# Biology and Geomorphology of Tropical Islands

Integrative Biology 158: Environmental Science, Policy, and Management 107

Research Papers: Fall 2003

Richard B. Gump South Pacific Biological Research Station:
Moorea, French Polynesia
University of California, Berkeley

# Biology and Geomorphology of Tropical Islands

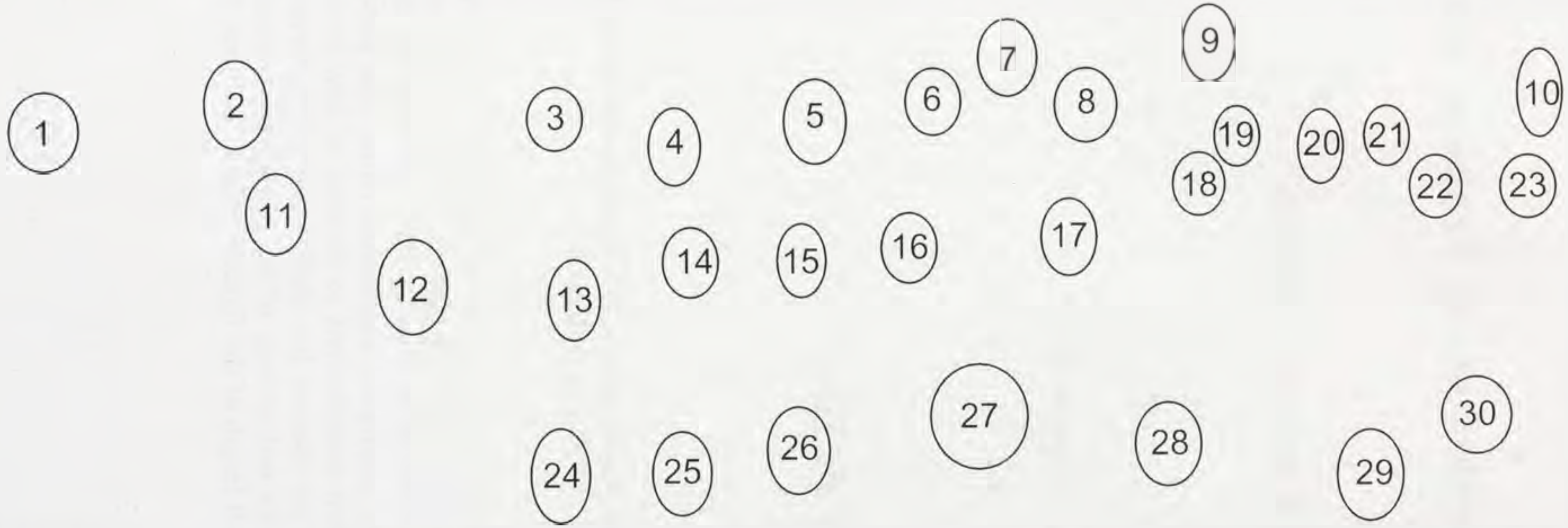
## Moorea Research Papers

## Volume 12

## Fall 2003

Integrative Biology 158; Environmental Science, Policy, and Management 107
University of California, Berkeley

**Front Cover**: *Partula* sp., an individual in a relic wild population discovered in September 2003. All nine of the endemic partulid gastropod species that evolved on Moorea were thought to have been extinct in the wild by 1987, following the disastrous introduction of an invasive predatory gastropod, *Euglandina rosea*. The partulid tree snails of Moorea are famous for their contributions to theories of how evolutionary radiations occur. Ongoing research on Moorea has shifted toward conservation and understanding the population dynamics and ecology of the precarious remnants of the indigenous terrestrial snail biota. Shell length of the figured adult = 15.5 mm. Photo by Carole Hickman.



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**View southeast across Cook's Bay from the Gump Station with Mt. Mouaputa. Photograph by Jere Lipps.**

# The Moorea Class 2003

## Introduction

The Moorea Class is a very special experience for undergraduates. Officially known as "Biology and Geomorphology of Tropical Islands" (Environmental Sciences and Policy Management 107 and Integrative Biology 158), it is a single semester-long class spent on the Island of Moorea, just 11 kilometers from Tahiti in French Polynesia. Moorea is the perfect teaching situation for field science--a tropical paradise with much geology, oceanography, anthropology and biology visible all around. For the Berkeley undergraduates who have taken the course there, Moorea changed their lives. We intend that the course will take these students from lecture hall into the world of professional biologists, geologists or whatever, through the creation, design and implementation of their own original research project. The course is designed much like a research expedition—planning and supply, field reconnaissance, field research, and presentation of the final results. We spend three weeks at Berkeley preparing and equipping ourselves to go into the field on Moorea. Once there a week or so is spent in exploring all the many environments and opportunities of the island and of Tahiti nearby. Then comes research, and Moorea holds many unique research opportunities, from the tops of the spectacular mountains to the depths of the forereef. Unique plants and animals are found there, as well as rock formations, soils, and human activities spanning 1500 years. Capt. James Cook and Mr. Charles Darwin explored these islands and came away with great insights. Our students have also come away from their two months on the islands with similar insight into scientific subjects, as well as themselves. Each student selected their own research topic and pursued it more or less in their own way. Back in Berkeley during the last two weeks of the semester, the students finalized their work and delivered an oral and written presentation.

Richard B. Gump, of San Francisco department store fame, donated land and facilities on Cook's Bay, Moorea, to UC Berkeley in the mid-1980s to build a research facility. UCB students and faculty are indeed fortunate that he did so, and that the development of the Richard B. Gump South Pacific Research Station has been enhanced by the Gordon and Betty Moore Foundation over the years, so that these experiences could be available to undergraduate and graduate students, and to faculty researchers.

Faculty members and Graduate Student Instructors with expertise in terrestrial biology, botany, marine biology, and geology, from both IB and ESPM teach the course. Some of the team gave lectures at Berkeley while others provided instruction and assistance on Moorea. Five faculty took part in the field instruction for several weeks each, and three GSIs lived and worked with the class for the entire nine weeks on Moorea.

The Moorea course was started in 1991, and has been offered every Fall semester since then. Over 200 students have done research in the course on their own original projects, presented their results in the annual Symposium on the Biology and Geomorphology of Tropical Islands, and wrote scientific papers published in this series of books. These books are widely distributed to libraries and personnel at Berkeley, on Moorea and Tahiti, as well as elsewhere. Many of the students' research results have also been published in regular scientific journals.

Once again in 2003, the course was immensely successful. Twenty-two students did research on plants, animals and physical processes on Moorea. It was a creative and stimulating experience, and it changed all of lives in many ways. This book presents the written research results produced by the class of Fall 2003.

## Acknowledgments

The Moorea field course is a complex undertaking for students and instructors alike. It could not be done successfully by any single individual. In fact, we owe a large debt of gratitude to the students, faculty, Graduate Student Instructors, and our colleagues at Berkeley and on Moorea who made the 2003 class successful. We all appreciated and remember with wonderful feelings the good times, camaraderie and excitement we shared with them. 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.

At Berkeley, we received help from a number of other faculty and staff who presented lectures and workshops on a variety of topics. These people included Brigette Bankay (UCB Environmental Health and Safety), Jim Hayward (UCB Diving Safety Officer), Norma Kobzina (Bioscience and Natural Resources Library), David Lindberg and Brent Mishler (Integrative Biology), and David Smith and Pang Wai Chan (VLSB Visualization Center). We especially thank Steve Owen, Tim Herrlinger, Rebecca Pauling, and Robert Shaw (Integrative Biology) and Gleoria Bradley-Sapp (ESPM), who kept the course going administratively. The staff of the University and Jepson Herbaria, the Museum of Paleontology, the Bioscience and Natural Resources Library, and the Visualization Center provided assistance with and use of their resources.

On Moorea, we also are grateful to many people, especially the staff of the R. B. Gump South Pacific Research Station, without whom none of this would have been possible. Frank and Hinano Murphy of Moorea and Tahiti, and many other Mooreans, provided much assistance and interaction. The staff of the French research station on Moorea (CRIOBE) provided access to their library and collections. Gordon and Betty Moore have continued to support the Gump Research Station, making it one of the finest field laboratories in the tropics.

Without all this help of such various kinds, our students would not have had this special opportunity to learn about science, a unique environment, a new culture, and especially, themselves. They have been changed forever!

Jere H. Lipps, Professor, Integrative Biology. Course Coordinator.
Rosie Gillespie, Professor, ESPM
Carole Hickman, Professor, Integrative Biology
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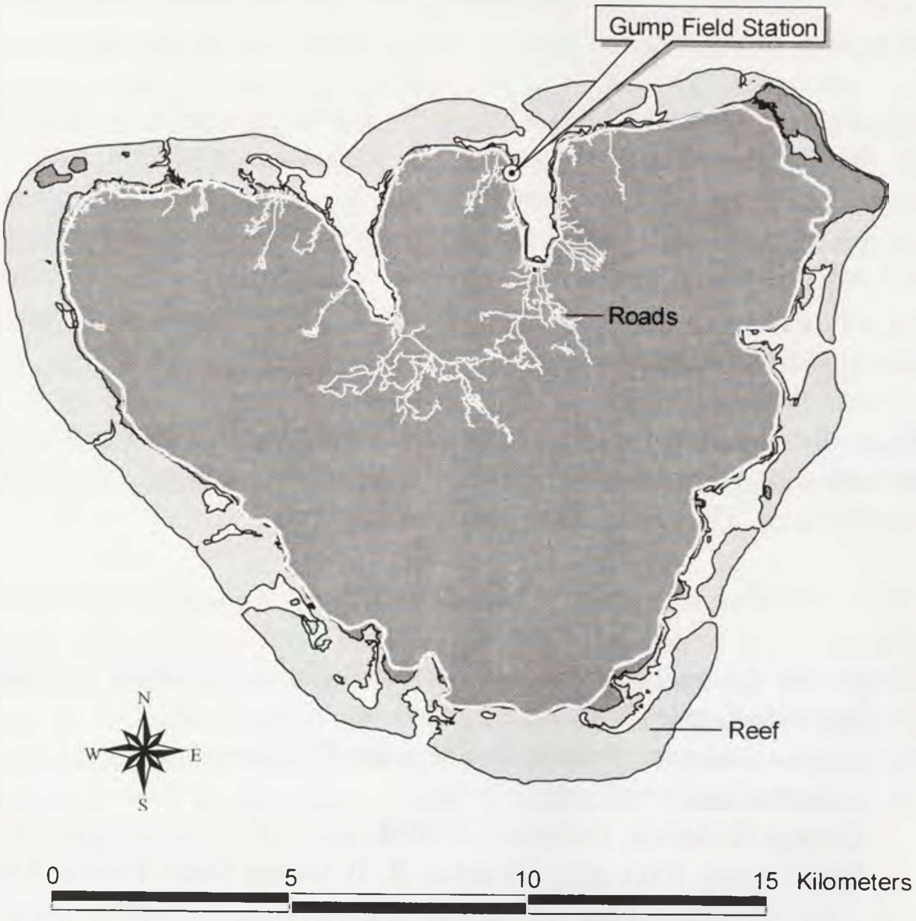
Island of Mo'orea, Society Islands, French Polynesia



# Biology and Geomorphology of Tropical Islands

Moorea Student Papers

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## CONTENTS

# Feeding Biology of the Cushion Sea Star, *Culcita novaeguineae*, in Moorea, French Polynesia

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ABSTRACT. The cushion sea star *Culcita novaeguineae* is a corallivore that often exhibits preferential feeding patterns in reef communities. In this study, a general survey was done to determine the time of day for feeding, feeding patterns, and the prey choice of *C. novaeguineae* individuals found on the fringing reef located next to the University of California - Berkeley Gump Research Station in Moorea, French Polynesia. It was found that *C. novaeguineae* is typically a night feeder and has a feeding preference for coral rubble while significantly avoiding sediment ($P < .00085$) and *Halimeda distorta* ($P < .03$). In laboratory experiments, *C. novaeguineae* shows a strong feeding preference for *Acropora austera* Dana over *Montipora efflorescens* Bernard, *Porites lobata* Dana, *Fungia horrida* Dana, *Actinodiscus ? sp.*, *Halimeda distorta*, sediment, rocks covered with *Padina boryana*, and coral rubble. In additional laboratory studies, *C. novaeguineae* exhibits a preference for *Pocillopora meandrina* Dana over *Pocillopora damicornis* (L.) and *Acropora austera* Dana. *Culcita novaeguineae* was not found to eat either type of *Pocillopora* during the current field observations, but was found to eat both in previous studies. These findings suggest that there is another factor influencing *C. novaeguineae* food choice in the wild other than individual preference. The small amount of *Acropora* present may have promoted *C. novaeguineae* to find other sources of food. The selective feeding of *C. novaeguineae* on young colonies of *Acropora* may affect the abundance of this coral in the reef system.

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## Introduction

Echinoderms are very distinctive organisms found throughout the world's ocean. This phylum includes feather stars, sea stars, brittle stars, urchins, sand dollars, and sea cucumbers. All echinoderms are exclusively marine and are identified as having pentamerous symmetry in adult form, developing an internal skeleton made of many dermal ossicles, and having a water vascular system (Brusca and Brusca, 2003). One subclass of the echinoderms is the asteroids, or sea stars. Asteroids are characterized as having a flattened central disc, typically five radial arms with open ambulacral grooves, and a highly adaptable stomach that is everted when feeding (Lutz, 1986). Because of their stomach, asteroids make unique and intriguing test subject for feeding studies.

Nearly all asteroids are carnivorous, feeding on many different types of organisms, from benthic invertebrates like molluscs, other echinoderms, and crustaceans, to pelagic vertebrates like fish (Lutz, 1986). Because not all areas of the world ocean contain the same organisms, asteroids can vary in food preference from one area to another. Several asteroids prefer particular food types, whereas others become scavengers and grazers (Gosliner *et al.*, 1996). For these reasons, it is impossible to extrapolate from one species of asteroid to another, concerning individual feeding preferences.

One species of asteroid, *Culcita novaeguineae* Muller & Troschel, 1842, is a common coral predator found in reef communities from the Indian Ocean to the Central Pacific Ocean (Marsh and Marshall, 1983). Glynn and Krupp (1986) conducted a study of this species of asteroid in Hawaii to determine if the sea stars had a feeding preference when consuming coral. They found that *C. novaeguineae* exhibits a stronger preference for *Pocillopora damicornis* (L.) and *Pocillopora meandrina* Dana over other coral species including *Porites compressa* Dana, *Montipora verrucosa* (Lamarck), and *Fungia scutaria* (Lamarck). This selective feeding led to the conclusion that *C. novaeguineae* could significantly affect the relative abundance of corals in Hawaiian reefs. Another study found *C. novaeguineae* periodically feeds on corals and other types of organisms that it does not primarily prefer (Potts, 1982). Menge (1972) explained this behavior by saying that sea stars will often consume unwanted prey if it is always abundant and readily available.

*Culcita novaeguineae* is also found in Moorea, French Polynesia along the fringing reef adjacent to the University of California - Berkeley (UCB) Gump Research Station.

However, unlike in Hawaii, the coral genus *Pocillopora* is extremely rare in this area. Instead, the asteroids are usually observed eating other types of coral including *Porites* cf. *lobata* Dana, *Montipora efflorescens* Bernard, and *Acropora austera* Dana. Moreover, the asteroids have also been found consuming larger quantities of sediment, algae and coral rubble than quantities of live coral. It is possible that the asteroids found in Moorea have a preference for these items over coral, differing from their relatives in Hawaii. It is also possible that these asteroids have the same preference as the *C. novaeguineae* found in Hawaii but because *Pocillopora* is found so rarely in their habitat, they eat whatever is more abundant. The objective was to determine what time of day the asteroids feed and what is their typical prey. The percent coverage of potential food source was assessed in the present study to see if there is a correlation between what the asteroids are feeding on and the abundance of the food item. This study was designed to test the hypothesis that *C. novaeguineae* shows preference when eating corals that are found near the UCB Gump Station. Furthermore, this research evaluated the concept that *C. novaeguineae* has adapted to consuming coral types other than species of *Pocillopora* because *Pocillopora* is found in such small amounts.

