadest in the middle, flowers white, showy, filaments long, red tipped

Araceae

*Colocasia esculenta* Taro Taro  
(*Arum esculentum*, *C. antiquorum*, *C. e. var. antiquorum*)  
Cultivated food crop with edible tubers and leaves, tubers large, petioles up to 1 meter long, often pink-red, leaves peltate, hastate to saggitate, spathe green to yellow-orange, spadix pistillate basally, staminate apically, sterile in between

Arecaceae (Palmae)

*Cocos nucifera* Niu, Haari, Tumu Ha'ari, Coconut, Cocotier  
Ahuahupuru  
Cultivated food crop, former cash crop for Moorea, tall palm, trunks often curved, leaves 6 m long or longer, pinnae roughly 1 meter long, inflorescence up to 2 meters long, staminate flowers yellow, pistillate flowers thick and globose, fruit orange at maturity

Bromeliaceae

*Ananas comosus* Painapo, Painapu Pineapple, Ananas  
(*Bromelia comosa*, *B. ananas*, *A. sativa*)  
Food crop, grown ornamentally on the Gump Station property, short-stemmed herb reaching 1 meter in height, leaves in dense rosettes, margins toothed, inflorescence capped by rosette of leaves, flowers numerous, densely clustered, forming syncarp with yellow edible flesh. The pineapple variety of French Polynesia is known as "Queen Tahiti" and is smaller and sweeter than the more common larger pineapples grown for juice

Cyperaceae

*Cyperus compressus*

(*Chlorocyperus c.*)

Tufted annual sedge with fibrous roots, culms erect, 3-sided, leaves basal, shorter than culm, spikelets 3-12 on up to 5 rays subtended by leaf-like bracts, fruit a 3-sided achene

*Cyperus rotundus*

Perennial 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

*Fimbristylis dichotoma*

(*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

*Kyllinga nemoralis*

Mo'u Upo'o, Matie upo'o, Matie tahiti, Mo'u upo'onui

(*Cyperus k.*, *K. cephalotes*, *K. monocephala*, *Thyrocephalon m.*)

Perennial, creeping via rhizomes, culms basally leafy, up to 50 cm tall, though generally much shorter, inflorescence a white terminal globose head subtended by 3 or 4 spreading bracts, fruit an achene

Dioscoreaceae

*Dioscorea alata*

Ufi, Uhi, Ubi, Patara

White Yam

Climbing vine, clockwise twining, growing from long, edible tubers, stems quadrangular, winged, leaves opposite, ovate-cordate, veins all starting from the same point basally and reconnecting apically, produces turbinate bulbils, perianth green-yellow

*Dioscorea bulbifera*

Hoi, Igame

Bitter Yam, Air Potato

(*D. sativa*, *Helmia b.*)

Climbing vine with short, bifurcated tubers with bright blue-purple flesh eaten only in time of famine, stems glabrous, reddish-green, cylindrical to quadrangular but not winged, producing axillary bulbils, pistillate and staminate flowers borne on different spikes

Heliconiaceae

*Heliconia bihai*, *H. rostrata* and other cultivars

(*Musa bihai*)

Heliconia, Lobster-Claw, Sexy-Pink

Balisier, Hanging Lobster Claws

Ornamental shrub, flowers erect (pendulous in *H. rostrata*), alternating on large inflorescence, petals fused into boat-shaped keel, red to pink, often with yellow to green tips or interiors, leaves with prominent midrib, long ovate

Musaceae

*Musa x paradisiaca ssp. sapientium* Meia

(*M. balbisiana x M. acuminata*)

Banana, Bananier

Tree-sized herb with huge leaves, the leaf bases forming a pseudo-trunk, leaves commonly 1-2 meters long, inflorescence pendulous, purple to maroon bracts containing pistillate and staminate flowers, producing sterile fruit in many varieties

Orchidaceae

*Vanilla planifolia*

Vanira

Vanilla, Vanille

Climbing vine, leaves alternate, glossy, lanceolate to elliptic, flowers green-yellow, fragrant, uncommon, bilateral, petals smaller than sepals. Much argument over this species. Fosberg considers the species on Moorea to be *V. planifolia* (alt. *V. fragrans*, *V. aromatica*, *V. mexicana*, *V. tiarei*, *Myrobroma fragrans*) the vanilla of trade, and considers *V. tahitensis* to be a separate species grown on Tahiti, Raiatea, and Tahaa. Other authors consider *V. tahitensis* to either be a hybrid (possibly of *V. planifolia x V. pompona*) or a contrived name. The Lycèe Agricolè on Moorea says that the species grown there is *V. tahitensis*, but admits it is in fact be a hybrid. Welsh mentions that *V. pompona* may be a synonym of *V. fragrans* and thus *V. planifolia*, so the hybrid theory may be moot. In short, there is a possibility that the vanilla grown here is a hybrid, but until a genetic workup has been completed, the vanillas of the Societies can be considered at least functionally as the same species - maybe.