## Methods and materials

### *Study Site*

All fieldwork was conducted at the UCB Gump Research Station, which is located on the western side of Cook's Bay in Moorea (17°30'S, 149°50'W), French Polynesia (Figure 1). The oceanic area adjacent to the station is characterized by a fringing reef that extends roughly 60-70 meters offshore. The reef region is mostly composed of sediment interspersed with coral platforms and live coral heads. Those coral genera dominating the area include *Montipora*, *Acropora*, *Fungia*, and *Porites*. The reef region ends in an abrupt slope that extends to the bottom of the bay. The study area ends at the beginning of this slope because very little live coral is found with increasing depth and those that are living are too difficult to access by free diving.

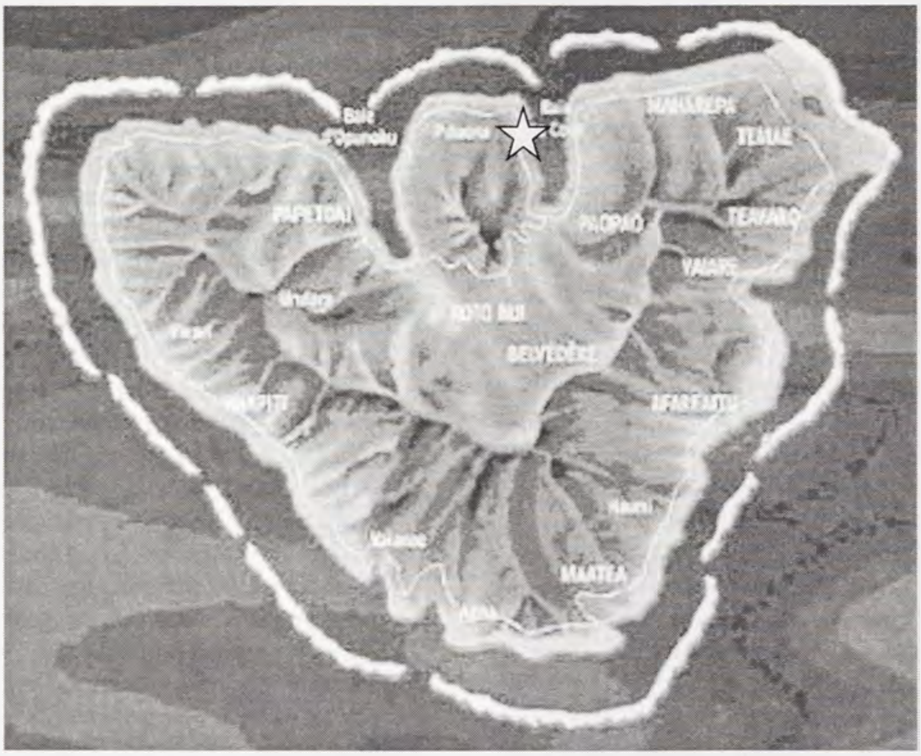

**Figure 1.** This figure is a map of Moorea, French Polynesia (Tahiti.org, 2003). The white star on the map of Moorea indicates the study site.

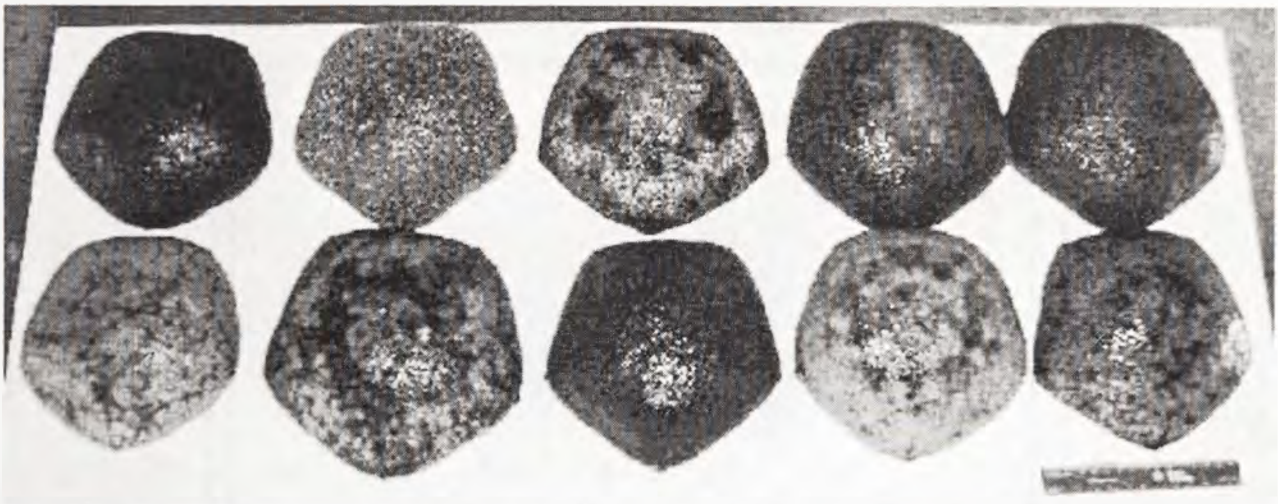

**Figure 2.** Test subjects used for the controlled feeding trials. To represent scale, a 15-centimeter ruler is located in the bottom right hand corner.

*Study Organism*

All asteroids studied were from the species *Culcita novaeguineae*, which are often found inhabiting barrier and fringing reefs in areas of the Indo-Pacific, including French Polynesia (Gosliner *et al.*, 1996). This species is characterized as having five radial arms that are highly webbed, causing the asteroid to look more like a pillow with five rounded corners. Coloration of *C. novaeguineae* is highly variable ranging in colors from purple to orange to green, with many organisms displaying several colors simultaneously.

*Fieldwork*

For one week, fieldwork was conducted three times a day (5 a.m., 1 p.m., and 9 p.m.) to observe what times the asteroids were feeding and what they were feeding on. At each time indicated, snorkeling was done along the reef edge for a distance of approximately 80 meters. When an asteroid was spotted, the color of the individual was recorded. Then, the asteroid was flipped over to see if the stomach was everted, meaning that the asteroid was ingesting material. If the asteroid was eating, the type of food was also recorded. This snorkeling was repeated for one day at the end of the laboratory work to help insure that what was found was not a weekly variation or random finding.

*Percent Coverage of Food Items*

Percent coverage was determined for each type of food item (*Montipora efflorescens* Bernard, *Acropora austera* Dana, *Porites lobata* Dana, *Actinodiscus ? sp.*, *Fungia horrida* Dana, *Halimeda distorta*, sediment, rocks covered with *Padina boryana*, and coral rubble) on and along the edge of the reef, covering an area of approximately 882 $m^2$. Percent coverage was determined by swimming in a zigzag pattern over the study area. Over 250 two meter by two meter quadrants were used to cover the entire study area. In each quadrant, the estimated percent coverage of each item was recorded. After all transects had been performed, all percentages were summed together for each of the nine potential food sources. To determine the percent cover for each food type, these sums were divided by the total area studied.

*Food Preference*

Laboratory controlled feeding experiments were conducted to determine the feeding preference for each asteroid collected. Ten different individuals (Figure 2) were collected from the study area and held in a flow-through tank in the station's wet lab. After collection, each asteroid was left without for 24 hours so as to purge their digestive system. Nine different food items were collected from the study site and offered to the specimens. These items were *Acropora austera* Dana, *Montipora efflorescens* Bernard, *Porites lobata* Dana, *Fungia horrida* Dana, *Actinodiscus ? sp.*, *Halimeda distorta*, sediment, rocks covered with *Padina boryana*, and coral rubble. Each food item was placed equal distant from each other around the circumference of a circle that was placed within a 1.25 m. by 2.45 m. outdoor tank adjacent to the wet lab. The asteroid was placed in the center of the food circle and observed

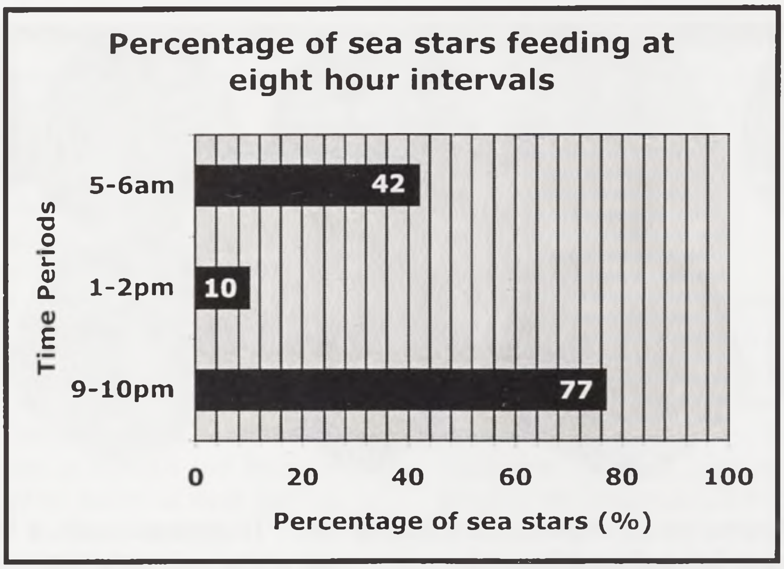

**Figure 3.** The percentage of sea stars feeding at eight-hour intervals as found in six days of field observations.

every half hour from 6 pm to 6 am. At each time interval the location and feeding status of the asteroid was recorded. So as not to disturb the normal behavior of the cushion stars, all observations were made under a red light.

To determine if the Moorean cushion stars differed from their Hawaiian relatives in food preference, another feeding test was conducted using the same ten asteroids. Prior to the experiment, the asteroids were left without food for 48 hours to once again purge their system. Ten tanks were set up with *A. austera*, *P. meandrina*, and *P. damicornis* placed in a triangle on the bottom of the tank. The asteroids were placed in the middle of the triangle and observed every half hour from 6 pm to 6 am. At each time interval the location and feeding status of each asteroid was recorded. Once again, a red light was used to make the visual observations.

*Data Analysis*

To determine if a correlation between food abundance and types of food being consumed in the wild existed, a binomial test was used. Each time that the asteroid was found eating a given food item counted as a success. The number of successes for each food type was divided by the total number of successes for all food choices to determine the percentage observed. The percent cover of each food item was used as the probability that a success would occur. All of this information was entered into the binomial test to find the z value. Using the z value, the normal distribution for each item was determined and this number was subtracted from one to get the P values (Table 1). The same statistics were also applied to the controlled feeding experiments (Tables 2 and 3).

## Results

*Field Observations of Feeding*

As a first step in evaluating the feeding patterns of *Culcita novaeguineae*, sea stars were observed in the wild. Upon examining *C. novaeguineae* in the field, it was found that a large percentage of sea stars were feeding primarily at night (Figure 3). Less than half (42%) of the cushion stars ate during the time period 5am to 6am. Only 10% of the animals were found consuming food from 1pm to 2pm while 77% were discovered eating from 9pm to 10pm.

During field observations, the types of food that *C. novaeguineae* was found consuming were recorded. The types of food that *C. novaeguineae* was found ingesting included hard corals, algae, sediment, and soft coral (Figure 4). Coral rubble was the food type that the cushion stars were found eating most often (28 out of 85 observations). Sediment and algae covered rocks were preferred 22 and 23 times out of 85, respectively. *Porites* was consumed six out of 85 times and *Acropora* was consumed only three out of 85 times. Those items being consumed only once consisted of *Montipora*, *Halimeda*, and *Actinodiscus*. *Fungia* was spotted being consumed by the cushion stars during preliminary observations but was not observed to be eaten by the sea stars during this study period.

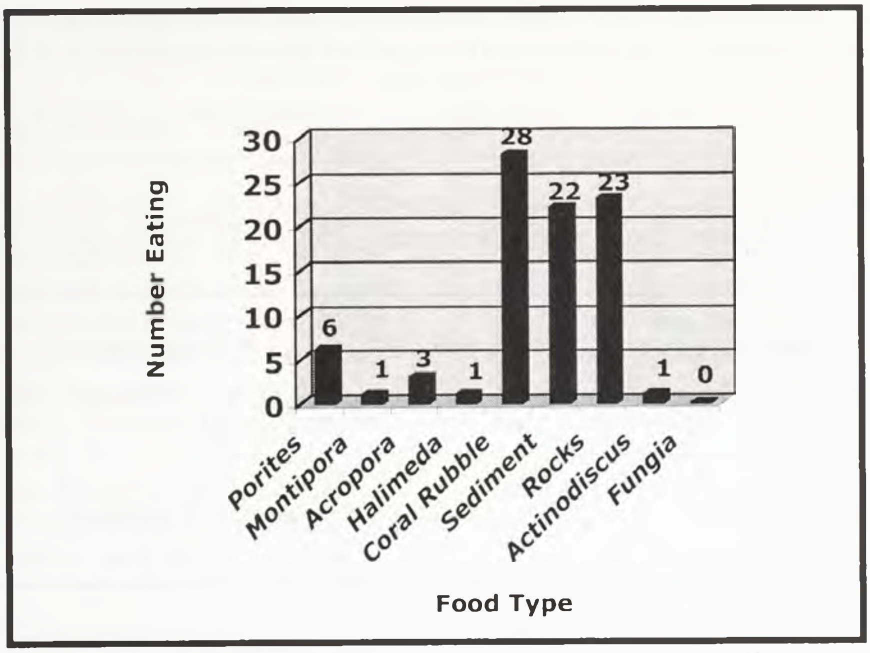

**Figure 4.** Found eating distribution for the asteroids. This data was collected from Sept. 21, 2003 to Sept 29, 2003 during 18 field observations.

*Percent Coverage of Food Items*

To better understand the amount of food available to the cushion stars, the percent coverage of each food item was estimated. The study area was composed mostly of sediment (41.39%) and rock and coral platform (33.85%) with occasional colonies of coral and algae interspersed (Figure 5). Coral rumble was the third most dominant feature at 10.12%. *Porites* and *Acropora* were the two most dominant corals present (8.97% and 1.06% respectively). All other corals were present at less than 1% (*Montipora* at 0.36%, *Fungia* at 0.19%, and *Actinodiscus* at 0.05%). The only type of algae measured in this study was *Halimeda* and it comprised 4% of the covered area.

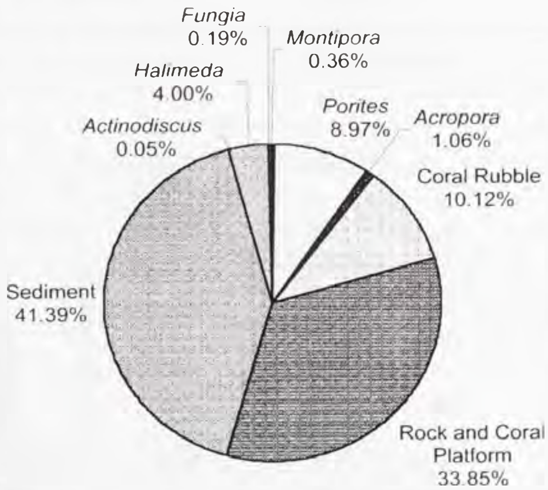

**Figure 5.** The percent coverage of each of the nine food items along the edge of the reef next to the UCB Gump Station after evaluating over 250 different quadrants from the area.

**Table 1.** Binomial test results for the correlation between food abundance and types of food being eaten in the wild.

| | *Montipora* | *Porites* | *Acropora* | Coral Rubble | Rock | Sediment | *Actinodiscus* | *Halimeda* | *Fungi* |
|---|---|---|---|---|---|---|---|---|---|
| number eating in field | 1 | 6 | 3 | 28 | 23 | 22 | 1 | 1 | |
| expected number eating | 0.306 | 7.6245 | 0.901 | 8.602 | 28.7725 | 35.1815 | 0.0425 | 3.4 | 0.27 |
| P value | 0.422637252 | 0.316969721 | 0.173629568 | 6.47172E-06 | 0.099001898 | 0.000843372 | 0.322680912 | 0.027984489 | 0.7615220 |

**Table 2.** Controlled feeding trial results for ten different asteroids.

| | Rock | Sediment | *Acropora* | *Montipora* | *Fungia* | *Halimeda* | Coral Rubble | *Actinodiscus* | *Pori* |
|---|---|---|---|---|---|---|---|---|---|
| Total number eating | 0 | 0 | 48 | 0 | 3 | 2 | 0 | 18 | |
| Expected Number Eating | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | |
| P value | 1.7733E-68 | 1.7733E-68 | < 1E-68 | 1.7733E-68 | 0.004809736 | 5.54858E-05 | 1.7733E-68 | 0.004371127 | 1.7733E |

*Correlation Results*

To determine if a correlation existed between the abundance of individual food choices and the number of times *Culcita novaeguineae* was found consuming the item, a binomial statistics test was run. For most of the food choices, the experimental data did not significantly deviate from expected values (Table 1). This finding indicates that *C. novaeguineae* did not prefer nor avoid eating these prey items. There were three food items that *C. novaeguineae* did show preferential feeding patterns for. *Culcita novaeguineae* showed a feeding preference for coral rubble ($P < .000007$). However, *C. novaeguineae* significantly avoided sediment ($P < .00085$) and *Halimeda* ($P < .03$).

*Food Preference*

To better understand individual feeding preferences, controlled laboratory feeding trials were run. During these feeding experiments, *C. novaeguineae* showed a significantly stronger preference for *Acropora* over all other food options (Table 2), eating it 48 times out of 71 ($P < 1\mathrm{x}10^{-68}$). *Culcita novaeguineae* showed a slight preference for *Actinodiscus*, eating it 18 times out of 71 ($P < 0.0044$). *Fungia*, eaten 3 out of 71 times, and *Halimeda*, eaten 2 out of 71 times were both significantly avoided by *C. novaeguineae* ($P < 0.0049$ and $P < 5.6\mathrm{x}10^{-5}$, respectively). All other food choices were not eaten and therefore were strongly significantly avoided by *C. novaeguineae* (all with $P < 1.8\mathrm{x}10^{-68}$).

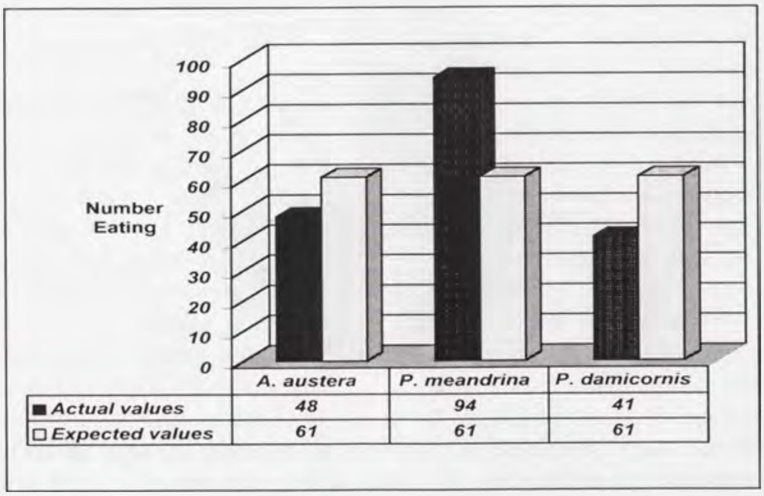

**Figure 6.** The results from the *Acropora* versus *Pocillopora* controlled feeding test.

**Table 3.** P values for the results from the *Acropora* versus *Pocillopora* controlled feeding test.

| | *A. austera* | *P. meandrina* | *P. damicornis* |
|---|---|---|---|
| P values | 0.017836987 | 7.68082E-07 | 0.000272961 |

In the second controlled feeding experiment, it was found that *C. novaeguineae* significantly exhibited a high food source preference for *P. meandrina* (Figure 6 and Table 3). Of the total 183 times the cushions stars were found eating, they were consuming *P meandrina* 94 times, 33 more times than the expected value of 61 ($P < 7.7x10^{-7}$). *Culcita novaeguineae* was found to significant avoid both *A. austera* ($P < 0.018$) and *P. damicornis* ($P < .0003$), eating them only 48 and 41 times respectively.

## Discussion

Previous studies have shown that *C. novaeguineae* is a coral predator in many reef communities, showing preference for certain corals over others (Goreau *et al.*, 1972; Glynn and Krupp, 1986). Those preferred by the cushion stars include *Pocillopora*, *Acropora*, and *Porites*. The objective of this study was to determine if these preferences were also valid for the Moorean cushion stars located on the fringing reef adjacent to the UCB Gump Research Station by testing the hypothesis that *Culcita novaeguineae* prefers to eat *Acropora* to other food types available in the reef system.

Initial field observations indicated that *C. novaeguineae* is primarily a night feeder, eating only occasionally during the day. Day feeding most likely occurs when the cushion star does not obtain enough food during the night. Field results also indicated that *C. novaeguineae* prefers to eat coral rubble to all other available food options. However, laboratory studies found that *C. novaeguineae* does show the strongest preference for *Acropora* when presented with an equal opportunity to all nine food choices tested. These findings suggest that there is another factor, other than individual preference, that is influencing prey choice in the wild. *Culcita novaeguineae* has rather short arms, making it difficult for the star to climb up large pieces of coral and causing it to preferentially eat smaller colonies of coral (Goreau *et al.*, 1972). Coral rubble was typically found on the bottom in easy reach of the cushion stars while most of the *Acropora* colonies found within the study site were growing on top of large colonies of *Porites*. By growing on top of other corals, *Acropora* may escape being eaten by the cushion stars simply because they cannot reach them. Those *Acropora* colonies that were found growing on the bottom were usually dead and often with a sea star next to them indicating that the star may have eaten the colony. Therefore, it is possible that *C. novaeguineae* is hindering the growth of *Acropora* colonies on the bottom substrate and influencing them to grow on top of other large coral colonies.

In the second laboratory study, *C. novaeguineae* was found to prefer *Pocillopora meandrina* to both *Acropora austera* and *Pocillopora damicornis*. The reasons why the cushion stars were never found eating these corals in the wild were simply because only one colony of *P. meandrina* and no colonies of *P. damicornis* found within the study area. However, because the cushion stars still show the highest preference for *P. meandrina*, the Moorean cushion stars are no different in feeding preference from their Hawaiian relatives, suggesting that perhaps *P. meandrina* was once more abundant in the area than at present. It is possible, however, that *Culcita novaeguineae* ate the *Pocillopora* simply because it was something new or possibly in better health than the *Acropora* it was offered. In the future, longer term studies would need to be performed to insure these trends continue over a longer period of time.

## Conclusions

*Culcita novaeguineae* is an important predator in reef communities. By focusing its feeding on only certain types of corals, *C. novaeguineae* holds the ability to influence both the abundance and locality of corals within the reef system. In the reef community located next to the UCB Gump Research Station in Moorea, French Polynesia, *C. novaeguineae* appears to be influencing *Acropora* to grow on top of other coral types while killing off those that begin growing on the bottom substrate. Furthermore, it is possible that *C. novaeguineae* has had a similar influence on other corals in the past and may continue to affect the composition and location of coral within the reef community in the future. In the future, work needs to be done at other sites around the island and throughout

French Polynesia to see if this trend continues. The impact of *Culcita novaeguineae* in the coral reefs of French Polynesia needs to be understood before the possible loss of coral species richness becomes a reality.

## Acknowledgements

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## LITERATURE CITED

Brusca RC, Brusca GJ (2003) Invertebrates, Second Edition. Sinauer Associates, Inc., Sunderland, Massachusetts, pp. 801-837

Goreau TF, Lang JC, Graham EA, Goreau PD (1972) Structure and ecology of the Saipan reefs in relation to predation by *Acanthaster planci* (Linnaeus). Bulletin of Marine Science 22:113-152

Gosliner TM, Behrens DW, Williams GC (1996) Coral Reef Animals of the Indo-Pacific: Animal Life from Africa to Hawai'i exclusive of the vertebrates. Sea Challengers, Monterey, California, p. 255

Glynn PW, Krupp DA (1986) Feeding biology of a Hawaiian sea star corallivore, *Culcita novaeguineae* Muller & Troschel. Journal of Experimental Marine Biology and Ecology 96(1):75-96

Lutz PE (1986) Invertebrate Zoology. Addison-Wesley Publishing Company, Reading, Massachusetts, pp. 639-696

Marsh LM, Marshall JI (1983) Some aspects of the zoogeography of Northwestern Australian echinoderms (other than holothurians). Bulletin of Marine Science 33(3):671-687

Menge BA (1972) Foraging strategy of a starfish in relation to actual prey availability and environmental predictability. Ecological Monographs 42(1):25-50

Tahiti.org (2003) The Tahitian information and tourism center. Retrieved December 15, 2003 from http://www.tahiti.org/images/maps/moorea.jpg

Potts DC (1982) Crown-of-thorns starfish – man induced pest or natural phenomenon? In: The ecology of pests, some Australian case histories, (eds) RL Kitching, RE Jones, CSIRO, Canberra, Australia, pp. 55-86

# Feeding and Habitat Selection of the Sea Cucumber *Holothuria leucospilota* in Moorea, French Polynesia

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ABSTRACT. The distribution of a holothurian species *Holothuria leucospilota* is limited to only two populations found in a shallow channel and lagoon at Point Aroa reef on Moorea, French Polynesia. As a deposit feeder, this holothurian species ingests sediment for food resources. This study examined whether sediment grain sizes and organic matter content affect their habitat selection. Feeding experiments compared sediment samples from the channel and lagoon to those in designated reef zones, where *H. leucospilota* is absent. This study also compared the organic matter absorption rates and sediment turnover rates between the two populations. Grain sizes did not affect preferences for sediment from any location, as this species selected for large-sized (1.8-2.0 mm) particles in a randomly given sample. However, *H. leucospilota* showed some preference for sediment with higher organic matter, as in both the channel and lagoon. The mean organic matter absorption rate for the lagoon population was 4.20 g/day and for the channel population 4.06 g/day. The annual sediment turnover rates were similar between these two populations, which averaged 5974 $g/m^2$/year for the lagoon and 5128 $g/m^2$/year for the channel. Both the organic matter absorption rate and sediment turnover rate were proportional to holothurian mass. The large uptake of organic matter and the rapid turnover of sediment indicate that *H. leucospilota* play a vital role in biologically changing the substratum composition of their habitat.

## Introduction

Holothurians (Echinodermata: Holothuroidea), commonly known as "sea cucumbers," are marine invertebrates that have a cylindrical and elongate body form. Tube feet on the ventral side allow them to move and attach to substrate. *Holothuria leucospilota* (Brandt, 1835) is a deposit feeder most commonly found curled under coral or rocks, with anterior ends stretched out to feed on nearby sediment. This species has irregular periods of feeding, with no consistent times of the day. Its feeding tentacles are elaborately branched, and are extended when feeding to grasp particles and deliver them into the mouth. While the holothurian feeds, it removes organic matter from the sediment and excretes nutrient-depleted sediment from its anus in the form of fecal pellets. This continual process significantly alters the sediment quality of the ocean floor, thereby impacting the ecosystem and the other fauna that live within it.

*Holothuria leucospilota* is a localized holothurian in Moorea, as I found only two distinct populations in a shallow channel and lagoon at Point Aroa. This species is absent in the lagoonal environment leading up to the reef edge, though oddly, other holothurian species dominated this area. There are many factors that may explain why they prefer the channel and lagoon. The purposes of this study are (a) to determine whether food selection influences habitat selection and (b) to observe the role of holothurians in bioturbation, the process of turning over sediment.

Sediment is consistently altered by both physical and biological processes in the ocean. Biological processes seem to dominate most coral reefs, as calcium carbonate deposits from corals and other organisms contribute loose sediment to the seafloor (Scoffin 1992). According to Scoffin's review of taphonomy, the study of the processes of dead organisms in sedimentation, the greatest amounts of loose sediment are most prevalent in channels—where sediment is transported by tidal currents—and lagoons, where sediment is shifted by burrowers. These are the types of environments where *H. leucospilota* are found at Point Aroa. Sediment generally contains inorganic elements (such as silica), organic detritus, the fecal matter of organisms, and microorganisms (diatoms, foraminifera, and bacteria) (Massin 1982b). Holothurians, among many deposit feeders, ingest all this matter when sediment passes through their digestive tract. Muscles in the pharyngeal bulb, stomach, and posterior intestine mechanically grind sediment and absorb the organic matter from particles. The stomach maintains a nearly neutral pH of 5-7 and seawater also serves as a buffer in the digestion process (Massin 1982a).

Previous research has shown a positive correlation between holothurian densities and the amount of organic carbon available in their environment (Sibuet 1984). A specific study on the distribution of another species, *Holothuria scabra*, indicated that grain size and organic matter of sediment affected its distribution (Mercier et al 2000). No similar studies have been done on *Holothuria leucospilota* to understand its feeding ecology and how that influences its habitat selection and the role in changing its habitat through bioturbation. Three holothurian studies have been conducted on Moorea within the last 15 years. Dr. John Pearse of the University of California, Santa Cruz, in a 1989 survey discovered 19 distinct holothurian species on the island. In 1996, Filiatrault conducted a survey on the distribution of 15 holothurian species, including *H. leucospilota*, to find that sediment grain size did not affect distribution and concluded that *Bohadschia argus* and *Holothuria atra* were generalists in terms of feeding, but no statements were made regarding the feeding mechanism of *H. leucospilota*. The most recent holothurian study in Moorea was completed in 1999, when Brusch observed the sediment turnover rate of *H. atra*.

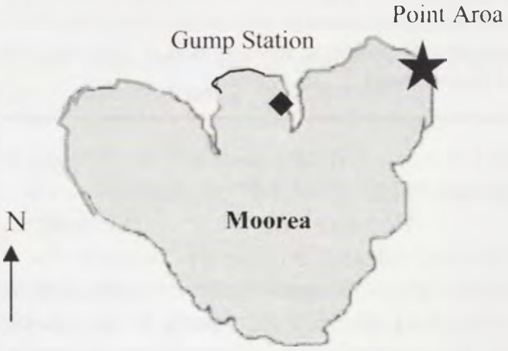
The present study contains four parts in analyzing the feeding ecology of *H. leucospilota*:
(1) Feeding experiments tested whether this species preferred one zone's sediment to another based on grain size and/or organic matter content of each sample.
(2) If there is no preference, whether this species has the ability to select for a certain grain size from any random sample.
(3) Organic matter absorption rates were determined to predict amounts of organic matter removed from the environment.
(4) Sediment turnover rates suggested how this species affected its habitat by moving sediment around.

## Materials and Methods

### *Site of study*

This research was conducted from October to November of 2003 on the island of Moorea, French Polynesia (17°30'S, 149°50'W), located in the South Pacific (Fig. 1). The island is 1.2 million years old, covering 125 km$^2$ of area. Field studies were made at Point Aroa (17°28.402'S, 149°46.419' W), a barrier reef located on the northeast side of the island. The reef contains a variety of corals and a rich diversity of flora and fauna. On land, a rocky carbonate platform constructed from ancient eroded coral meets the shore. Sections of the platform isolate a narrow channel and back lagoon from the reef. *H. leucospilota* is limited to only these two areas and is absent in the lagoonal environment leading to the reef edge. Interestingly, this lagoonal environment contained other holothurian species. The lagoonal environment was divided into four different zones (Fig. 2) for sediment collection. Laboratory experiments were performed at the University of California, Berkeley's Richard B. Gump South Pacific Research Station (17°24.4'S, 149°33.0'W) at the edge of Cook's Bay.