Pandanaceae

*Freycinetia impavida*

Ieie, Iare, Fara-Pepe

Freycinetia

(*Victoriperra i.*, *F. victoriperra*, *F. parksii*, *F. demissa*)

Climbing vine, leaves long lanceolate with spiked midrib, spreading asexually via complex networks of stolons (see Des Marais, 1999), flowers and fruit rare. Planted October 1999, may not persist.

*Pandanus tectorius*

Fara

Screwpine, Pandanus

Shrub to tree, branches erect with conspicuous aerial prop roots, leaves clustered at branch tips, leaves linear, commonly 1 meter long, bearing spikes along margin and midrib, staminate spadices elliptic, pistillate spadices pedunculate, fruit a large conglomerate head. This species name is tentative at best, with well over 500 spp. within the genus along with the fact that *Pandanus* is known to have high levels of intraspe-

cific variation (plus the plant on the Gump property appears to be an ornamental cultivar).

#### Poaceae (Gramineae)

- Chrysopogon aciculatus* Papapa Golden Grass, Golden Beardgrass  
(*Andropogon a.*, *Rhaphis aciculata*, *Andropogon acicularis*)  
Creeping mat-forming perennial grass spreading via stolons, culms erect to ascending, leaves mostly basal, inflorescence a loose panicle, spikelets 3, purple, 1 sessile, glumes as long as spikelet, the upper with a short awn, second lemma with one long awn
- Cynodon dactylon* Bermuda Grass  
(*Panicum d.*, *Cabriola d.*)  
Rhizome spreading lawn grass, culms erect or ascending, often red-green, leaf slightly hairy, inflorescence a whorl of 3-7 racemes with a purple hue, lemmas ovate, keeled
- Echinochloa colona* Barnyard Grass, Jungle Rice  
(*Panicum colonum*)  
Tufted annual grass, culms erect or ascending, leaf glabrous to minutely hairy, inflorescence a panicle of alternating compact racemes with red-maroon color, glumes ovate
- Eleusine indica* Tamamau Goose Grass  
(*Cynosurus indicus*)  
Tufted annual grass forming clumps, culms prostrate to ascending, leaf folded along conspicuous midrib, inflorescence a whorl of 4-6 spikes with one extra spike arising visibly below the others, spikelets 3-7 flowered, glumes lanceolate-ovate
- Melinis repens* Natal Grass, Natal Redtop  
(*Rhynchelytrum r.*, *Tricholaena rosea*, *Saccharum r.*)  
Annual grass, culms loosely tufted, erect, leaf extends horizontally from near midpoint of culm, inflorescence a red-pink oblong panicle with ascending branches, spikelets with long hairs
- Oplismenus compositus* Basket Grass  
(*Panicum compositum*)  
Stoloniferous creeping perennial grass, culms slanting, glabrous, leaf blade lanceolate, up to 3 cm wide, margins wavy, inflorescence a panicle bearing alternating racemes, lower glume with purple awn
- Paspalum conjugatum* Sour Paspalum, T-Grass, Hilo Grass  
Creeping perennial grass, culms erect, spreading via reddish stolons, leaves mostly glabrous, inflorescence consisting of two spreading racemes, lower glume absent
- Paspalum paniculatum* 'Ofe' ofe  
Perennial grass, culms erect to ascending, up to 1 meter long, leaves up to 40 cm long, partially hairy with long hairs basally, inflorescence consisting of 15-20 spreading racemes, lower glume absent
- Paspalum scrobiculatum* Nonoha  
(*P. orbiculare*, *P. s. var orbiculare*)  
Tufted perennial grass, culms erect, leaves narrow, up to 25 cm long, inflorescence a panicle of 2-6 spikes, spreading or ascending, spikelets brown

#### Zingiberaceae

- Alpinia purpurata* Red Ginger  
(*Guillania p.*, *Languas p.*)  
Ornamental herb, leaves up to 70 cm long, inflorescence terminal, up to 20 cm long, consisting of bright red-pink bracts mostly concealing white flowers, capsules subglobose

#### PTERIDOPHYTES

##### Davalliaceae

- Davallia solida* Ti'ati'a mou'a Giant Hake's Foot, Leather Fern  
(*D. elegans*)  
Highly dissected fern, terrestrial or epiphytic, pinnae triangular, sori oblong, indusium tubular opening towards margin, rhizome used medicinally

##### Dryopteridaceae

- Nephrolepis hirsuta* Amoa  
Pinnate fronds, leaflets basally spurred, sori near margin with reniform indusia

##### Polypodiaceae

- Polypodium vitiense* Maire  
(*P. pustulatum*)  
Pinnately lobed fern growing epiphytically or from a spreading rhizome, sori large, lacking indusia

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