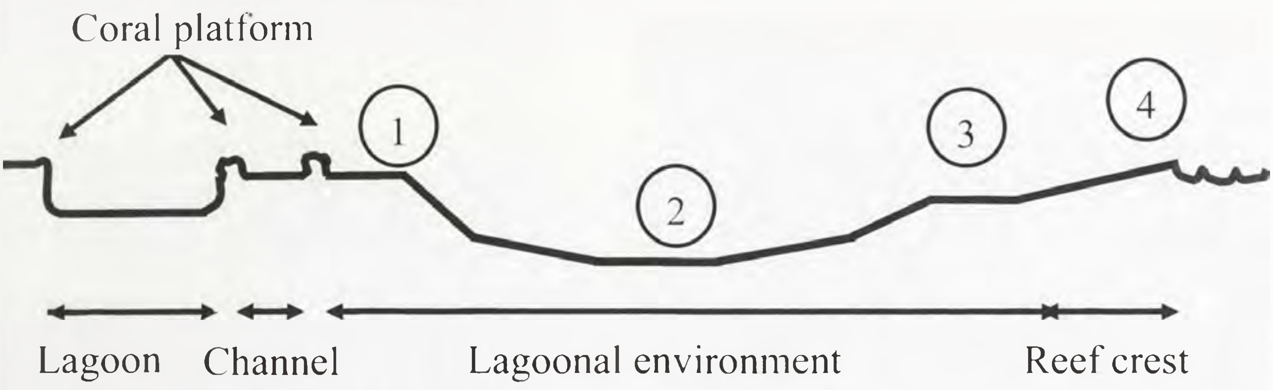
**Figure 1.** Map of Moorea, French Polynesia.



### *Preliminary observations*

Preliminary studies were conducted on the sediment grain size distribution and *H. leucospilota's* feeding behavior. In the wet lab, by sieving sediment samples collected from the lagoon, channel, and various zones leading up to the reef edge, the percentage weight of different grain sizes showed some degree of difference among the samples. Sediment was also observed under a dissecting microscope to determine shapes of grains and presence of algae covering the outside of grains. In the field, four individuals of this species were removed from the lagoon and placed in the various zones, where none was previously found, to observe whether they would feed on this new sediment. Each extended its tentacles to sample the new sediment around them, and retracted them immediately without feeding. Observations to determine whether feeding occurred were made every 15 minutes. After 45 minutes, only one of the four started ingesting this new sediment.

**Figure 2.** Reef zonation at Point Aroa. Sediment samples collected from the lagoon, channel, and four designated zones.



Four other individuals were also used as controls to test whether stress from an unfamiliar environment was the cause of the previous four not feeding. These four controls were lifted from their feeding area in the lagoon to another location in the lagoon a few meters away. Immediately they all began feeding. All eight holothurians were removed from their original area while in the process of feeding. These preliminary observations suggested that sediment preference may play a role in habitat selection.

*Measuring densities*

The densities of both populations were mapped in the channel and lagoon. Using 50 m-transect tape, the length and width of the channel and lagoon were measured. One-meter lanes were established along the length of each area with colored flags as lane markers. By snorkeling and wading through each lane, the number of holothurians found was counted separately for each population. The density was obtained by dividing the number of individuals by each area.

*Collection of specimens and sediment*

Twelve individuals were collected from the channel and twelve individuals were collected from the lagoon to obtain a total of twenty-four specimens. These specimens were transported back to the Gump Research Station and maintained in a circular cement tank ($c = 7.22$ m, $r = 1.14$ m, $h = 0.56$ m) at an outdoor wet lab facility. The tank was filled to a sediment height of 3.00 cm and a drainpipe maintained a water depth of 0.55 m. Fresh seawater (30°C, 37 o/oo) was recirculated through the tank at a flow rate of 6.00 L $\text{min}^{-1}$. Returning to Point Aroa with buckets ($c = 1.00$ m, $r = 0.14$ m, $h = 0.53$) and troughs, 0.0216 $m^3$ of sediment nearby holothurian individuals was collected from both the channel and lagoon. Because this holothurian species did not burrow, I extracted only the upper 10 cm of surface sediment. There were 0.0108 $m^3$ of sediment collected from each of the four designated zones in the lagoonal environment (Fig. 2), perpendicular to shore and 65 m east of the light post on the carbonate platform as a marker. A total of six buckets of sediment were collected from these six different areas. Temperature and salinity measurements were taken from each area. The different experiments performed in the wet lab required multiple returns to the site to make separate sediment collections of the same amounts for every feeding trial conducted and for both the grain size partitioning analysis and organic matter analysis.

*Feeding trials*

Feeding experiments were conducted in a water table (2.36 x 0.99 x 0.15 m) partitioned by Plexiglas into ten feeding cells (48 x 33 cm) and ten blank cells (48 x 17 cm) (Fig. 3A). Each feeding cell was further divided in half by wooden sticks to hold different sediment samples collected from the six different locations. A drainpipe maintained a water depth of 0.10 m, with recirculating seawater (30°C, 37 o/oo) entering at a flow rate of 1.029 L $\text{min}^{-1}$.

**Figure 3.** Feeding trials water table design. (A, top) Image of entire water table in wet lab facility during a feeding trial. (B, bottom) Schematic diagram identifying the contents of each cell.

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Channel | Zone 1 | Channel | Zone 2 | Channel | Zone 3 | Channel | Zone 4 | Channel | Lagoon |
| Lagoon | Zone 1 | Lagoon | Zone 2 | Lagoon | Zone 3 | Lagoon | Zone 4 | Lagoon | Channel |
| Blank | | Blank | | Blank | | Blank | | Blank | |
| Blank | | Blank | | Blank | | Blank | | Blank | |

**Figure 4.** Specimen images. (A, left) Branched feeding tentacles protruding from anterior end of specimen to grasp sediment. (B, right) Identification of specimens by tagging.

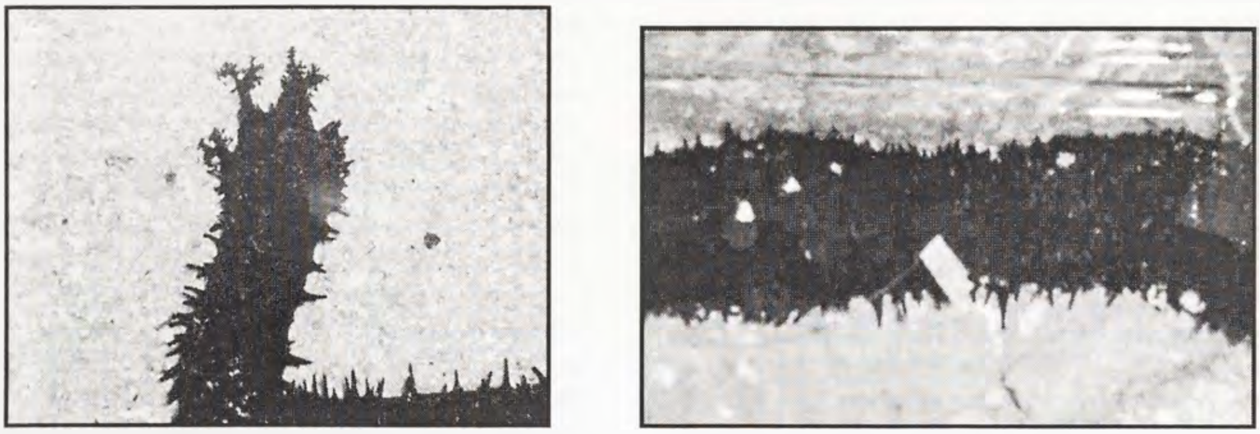


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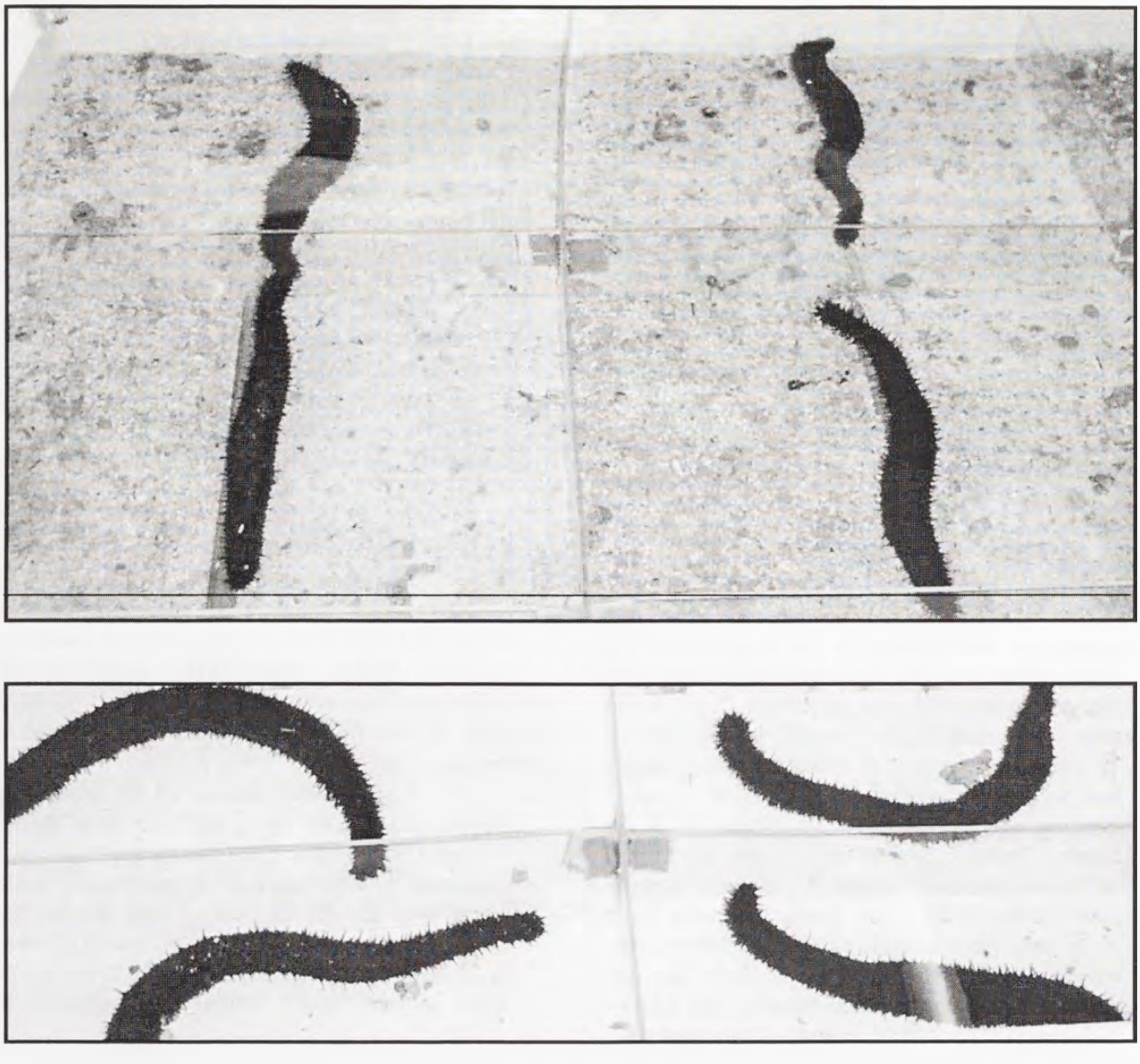
**Figure 5.** Close-up images of cells in water table. (A, top) Four feeding cells depicted with specimens aligned along center of each cell. (B, bottom) Four blank cells with specimens excreting fecal pellets.



Combinations of varying types of sediment from the six different locations filled each cell to a sediment height of 2.00 cm according to the diagram in Figure 3B. The channel versus lagoon cells served as controls in which no preference was expected.

Before beginning feeding trials, 5.0 g of each sediment type (channel, lagoon, zones 1-4) were removed from the water table and placed in six 250 ml beakers for measuring organic matter later. These samples were dried in a Fisher Scientific Isotemp oven at 60°C for 24 hours and preserved in a freezer at 8°C. Another 200 g of each sediment type was removed and sieved through 2 mm, 1.8 mm, 500 µm, 250 µm, and 125 µm sieves. These samples were also dried at 60°C for 24 hours and weighed.

Ten specimens were used for these feeding experiments, five from the channel population and five from the lagoon population (Fig. 4A). They were transferred from the circular tank to the ten blank cells in the water table to remain in these cells for 24 hours excreting fecal pellets. This "starvation period" purged their digestive tracts so that they would begin feeding trials with a clear gut. Fecal pellets were removed periodically, at least every six hours, to prevent holothurians from re-ingesting the fecal pellets. After 24 hours, each specimen was identified by tying fishing line with numbered tags around the circumference of the body (Fig. 4B). Each specimen was weighed on an OHAUS Portable Advanced C7600 balance 60 seconds after it was removed out of the water, allowing expulsion of water out of the anus, to obtain the weight of each specimen without water in the gut.

To begin a feeding trial, each specimen was placed in the center of each feeding cell, aligning their bodies along the wooden stick that separated the two types of sediment in the cell (Fig. 5A). The five specimens from the channel population were placed in the first row of the water table and the five specimens from the lagoon population were placed in the second row. The holothurians were allowed to feed for 12 hours and the side of the cell each specimen was feeding on was recorded every 30 minutes. Feeding was indicated by the extension of the buccal tentacles around the mouth that grasp sediment particles to deliver into the mouth. Five feeding trials were conducted, with three night trials from 6:00 pm to 6:00 am and two day trials from 6:00 am to 6:00 pm. Both day and night trials were conducted because this species had irregular periods of feeding. Each specimen was rotated to a different cell in its own row for each trial to ensure each specimen feeds on all the combinations of sediment offered. Between each trial, the specimens were removed from the feeding cells and placed in the blank cells to starve for 24 hours before beginning the next trial (Fig. 5B). Fecal pellets were collected with a baster in ten separate 40 ml beakers after each trial, dried and weighed according to the methods previously used for samples taken from the water table.

### *Grain size partitioning analysis*

An aquarium tank (0.80 x 0.52 x 0.43 m) was filled with 3.00 cm high of randomly chosen sediment from one of the six locations. Prior to starting experiment, approximately 200 g of sediment sample was extracted from the tank, sieved through 2 mm, 1.8 mm, 500 µm, 250 µm, and 125 µm sieves, dried at 60°C for 24 hours, and weighed.

The ten specimens previously used in the feeding trials were starved for 24 hours in the blank cells of the water table prior to this experiment with fecal pellets periodically removed. Then all ten specimens were placed in this tank and allowed to feed for 12 hours. After feeding, the specimens were transferred back to the blank cells to starve for 24 hours with fecal pellets removed. Because the amount of fecal matter produced per individual was too small to sieve through, the fecal pellets of all ten individuals were combined. The experiment was repeated over a period of five days to obtain a larger sample size. This accumulated fecal sample was sieved through the same sieves, dried and weighed the same way the tank sample was treated.

### *Organic matter analysis*

Six aquarium tanks (0.52 x 0.30 x 0.43 m) were each filled with 3.00 cm high of sediment taken from the six different locations (channel, lagoon, zones 1-4). Approximately 5.00 g of sediment were extracted from each tank, dried at 60°C for 24 hours and preserved in the freezer at 8°C.

For this experiment, all 24 specimens originally collected from the site were placed through a 24-hour starvation period, then randomly divided into four specimens per tank, where they fed for 12 hours. They starved for another 24 hours and fecal pellets were collected in 24 different 40 ml beakers. Once dried, all 24 fecal samples were weighed and placed in separately labeled plastic bags (16.51 x 14.92 cm) for storage in the freezer.

Upon returning to the University of California, Berkeley laboratory, all preserved samples were measured for the amount of organic matter contained per gram of dried sediment. Approximately 3.00 g of each sample was measured on a Mettler AE 240 balance and ashed in a Thermadyne 30400 muffle furnace at 500°C for 30 hours. Each sample was weighed again. The amount of organic matter removed was determined by the difference between the initial and final masses of each sample. The rate of organic matter absorption by each individual holothurian was calculated based on the amount of fecal matter produced per day.

## Results

### *Feeding trials*

The amount of time spent feeding on each type of sediment was tabulated. Since both day and night trials were conducted, a t-test was applied to determine whether data obtained were statistically similar. The t-test showed that data obtained from both day and night trials were 96% statistically similar. A binomial test was then applied to the data to determine whether there is a preference for one sediment type over the other in the binary comparison (Table 1). If $Z > 1.960$ (95% confidence), then there is preference, apparent in 3 out of the 10 cells tested: Channel vs. Zone 3, Channel vs. Zone 4, and Lagoon vs. Zone 1. All six sediment samples are composed of mostly large grains (1.8-2.0 mm) and small grains are minimal (Table 2). The organic matter content varied, with the greatest amounts in the lagoon and channel and some organic matter in zone 1. Zones 2, 3, and 4 contained the least amount of organic matter (Table 3).

The amount of fecal matter produced for each specimen was recorded for each of the five trials (Table 4). The average amounts of fecal matter produced by each individual over the five trials were graphed against each individual's body mass to determine if there is a correlation (Fig. 6). A positive correlation was found ($R^2 = 0.94$, $P < 0.001$). The average fecal matter produced per individual in a population was computed, 4.62 g ($s = 2.20$) per individual in the channel and 5.20 g ($s = 1.73$) per individual in the lagoon. These averages were used in extrapolating the sediment turnover rates in each population.

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**Table 1.** Summary of Z-values from binomial test results for feeding trials. Each Z-value represents degree of preference for the sediment samples compared. There is preference if $Z > 1.960$.

| | Zone 1 | Zone 2 | Zone 3 | Zone 4 | Lagoon |
|---|---|---|---|---|---|
| Channel | 0.42 | 1.60 | 2.28 | 5.39 | 0.43 |
| Lagoon | 2.18 | 0.15 | 0.85 | 1.50 | 1.33 |

**Table 2.** Grain size distribution by percent weight in each sediment sample.

| Sediment | > 2 mm | > 1.8 mm | > 500 μm | > 250 μm | > 125 μm | < 125 μm |
|---|---|---|---|---|---|---|
| Lagoon | 43.0% | 42.6% | 11.1% | 2.0% | 0.8% | 0.9% |
| Channel | 19.9% | 40.8% | 25.0% | 11.9% | 1.2% | 1.2% |
| Zone 1 | 13.7% | 24.6% | 49.8% | 9.9% | 0.5% | 1.5% |
| Zone 2 | 15.9% | 37.0% | 35.7% | 9.9% | 1.2% | 0.3% |
| Zone 3 | 12.4% | 51.1% | 26.4% | 7.9% | 0.9% | 1.4% |
| Zone 4 | 25.7% | 27.1% | 42.2% | 3.8% | 0.8% | 0.5% |

**Table 3.** Organic matter content expressed as the mass per gram dry sediment sample.

| Sediment | OM (g/ g dry sed) |
|---|---|
| Lagoon | 1.736 |
| Channel | 1.611 |
| Zone 1 | 0.7175 |
| Zone 2 | 0.1427 |
| Zone 3 | 0.1497 |
| Zone 4 | 0.1317 |

**Table 4.** Mean fecal matter produced per population. Results were averaged from five feeding trials.

| **Specimen id.** | **Holothurian Mass (g)** | **Fecal Mass (g)** | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | **Trial 1** | **Trial 2** | **Trial 3** | **Trial 4** | **Trial 5** | **Average over 5 trials** | **Average for population** |
| Channel - 1 | 202.5 | 8.5 | 0.6 | 2.8 | 6.2 | 5.6 | 4.74 | |
| Channel - 2 | 298.6 | 23.5 | 0.7 | 9.0 | 1.0 | 3.8 | 7.60 | |
| Channel - 3 | 238.2 | 6.7 | 9.8 | 2.2 | 5.9 | 2.7 | 5.46 | |
| Channel - 4 | 115.9 | 3.8 | 0.0 | 2.0 | 1.3 | 1.1 | 1.64 | |
| Channel - 5 | 176.6 | 8.1 | 3.1 | 1.6 | 3.5 | 1.9 | 3.64 | **4.62 (s = 2.20)** |
| Lagoon - 1 | 219.7 | 5.5 | 0.9 | 7.7 | 5.9 | 4.6 | 4.92 | |
| Lagoon - 2 | 243.3 | 0.4 | 8.9 | 6.7 | 13.4 | 5.1 | 6.90 | |
| Lagoon - 3 | 257.0 | 11.7 | 16.6 | 0.6 | 4.5 | 0.8 | 6.84 | |
| Lagoon - 4 | 152.8 | 3.2 | 3.3 | 4.9 | 1.6 | 0.8 | 2.76 | |
| Lagoon - 5 | 182.3 | 10.5 | 5.2 | 3.0 | 3.6 | 0.7 | 4.60 | **5.20 (s = 1.73)** |

**Figure 6.** Holothurian mass compared to mean fecal mass obtained over five trials.

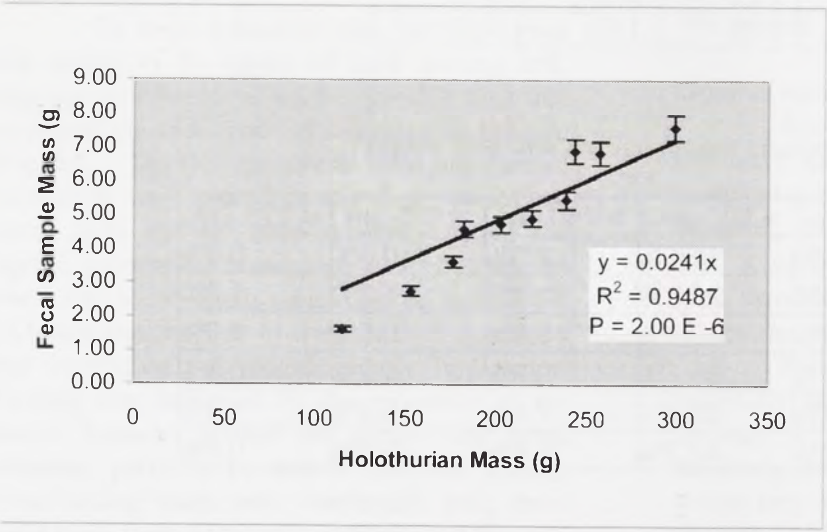
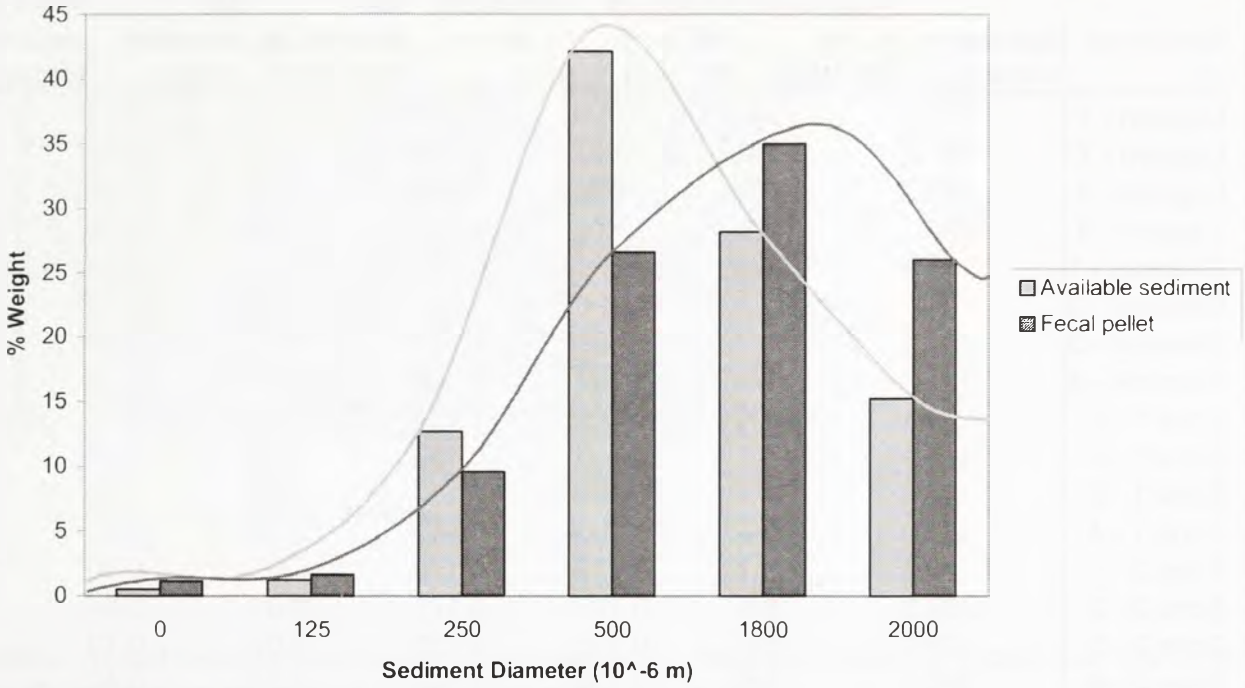


**Figure 7.** Sediment grain size frequency distribution. Trend lines compare grain sizes available for feeding and which sizes were ingested.



*Grain size partitioning analysis*

Grain sizes of both the available sediment and fecal pellets were compared (Fig. 7). The middle-sized grains (>500 μm) are the most abundant in this random sediment sample. There is, however, a trend towards selection for larger grains (1.8-2.0 mm). Non-selection for small grains cannot be explained by whether holothurians were not choosing them or whether not enough small grains were available for them to choose from.

*Organic carbon analysis*

The organic matter content in samples was expressed as the amount of organic matter per gram of dried sediment (Table 5). The organic matter removed by the holothurian during digestion as sediment passes through the gut was the difference between the amounts of organic matter found in the fecal pellets and the sediment available for feeding. The OM absorbed was calculated by multiplying the OM removal by the fecal mass produced in a day. OM absorption rates were compared between the channel and lagoon populations and a t-test indicated that these rates were 91% statistically similar, with no significant difference between the two populations. Means were computed for the OM absorption rates observed in the channel and lagoon populations. The body masses and fecal masses of these 8 specimens were also used in graphing purposes to determine their relationships with OM absorption. There is a direct proportion between holothurian mass and OM absorption ($R^2 = 0.8960$, $P<0.001$, Fig. 8) and between fecal mass and OM absorption ($R^2 = 0.9681$, $P<0.001$, Fig 9). This confirms the positive correlation between holothurian mass and fecal mass demonstrated in the feeding trials previously discussed.

*Sediment turnover rates*

Data was collected from the feeding trials. In a 12-hour feeding period, holothurians only spend about 5 hours of that time actually feeding. The average fecal mass produced for that feeding time was used to predict how much fecal matter was produced in a given day and year, extrapolated over both populations, based on their densities measured in the field, to obtain an annual sediment turnover rate (Table 6).

**Table 5.** Organic matter absorption rates. OM removal is the difference between the sediment and feces OM. OM absorbed per day is determined by OM removal times the fecal mass produced in a day.

| Specimen id | Specimen mass (g) | Fecal mass (g dry sed/day) | Sediment OM (g/ g dry sed) | Feces OM (g/ g dry sed) | OM removal (g/ g dry sed) | OM absorbed (g/day) | Mean OM absorbed (g/day) |
|---|---|---|---|---|---|---|---|
| Lagoon - 1 | 331.5 | 4.4 | 1.616 | 0.348 | 1.27 | 5.58 | |
| Lagoon - 2 | 141.2 | 2.2 | 1.616 | 0.188 | 1.43 | 3.14 | |
| Lagoon - 3 | 253.2 | 2.6 | 1.616 | 0.068 | 1.55 | 4.02 | |
| Lagoon - 4 | 294.1 | 2.8 | 1.616 | 0.166 | 1.45 | 4.06 | 4.20 |
| Channel - 1 | 195.0 | 2.5 | 1.396 | 0.152 | 1.24 | 3.11 | (s = 1.01) |
| Channel - 2 | 306.4 | 3.7 | 1.396 | 0.144 | 1.25 | 4.63 | |
| Channel - 3 | 372.4 | 5.2 | 1.396 | 0.145 | 1.25 | 6.51 | |
| Channel - 4 | 114.1 | 1.6 | 1.396 | 0.158 | 1.24 | 1.98 | 4.06 |
| Zone 1 - 1 | 239.1 | 11.6 | 0.703 | 0.162 | 0.54 | 6.27 | (s = 1.96) |
| Zone 1 - 2 | 146.1 | 14.2 | 0.703 | 0.153 | 0.55 | 7.80 | |
| Zone 1 - 3 | 152.0 | 14.3 | 0.703 | 0.157 | 0.55 | 7.80 | |
| Zone 1 - 4 | 147.0 | 13.6 | 0.703 | 0.141 | 0.56 | 7.65 | |
| Zone 2 - 1 | 150.3 | 6.0 | 0.178 | 0.144 | 0.03 | 0.20 | |
| Zone 2 - 2 | 252.3 | 6.5 | 0.178 | 0.171 | 0.01 | 0.04 | |
| Zone 2 - 3 | 178.0 | 5.7 | 0.178 | 0.156 | 0.02 | 0.12 | |
| Zone 2 - 4 | 340.0 | 9.6 | 0.178 | 0.137 | 0.04 | 0.40 | |
| Zone 3 - 1 | 145.3 | 19.8 | 0.150 | 0.141 | 0.01 | 0.18 | |
| Zone 3 - 2 | 171.2 | 10.9 | 0.150 | 0.142 | 0.01 | 0.08 | |
| Zone 3 - 3 | 168.8 | 13.8 | 0.150 | 0.149 | 0.00 | 0.02 | |
| Zone 3 - 4 | 202.6 | 14.6 | 0.150 | 0.139 | 0.01 | 0.16 | |
| Zone 4 - 1 | 183.6 | 13.0 | 0.156 | 0.146 | 0.01 | 0.13 | |
| Zone 4 - 2 | 264.5 | 6.2 | 0.156 | 0.147 | 0.01 | 0.06 | |
| Zone 4 - 3 | 265.8 | 6.4 | 0.156 | 0.145 | 0.01 | 0.07 | |
| Zone 4 - 4 | 199.2 | 7.2 | 0.156 | 0.147 | 0.01 | 0.07 | |

**Figure 8.** Holothurian mass is compared to organic matter absorption for the four specimens from the channel and four specimens from the lagoon.

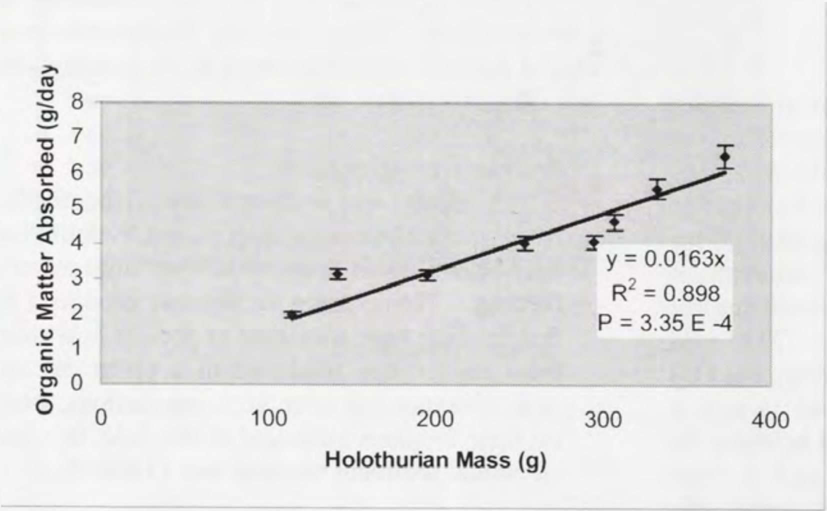


**Figure 9.** Fecal mass is compared to organic matter absorption for the four specimens from the channel and four specimens from the lagoon.

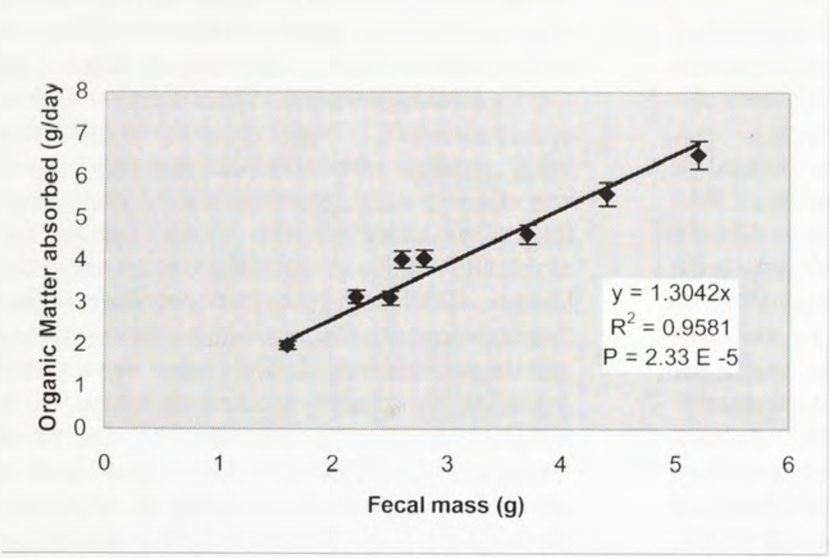


**Table 6.** Annual sediment turnover rate for each population. Fecal production and feeding times determined from the experiments extrapolated to annual sediment turnover rate.

| | Channel | Lagoon |
|---|---|---|
| Average feeding time (hrs) | 5.8 | 5.4 |
| Average fecal mass per individual per feeding time (g $indiv^{-1}$ $hrs^{-1}$) | 4.6 | 5.2 |
| Average fecal mass per individual per day (g $indiv^{-1}$ $day^{-1}$) | 19.0 | 23.3 |
| Average fecal mass per individual per year (g $indiv^{-1}$ $yr^{-1}$) | 6930.0 | 8498.5 |
| Density (indiv $m^{-2}$) | 0.7 | 0.7 |
| Annual sediment turnover rate (g $m^{-2}$ $yr^{-1}$) | 5128.2 | 5974.5 |

## Discussion

### *Feeding trials*

The organic matter content of sediment affects the habitat selection of *H. leucospilota*, not particle grain size. Hammond, in a 1982 study of grain size selection in other holothurian species, concluded that there was no selection because adhesive mucus on the feeding tentacles extracts any size sediment in its habitat (Hammond 1982). Sediment grain sizes did not affect preference as these grain sizes get redistributed by wave action among the channel, lagoon, and zones 1-4 without addition input from land, or at least bioerosion on land occurs too slowly to create immediate changes in grain size distribution. However, organic matter constantly enters the channel and lagoon from land runoff. This species was found in the channel and lagoon behind the carbonate platform, where the sediment in both places was darker in color than sediment in the four designated zones leading up to the reef edge. This dark color suggested more organic matter content. When sediment from the channel and lagoon were observed under the microscope, grains were enclosed in algal clumps that indicated algae to be a possible source of organic matter among other types biological input, such as contribution from other organisms. No algae were found on grains from zones 1-4. Results confirmed that both channel and lagoon sediment were higher in organic matter content than the other zones. Zone 1, however, did contain more organic matter than zones 2, 3, and 4. These differences played a role in the holothurian's preference for sediment from one zone over another.

Of the 10 cells tested in the feeding trials, 3 indicated that preference was apparent between the channel and zone 3, the channel and zone 4, and the lagoon and zone 1. In each case, the holothurians preferred either the channel or lagoon sediment to sediment from the other zone in the binary comparison. Why no preference was shown when the channel and lagoon were compared to zone 2 is unclear; however, some specific characteristics about each of the other zones must be a factor as to why preference resulted in comparisons to zones 1, 3, and 4. The results suggest that when OM amounts differed significantly between zones, no preference was apparent. However, when OM amounts were close, as in the lagoon and zone 1, the holothurians chose the sediment that contained the higher amount. In the field, zone 3 was observed to contain more of an abundance of *Porites* coral and *Halimeda* algae and zone 4 was dominated by *Sargassum* algae. These organisms can contribute more organic matter to the sediment. Furthermore, *Halimeda* would supply more loose sediment than corals because of its higher rate of calcium carbonate production (Scoffin 1992). Abundance of coral and algae houses a greater species diversity where other animals may also supply organic matter to the environment. A decaying fish that occurs in zone 3 or 4 can present a rare case in which organic matter would increase in the sediment significantly. Once again, when OM amounts were similar between two sediment samples compared, the holothurians still chose the one with a higher OM amount. A closer study of these zones and their biological components is necessary to determine OM sources and to assess exactly why preference was observed with these locations. Exact sources of sediment are difficult to identify because all organisms contributing loose sediment undergo different stages of partial breakdown that render taxonomic identification almost impossible (Scoffin 1992).

The results of the feeding trials do not serve to isolate food availability as the only factor in this species' habitat selection. Obviously, preference is only apparent when holothurians are given the choice, as in the laboratory. Other factors not tested in this study may explain why this species is only found in the channel and lagoon. Predation is not a possible reason because the only predators that holothurians generally are susceptible to are much larger echinoderms, such as *Pycnopodia*, a 10-armed animal. None were present at Point Aroa. Salinity (34 o/oo) and temperature (31°C) may also be eliminated as factors because they are consistent among the channel, lagoon, and the four zones sampled. Water depth is also not a factor because at high tide, water is still able to enter through carbonate platform crevices into the channel and lagoon to increase depth there. Thus, the other possible factor besides food availability is the protection from extreme wave energy. The carbonate platform shelters these holothurians when waves wash into the channel and lagoon abruptly at high tide. Nevertheless, protection from wave action cannot stand as the only explanation for this species' distribution. Filiatrault concluded that this species' distribution depended heavily on the presence of shelter for hiding (Filiatrault 1996). There is not enough data to conclude that this is the sole factor, as preliminary observations made in this present study indicated that there were plenty of objects, such as large corals, for *H. leucospilota* to hide under in zones 1 through 4.

### *Grain size partitioning analysis*

As indicated in their fecal matter, *H. leucospilota* selected for large grain sizes (1.8-2.0 mm) from a random sediment sample, despite the fact that more middle-sized grains (> 500 µm) were available in the sediment they were feeding on. The reason for why larger grains were selected is unknown. This is perhaps due to the structure and mechanics of the feeding tentacles and more study is required to understand their morphology. Some feeding tentacles are suggested to absorb dissolved OM (Massin 1982b). Massin also observed that there is an increase in selectivity with an increase in tentacle complexity. Organic matter selection may not even be influenced by feeding tentacles, as prior studies indicate that OM selection occurs in the pharyngeal bulb, not the tentacles (Massin 1982b). A study on the tentacular diversity of 12 different holothurian species revealed that the tentacles' structure indeed determined grain size selection (Roberts 1979).

There is a relationship between grain size and organic matter that may explain selection by holothurians. Usually the organic matter is stored in the small sediment grains as there is a larger total surface area. Thus, if there is grain size selection, I expect that holothurians would select for smaller grains. In another study of feeding behavior of two species *Holothuria atra* and *Holothuria scabra*, both selected for smaller grain sizes with more organic material (Wiedmeyer 1992). However, *H. leucospilota's* selection for larger grains may be for a different reason. Each individual large grain may exhibit ruggedness to hold more organic matter. This could not be determined in the simple microscopic observations in this study, as thorough rinsing is required to remove all the algal clumps that surrounded grains in order to analyze grain periphery for such ruggedness, if present. Larger grains may also settle more towards the surface of sediment as chips of coral continue to accumulate into loose sediment under large coral. Grain sizes are naturally sorted by waves and currents that cause larger, denser grains to settle as a deposit and the lighter grains to suspend (Scoffin 1992). Otherwise, *H. leucospilota's* selection for larger grain sizes could be due to just the nature of the sediment available at Point Aroa, in that not enough small grains are available for this species to choose for. A future study conducting feeding trials with pre-sorted sediment samples of different grain sizes may confirm selectivity.

### *Organic matter analysis*

The feeding trials established that the channel and lagoon contained higher OM amounts. OM amounts also varied in the fecal pellets collected from specimens feeding in different sediment types. Fecal pellet masses indicated the relative amounts of sediment ingested. Where sufficient OM was available, as in the channel and lagoon, holothurians ingested an amount of sediment proportional to their body mass to obtain the right amount of nutrition. Interestingly where zone 1 contains some available OM, holothurians ingest a greater amount of sediment in an attempt to gain enough OM from their food. This has been observed in a previous study in which holothurians will eat more to meet their metabolism when OM becomes scarce (Massin 1982a). However, when little OM to none were available to them in zones 2, 3, and 4, holothurians ingested the least amount of sediment, as if avoiding eating altogether. These results suggest that holothurians have the ability to detect and feed in OM-rich sediment as biomonitors. Nonetheless, overestimation of OM may occur, even if such cases are rare. Yingst ascribed the error to the mucus layer that holothurians make to shape and enclose their fecal pellets, as this mucus layer carried other microorganisms from the gut (Yingst 1976). Microbial activity within the gut may alter the organic matter present in fecal pellets once sediment has exited the holothurian (Scoffin 1992).

The OM absorption rates suggest that these holothurians play a role in recycling nutrients in the ecosystem. The average daily OM amounts absorbed per individual—4.20 g OM/ day for the lagoon population and 4.06 g OM/ day for the channel population—indicate that large amounts are simultaneously removed from the ecosystem. However, previous studies have shown an unusual case in which fecal pellets excreted back into the environment are richer in organic matter than sediment ingested, which could benefit other organisms (Wiedmeyer 1992). Consequently, organic matter is consistently renewed while holothurians are feeding. The upper layer of sediment contains the most nutrients (Yingst 1981). The mixing of this upper layer prevents calcium carbonate from being buried and lost, maintaining the carbon dioxide cycle (Massin 1982a). There was no significant difference in OM absorption rates between the channel and lagoon populations, as averages body masses were also not significantly different. The OM absorption rates are directly proportional to body mass—as the larger the holothurian, the more OM it absorbs—and proportional to fecal pellet mass—as the more the holothurian ingests, the more OM is absorbed. This is due to the direct proportional relationship between body mass and fecal pellet mass, as the larger the holothurian, the more sediment it ingests, and the more fecal matter it excretes. Evolution should drive individuals of this species to perform the same physiological functions; therefore, no differences should be observed between these two populations.

### *Sediment turnover rates*

As deposit feeders, holothurians such as *H. leucospilota* have a major contribution in bioturbation. The annual sediment turnover rate for the channel population is 5128 $g/m^2$/year and for the lagoon population is 5974 $g/m^2$/year. These rates were lower than the turnover rate observed by Brusch in the 1999 study on *Holothuria atra* because the densities of *H. leucospilota* in both the channel and lagoon were much lower. These rates, however, are high enough to create changes in not only organic matter content, but also grain size distribution especially when this species is selecting for the

1.8-2.0 mm grains. Sediment turnover rates correlate with the amount of OM contained, as the larger the grain sizes, the less the organic matter, but the more sediment turned over (Yingst 1981). The impact of bioturbation is relative to many factors, including the behavioral characteristics of different species and the type of habitat in which the holothurians are found. Bioturbation would be more significant if this species was a burrower that, while turning over sediment, it vertically partitioned the grain sizes in sediment, or if this species were in the deep sea where more OM-rich fecal pellets would be suspended throughout the water column instead of settling down to the ocean floor immediately as in shallow water.

If currents become too strong at high tide in Point Aroa, however, fecal pellets may still be transported. When these fecal pellets are moved, they can bury larvae of organisms, prevent sessile epifauna from sticking to substrate, or clog the filters of suspension feeders, which hang their feeding tentacles in the water to capture drifting particles (Massin 1982a). Fecal matter may also block the ambulacral system of other echinoderms (Scoffin 1992). Another study on the bioturbation rate of *Holothuria princeps* depicted how infaunal communities of gastropods and amphipods were also affected as their numbers decreased, as they also filter their food (Dahlgren et al 1999). Previous studies on other holothurian species in other habitats have shown how bioturbation diminishes the densities of meiofauna (Massin 1982a), microfauna, diatoms and cyanobacteria (Uthicke 1999) as well. On the contrary, meiofauna and bacteria may also serve to further break down fecal pellets into finer grains (Scoffin 1992); hence, it is still unclear whether bioturbation benefits or inhibits these microorganisms. Massin suggested that the holothurians' role in bioturbation is limited in shallow water because they are not the dominant macrofauna (Massin 1982a). However, both the channel and lagoon at Point Aroa seem to be an exception because both *H. leucospilota* populations at these locations are denser than that of other deposit feeders present, such as other holothurian species.

### *Future studies*

All the experiments and analyses conducted in this study may be extended for further investigation. A more in-depth analysis of the zonation at Point Aroa and the sources of sediment within each zone may offer a stronger basis for comparison to the channel and lagoon where *H. leucospilota* are found. Grain size selection requires more analysis to confirm the selection suggested by this present study. Feeding experiments may be altered to make binary comparisons of sediment of different grain sizes, pre-sorted, while taking advantage of the same design of the water table that offers an original system of rotation that allows each specimen to feed in all sediment sizes while experimenting with 10 specimens simultaneously. Grain size selection may be studied in relation to the morphology of feeding tentacles and the ontogeny of this species to determine preferences of larvae and juveniles as well as adults. A previous study on how the distribution of *Holothuria atra* was affected by the sizes of individuals indicated that larger individuals (the adults) preferred sand with little OM, smaller individuals (juveniles) preferred mud with more OM, new juveniles settle in seagrass beds with the richest OM, and all different holothurian sizes avoid fine silt altogether (Mercier et al, 2000). These results suggest that OM richness is not always found in fine sediment and that *H. atra* would only select for sediment sizes that would allow the holothurians to burrow more easily. In addition, since the relationship between bioturbation and meiofauna densities remain a mystery, measuring the densities of these microorganisms at Point Aroa in comparison to *H. leucospilota* densities may broaden the understanding of how nutrients are being recycled. A long-term study may also include monitoring the annual sediment turnover rates to predict how the sediment quality will continue to change in the future.

## Conclusions

*Holothuria leucospilota* will continue to influence sediment quality in the reefs it inhabits. Its food selection determines its habitat selection, showing preference for sediment with higher organic matter content. Grain sizes of sediment do not determine preference, as this species has the capability to partition grain sizes in any random sample and ingests only a particular size it selects for. *H. leucospilota* absorbs a large amount of organic matter from ingested sediment to meet its own metabolic needs while simultaneously recycling nutrients in the sediment as sediment re-enters the environment in the form of fecal pellets, which may be transported throughout an ecosystem. Consequently, bioturbation of sediment by this species would alter the grain size distribution of sediment and its organic matter content. Vast populations of *H. leucospilota* will continue to change the substrate of coral reefs for other organisms.

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## LITERATURE CITED

Brusch R (1999) Sediment turnover rate of the black sea cucumber *Holothuria atra*. Biology and Geomorphology of Tropical Islands, Student Research Papers. University of California, Berkeley, pp 11-19

Dahlgren CP, Posey MH, Hulbert AW (1999) The effects of bioturbation on the infaunal community adjacent to an offshore hardbottom reef. Bulletin of Marine Science 64(1): 21-34

Filiatrault DD (1996) Factors affecting the distribution of holothuroids on Viapahu Reef, Moorea, French Polynesia. Biology and Geomorphology of Tropical Islands, Student Research Papers. University of California, Berkeley, pp 60-71

Hammond LS (1982) Analysis of grain size selection by deposit feeding holothurians and echinoids Echinodermata from a shallow reef lagoon Discovery Bay, Jamaica, West-Indies. Marine Ecology-Progress Series 8(1): 25-36

Massin C (1982a) Effects of feeding on the environment: Holothuroidea. In: Jangoux M, Lawrence JM (eds) Echinoderm nutrition. Balkema Rotterdam p 493-497

Massin C (1982b) Food and feeding mechanisms: Holothuroidea. In: Jangoux M, Lawrence JM (eds) Echinoderm nutrition. Balkema Rotterdam p 43-55

Mercier A, Battaglene SC, Hamel J (2000) Period movement, recruitment, and size-related distribution of the sea cucumber *Holothuria scabra* in Solomon Islands. Hydrobiologia 440: 81-100

Roberts D (1979) Deposit feeding mechanisms and resource partitioning in tropical holothurians. Journal of Experimental Marine Biology & Ecology 37(1): 43-56

Scoffin TP (1992) Taphonomy of coral reefs: a review. Coral Reefs 11: 57-77

Sibuet M (1984) Quantitative distribution of echinoderms (Holothuroidea, Asteroidea, Ophiuroidea, Echinoidea) in relation to organic matter in the sediment, in deep sea basins of the Atlantic Ocean. Proceedings of the Fifth International Echinoderm Conference/ Galway/ 24-29 September 1984: 99-108

Uthicke S (1999) Sediment bioturbation and impact of the feeding activity of *Holothuria (Halodeima) atra* and *Stichopus chloronotus*, two sediment feeding holothurians, at Lizard Island, Great Barrier Reef. Bulletin of Marine Science 64(1): 129-141

Wiedmeyer WL (1992) Feeding behavior of two tropical holothurians *Holothuria (Metriatyla) scabra* (Jager 1833) and *H. (Halodeima) atra* (Jager 1833), from Okinawa, Japan. Proceedings of the Seventh International Coral Reef Symposium, Guam 2: 853-860

Yingst JY (1982) Factors influencing rates of sediment ingestion by *Parastichopus parvemensis* an epibenthic deposit feeding holothurian. Estuarine Coastal & Shelf Science 14(2): 119-134

Yingst JY (1976) The utilization of organic matter in shallow marine sediments by an epibenthic deposit-feeding holothurian. Journal of Experimental Marine Biology & Ecology 23: 55-69

# Distribution of the polycheate *Spirobranchus giganteus corniculatus* on various coral types

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ABSTRACT. *Spirobranchus giganteus corniculatus*, the Pacific Ocean sub-species of the christmas tree worm, is an obligate associate of coral. Its distribution on live corals was observed in two lagoon locations in Moorea, French Polynesia. Distribution was analyzed based on density (no. of worms/area of coral). Density was compared between study locations and coral types. Coral types were identified using morphological differences in corallite and polyp structure. Analysis of these data shows that colonization varies over coral type with a significant preference for two *Porites* species. This suggests either larval preference during settlement or differential survival rate after settlement, though previous studies of *S. giganteus* larvae suggest that larval preference is more likely. Density of worms varied significantly between study locations suggesting that the distribution of worms is associated with varying habitat types and environmental factors.

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## Introduction

Habitats are defined as "spatially bounded subsets of physical and biotic conditions among which population density of a focal species varies from other adjacent sites" (Morris 2003). Animals benefit when they choose habitats that will increase their survival and reproductive fitness. Individuals choose habitats in a non-random way to optimize protection, nourishment and reproduction. Increasing one's reproductive fitness by choosing a favorable habitat is evolutionarily advantageous and through time selection of habitat becomes species specific (Morris 2003, Munday 2001).

Coral reefs are highly complex, variable environments that consist of a multitude of available habitat types. Tropical island reefs are densely populated, resulting in increased competition for available habitat space. Increased competition results in commensal relationships as organism evolve to live together (Hunte 1990). These relationships can be observed in the distribution of sessile marine organisms. Previous studies of sessile marine invertebrates including barnacles, mussels, oysters and tubeworms (Pawlik 1991) have shown that distribution is regulated by larval preference at settlement or by differential mortality after settlement (Hunte 1990).

*Spirobranchus giganteus*, an obligate tubeworm of coral, is found throughout tropical and sub-tropical reef regions. The Atlantic Ocean is home to the sub-species *S. giganteus giganteus* and *S. giganteus corniculatus* lives in the Pacific Ocean. *S. giganteus* has a larval phase of 9-12 days in which the larvae are free living in the water column. The larvae then settle onto a coral head and build a calcareous tube to protect themselves. Metamorphosis is completed shortly thereafter (Hunte 1990, Marsden 1990, Smith 1984). Adult worms can live on the coral heads they inhabit for as long as forty years (Smith 1984). Studies by Hunte (1990), Marsden (1990) and Dai (1995) of larval settlement found distribution patterns in *S. giganteus* that suggest a selective commensal relationship between particular coral types and the tubeworms. These hypotheses can be drawn from field studies as well as controlled laboratory experiments. The current study tested for a similar relationship between *S. giganteus corniculatus* and the corals around Moorea, French Polynesia.

This investigation seeks to clarify the relationship between *S. giganteus* and coral. To do this, it is necessary to investigate the habitat selection of *S. giganteus* on differing coral types. This was accomplished by observing abundance of coral type in comparison with abundance of worms on each coral type. Further investigation involved testing for differences in worm density among coral types to determine whether the degree of worm colonization is correlated with coral type or coral size. This study sampled two locations around Moorea to determine whether distribution patterns are similar in different locations around the island.

## Methods and Materials

Moorea is the second youngest island in the Society archipelago. It was formed approximately two to three million years ago. Around the island lies an outer reef, commonly called a barrier reef. The outer reef is made up of the reef front, outer reef flat, inner reef flat, and lagoon zones. Lagoons are created by inner reef flat erosion that leaves a sandy bottom under a few meters of water. Lagoons have large, free standing coral heads. Growth can be very elaborate in lagoon areas because of minimal wave energy (Veron 1986). The current study was conducted in two similar locations on the north side of Moorea (See Appendix 3). Study site 1 was located between Opunohu and Paopao (Cook's) bay. This area is separated from the island by a large channel made up of a sandy bottom. Coral density increases with increasing distance from the channel. The lagoon area between the channel and the reef flat is spotted with dense patches of coral. These patches contain many different species of coral in varying densities. Study site 2 is located on the east side of Maharepa. The lagoon has a channel to the west named Irihonu pass. A boat channel passes in a latitudinal direction through the middle of the lagoon. These channels and the shore surround the study site (GPS coordinates for each quadrant are noted in Appendix 1).

Within the study locations seven types of coral were observed. These seven types consist of four genera: *Acropora*, *Montipora*, *Porites*, and *Pocillopora*. Within *Porites* there are four recognizable species termed, for the purposes of this study, *Porites* type I, II, III, and IV. *Porites* type I has 12 large denticle polyps in a clean circle just inside the septum. The septa are wider than they are tall. *Porites* type II consists of bright purple coral heads. Polyps are similar to type I but the type II corallites are smaller. The coral head has a small, columnar form. *Porites* type III has deep corallites with weakly developed polyps. Polyps rarely reach the edge of the septa. Septa are taller than they are wide. *Porites* type IV has 6 large and 6 small polyps in an alternating, star pattern. The corallites appear to be filled by polyps. The *Acropora* group consists of large coral heads in the family *Acroporidae*. The colonies are made of thin, branching coral. The *Montipora* observed was *M. efflorescens* which is a purple, encrusting coral (Pictures of all coral in Appendix 2).

A preliminary study was conducted prior to data collection to identify all the coral types. A multitude of detailed digital photographs were taken of all observed coral types. Coral types were categorized based on careful review of these photos so that identification of coral type could be accomplished during data collection. All photos were taken with a Nikon Coolpix 4500 digital camera in an Ikelite underwater housing.

Each study site consisted of five quadrants for a total of ten. Each quadrant was $100m^2$ in total area. Quadrants were chosen randomly by kayaking into an area of the lagoon where reef was present and dropping a weighted buoy. The position of the buoy marked the transect center. Measurements were standardized between sites by measuring five meters north of the buoy. This marked the north side of the quadrant. A ten meter by ten meter square was then measured and marked around the center point. Each corner was marked with a field flag and string was run around the flags.

Sites were surveyed for abundance of each coral type, shape of coral heads and abundance of worms on each coral type. Corals that were difficult to identify at the time of data collection were photographed and compared with previously categorized photographs. The abundance of each coral type was evaluated by measuring the circumference of every coral head. The abundance of worms was determined by counting the number living on each type of coral. Coral head color and gross shape were noted for each coral head.

Data were later entered into a Microsoft Excel spreadsheet. Area of coral was calculated from the circumference measured. All statistics were carried out using Excel's Analysis Toolpack.

## Results

Data from study sites 1 and 2 were combined to analyze the distribution of coral and worms. The abundance of coral was found to be uneven (Table 1). The abundance of worms on coral types was also found to be uneven (Table 1). A Kruskal-Wallis test was done to establish the organization of worms over coral type. The distribution was found to be non-random ($P<0.0001$). A binomial test was done to establish a preference for coral type. In all sites, the proportion of worms on *Porites* type II and III was found to be much higher than expected based on the relative proportions of those coral types. A regression of *Porites* type II and type III coral showed that both had a significant correlation with worm distribution, but a t-test provided insufficient support to say which of the two corals was more preferred.

The same statistical analyses were done for each study site. The binomial test for study site 1 showed that *Porites* type II and III had higher proportions of worms than what would be expected based on their relative proportions of coral. In study site 2 the proportion of worms was not higher than the relative proportion of coral for *Porites* type II. T-test results did not allow rejection of the hypothesis that site 1 was different from site 2 (t = 5.10 d.f. =1).

| Coral type | # of worms | Area of coral ($M^2$) | Proportion of worms | Proportion of coral | z-value | p-value |
|---|---|---|---|---|---|---|
| *Porites* I | 752 | 11.168 | 0.536 | 0.260 | 797.8 | 0.00000 |
| *Porites* II | 184 | 0.745 | 0.036 | 0.064 | 80.5 | 0.00000 |
| *Portites* III | 1906 | 5.297 | 0.255 | 0.660 | 1170.8 | 0.00000 |
| *Porties* IV | 12 | 0.864 | 0.043 | 0.004 | 109.8 | 0.00000 |
| *Acropora* | 32 | 2.444 | 0.117 | 0.011 | 306.3 | 0.00000 |
| *Montipora* | 3 | 0.269 | 0.013 | 0.001 | 25.4 | 0.00000 |

**Table 1.** Totals for all sites and results of binomial test. *Pocillopora* is left out of the analysis because it was not colonized.

Site 1

| Coral type | # of worms | Area of coral ($M^2$) | Density |
|---|---|---|---|
| *Porites* I | 621 | 6.3641 | 97.5783 |
| *Porites* II | 178 | 0.4611 | 386.0641 |
| *Porites* III | 1624 | 3.5333 | 459.6283 |
| *Porites* IV | 12 | 0.7280 | 16.4837 |
| *Acropora* | 15 | 1.5016 | 9.9892 |
| *Montipora* | 2 | 0.2245 | 8.9094 |

Site 2

| Coral type | # of worms | Area of coral ($M^2$) | Density |
|---|---|---|---|
| *Porites* I | 131 | 4.80439 | 27.2667 |
| *Porites* II | 6 | 0.28379 | 21.1427 |
| *Porites* III | 282 | 1.76397 | 159.8663 |
| *Porites* IV | 0 | 0.16628 | 0 |
| *Acropora* | 17 | 0.94244 | 18.0381 |
| *Montipora* | 1 | 0.04503 | 22.2087 |

**Table 2.** Abundance of worms and coral with density for each coral type calculated. *Pocillopora* is left out because it was not colonized

Regression analysis found that coral head area is correlated with worm abundance ($P<0.0001$), indicating that, as coral head size increases, there is more room for worms to live.

## Discussion

The distribution of coral types in the lagoons around Moorea is uneven. *Porites* type I makes up 54% of the total coral area and *Porites* type III makes up 26%. *Porites* is the most abundant coral genus overall. This could be because the lagoon area is a favorable place for *Porites* corals to live. *Porites* type I coral either grows faster than the other coral types or reproduces more successfully within the lagoon region.

Overall coral abundance is not related to the distribution of *S. giganteus*. The proportion of worms seen in Table 1 does not parallel the proportions of coral. This is due to either differential survival of worms on different coral types or habitat selection by larvae during settlement. Previous studies have indicated that larvae are attracted to exudates of coral and will choose a type of coral to colonize. Choice is related to the distribution of adults in the field (Marsden 1987, 1989, 1990). It is therefore assumed that worm distribution is due to habitat selection by larvae and not differential survival.

The proportion of worms inhabiting *Porites* type II and type III coral heads are higher than what is expected based on the relative proportion of those coral types. This indicates that these coral types are selected by *S. giganteus*. Alternatively, the other coral types are not selected. This is strongly supported by high Z-values (Table 1). The relationships of *Porites* type II coral heads and worm distribution changes between study sites. Study site 1 shows that type II is being selected for colonization and study site 2 shows that it is not selected. The t-test failed to show that the two sites differ in regards to distribution and coral type. The sampling of type II coral must have been different among study sites, possibly due to the low area of *Porites* type II coral found in study site 2. Or, it could be that there was a disproportionately high abundance of type II coral in the areas surveyed in study site 1. In either case, *Porites* type 3 seems to be more preferred for colonization than type II.

Studying distribution of this species allows us to hypothesize about its habitat selection. Habitat selection has been documented in *S. giganteus* numerous times. The selection of certain coral types is evident in both locations of lagoon sampled here. Hunte (1990) found that *S. giganteus giganteus* in Barbados (Atlantic Ocean) is most commonly found on *Diploria strigosa*. Dai (1995) found that *S. giganteus corniculatus* colonized the coral of Southern Taiwan (Pacific Ocean) unevenly, with most adults living on *Porites* corals. It is expected that coral preference varies between locations, especially ones as far apart as the Atlantic and Pacific Oceans. The identity and composition of coral varies in each of these studies but what remains the same is the preference for a particular coral type.

It is possible, based on current information, that there is habitat selection of *Porites* corals throughout the Pacific by *S. giganteus*. Further study of more locations in the Pacific might show the taxonomic level at which coral is chosen. More data are needed to determine what coral types are preferred throughout the geographic range of *S. giganteus*.

Habitat selection is based on the needs of the organism. Habitat selection in sessile marine organisms can only be accomplished by their free-living larvae. The habitats selected by the larvae become evident as distribution patterns in the adult worms. The distribution of adult worms can therefore be observed and we can infer which habitats are being selected. The relationship that has developed between *S. giganteus* and particular types of coral within *Porites* is dictated by larval settlement preference. The significantly high proportion of worms living on *Porites* type III coral heads suggests that this habitat is selected by the larvae during settlement. This coral type probably bestows some advantage on *S. giganteus* in juvenile and/or adult form. From the results of the current study, we can speculate that larvae capable of selecting *Porites* type III coral during settlement had higher reproductive success than other larvae that were unable to select a preferred habitat. These selective larvae have dominated the gene pool in the reefs of Moorea and have shown their preference through their distribution as adults.

## Conclusion

This study shows that coral abundance in the lagoons of Moorea is disproportionate to type. Furthermore, coral abundance does not seem to have an effect on the distribution of the obligate coral associate *S. giganteus*. There is a correlation between coral type and distribution such that *Porites* types II and III coral are preferred over all other types. Varying locations of the lagoon around the island are similar in distribution pattern. Furthermore, there is a correlation between coral head area and the abundance of worms found on each coral head. This study further supports the idea that *S. giganteus* colonizes specific coral types based on selective advantage.

## Acknowledgements

Thank you to the Richard P. Gump research station for the use of their facilities, research equipment and living space during my stay in Moorea. Special thanks to the instructors: Jere Lipps, Carole Hickman, Vince Resh, George Roderick, and Rosemary Gillespie for their guidance and support and for allowing me to have this amazing opportunity. I would like to thank Vicki Bertics, Sarah Valencia and Eva Bauer for their assistance in the field. Thank you to the graduate student instructors Curtis Pehl and Blake Suttle for statistical advice and Jan Nakamura for advice on project planning and design. Further thanks to the graduate students for their hard work and for making this trip a success for all involved.

## LITERATURE CITED

Dai, Chang-Feng & Yang, Hsiao-Pei. (1995) Distribution of *Spirobranchus giganteus corniculatus* (Hove) on the coral reefs of southern Taiwan. Zoological Studies 34(2): 117-125

Hunte, et. Al. (1990) Habitat selection in the tropical polychaete *Spirobranchus giganteus* I. Distribution on corals. Marine Biology 104: 87-92

Hunte, et. Al. (1990) Habitat selection in the tropical polychaete *Spirobranchus giganteus* III. Effects of coral species on body size and body proportions. Marine Biology 104: 93-99

Marsden, J.R. & Meeuwig, J. (1990) Preferences of planktonic larvae of the tropical serpulid *Spirobranchus giganteus* (Pallas) for exudates of corals from a Barbados reef. Exp. Marine Biology 137:95-104

Marsden, et. Al. (1990) Habitat selection in the tropical polychaete *Spirobranchus giganteus* II. Larval preference for corals. Marine Biology 104: 93-99

Marsden, J.R. (1987) Coral preference behaviour by planktotropic larvae of *Spirobranchus giganteus corniculatus* (Serpulidae: Polycheata). Coral Reefs 6: 71-74

Morris, Douglas W. (2003) Toward an ecological synthesis: a case for habitat selection. Oecologia 136: 1-13

Munday, Philip. (2001) Fitness consequences of habitat use and competition among coral-dwelling fishes. Oecologia 128(4): 585-593

Pawlik, J.R., Butman, C & Starczak, V. (1991) Hydrodynamic facilitation of gregarious settlement of a reef-building tube worm. Science 251(4992): 421-424

Pichon, Michael. Scleractinia. James Cook University of No. Queensland. Species list from CRIOB station.

Smith, Richard. (1984) Development and settling of *Spirobranchus giganteus* (Polychaeta; Serpulidae). The Linn. Society of New South Wales, pp 461-483

Veron, John. (1986) Corals of Australia and the Indo-pacific. University of Hawaii

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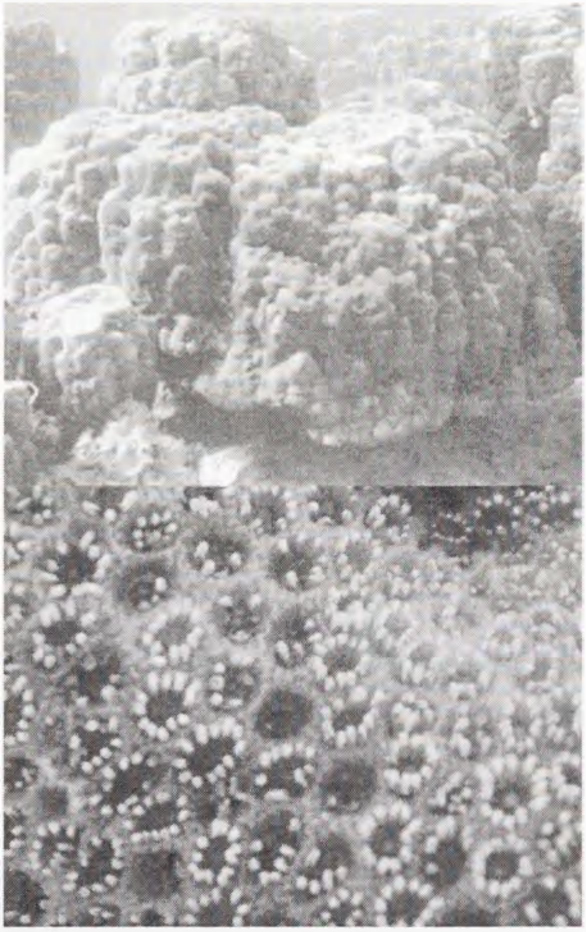
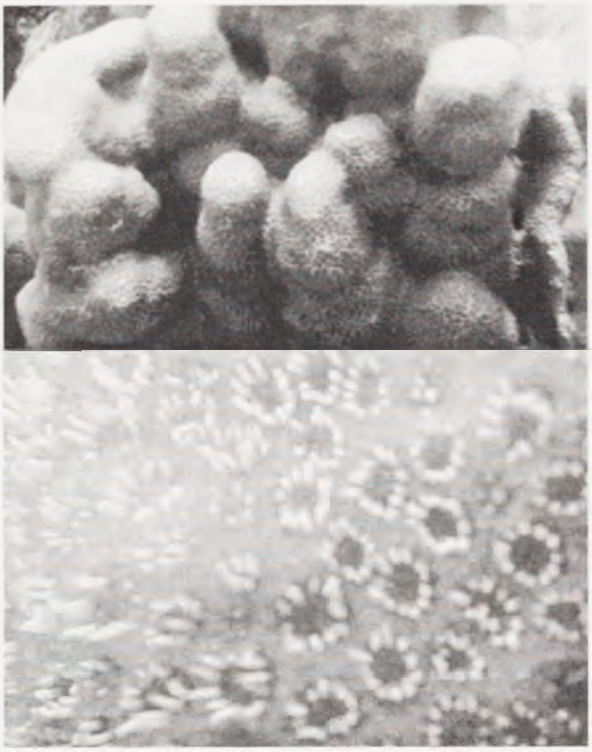
**Appendix 1:** GPS locations of quadrants

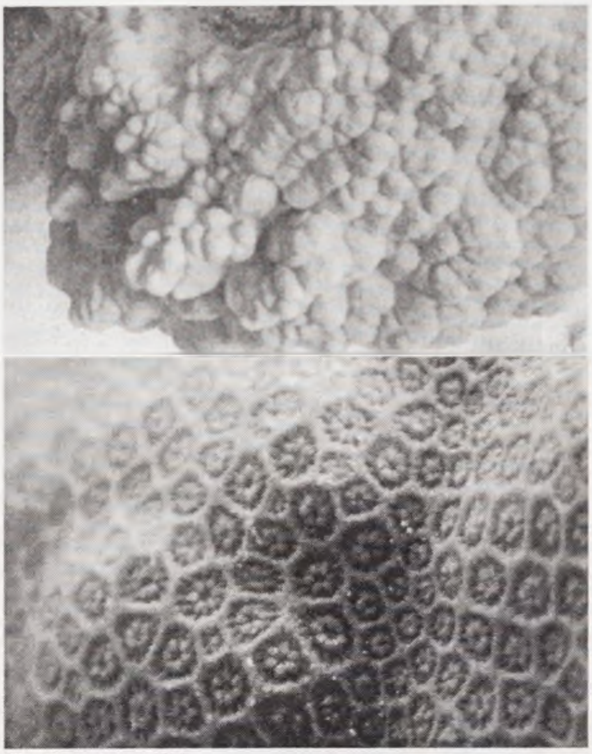
| Quadrant # | GPS Location |
|---|---|
| 1 | S $17^{0}$ 28.983’, W $149^{0}$ 49.885’ |
| 2 | S $17^{0}$ 28.962’, W $149^{0}$ 49.891’ |
| 3 | S $17^{0}$ 28.976’, W $149^{0}$ 49.905’ |
| 4 | S $17^{0}$ 28.934’, W $149^{0}$ 49.914’ |
| 5 | S $17^{0}$ 28.940’, W $149^{0}$ 49.895’ |
| 6 | S $17^{0}$ 28.721’, W $149^{0}$ 47.617’ |
| 7 | S $17^{0}$ 28.737’, W $149^{0}$ 47.621’ |
| 8 | S $17^{0}$ 28.725’, W $149^{0}$ 47.590’ |
| 9 | S $17^{0}$ 28.742’, W $149^{0}$ 47.587’ |
| 10 | S $17^{0}$ 28.753’, W $149^{0}$ 47.604’ |

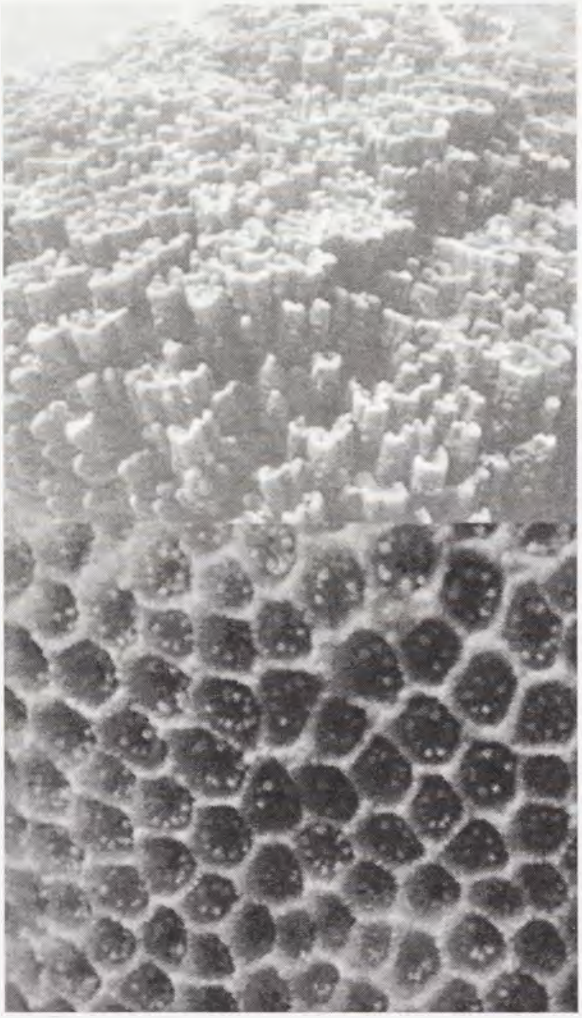
**Appendix 2:** Pictures of coral types



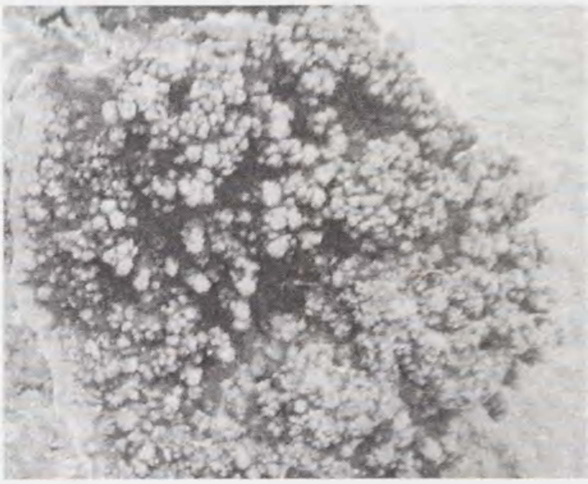
*Porites* type I


*Porites* type II

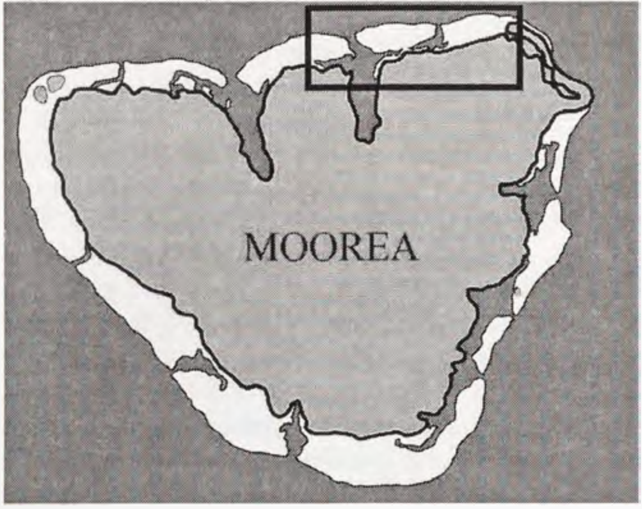

*Porites* type IV


*Porites* type III

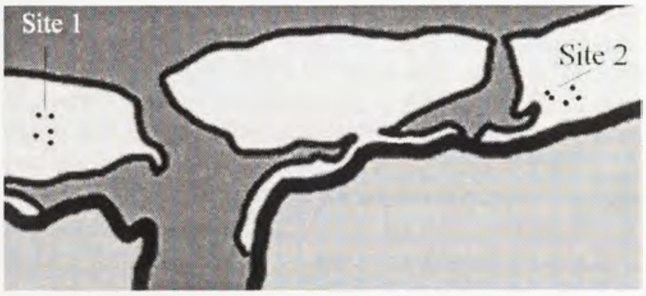

*Acropora*


*Montipora*

## **Appendix 3:** Map of Moorea and study sites



View of Moorea



Enlarged view of north side lagoons with study sites marked.

# Feeding Preference of Two Species of Nudibranchs in Moorea, French Polynesia

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ABSTRACT.

Dietary preferences of two closely related nudibranchs, *Glossodoris cincta* and *G. hikeurensis*, were studied and compared against food availability. In a preliminary investigation, individuals were observed in the field to establish daily feeding patterns and food breadth. Food selection in the field was noted and preference trials were run in the lab using the 4 most frequently selected items. Percentage cover estimates of food availability yielded 0.5% *Hyrtios erecta*, 5% *Halimeda*, 2.5% *Padina*, 1% *Dictyota*, and 51% epithelial algal covering, or algal turf, and the frequency of food selection was compared to these percentages. Results indicate one species of sponge (*H. erecta*) was significantly preferred relative to abundance in both the lab and the field.

Sponges often contain toxins and many nudibranchs sequester these toxic metabolic compounds as a defense against predation. A previous study found heteronemin, a compound found in *H. erecta*, to play a role in nudibranch defense. Most sponge-preying nudibranchs are characterized as obligate specialists, but this study suggests other possible food sources in addition to *H. erecta*. Further work is necessary to determine whether nutritional and defense needs can be met by a diet lacking *H. erecta*.

Keywords: Nudibranch, Opistobranch mollusk, feeding biology, preferential dietary selection, tropical ecology, sponge feeder.

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## Introduction

Nudibranch mollusks commonly occur in marine communities worldwide, from the deep icy waters of Antarctica to shallow coral reef systems in the tropics. Ecologically they exhibit a great deal of diversity and have evolved numerous feeding strategies, allowing them to inhabit a range of settings (Todd, 1981). Despite this diversity, dorid nudibranchs are often characterized in scientific literature as obligate specialists preying on sponges, bryozoans, or tunicates. Feeding biology is very important to a comprehensive understanding of nudibranchs as many characteristics separating opistobranchs from other gastropods arose from the coevolution of nudibranchs and their food sources (Avila, 1995). Few animals prey on chemically defended organisms; this allows nudibranchs to exploit a dietary resource unavailable to other predators. The toxic metabolic compounds they ingest are incorporated into their bodies, allowing nudibranchs to forgo other defensive strategies and resulting in their characteristic aposematic coloration and lack of shell (Faulkner and Ghislen, 1983).

Chemical aspects of nudibranch feeding biology are well studied. Extensive studies have assessed the origins, structures, and functions of the secondary metabolic compounds incorporated into the mantle and other body parts of nudibranchs (Cimino et al, 1982, Mebs, 1985). Avila and Paul (1997) investigated how the location of these compounds affects feeding deterrence, while Becerro, Paul and Starmer (1998) have investigated the predatory fish deterred by various icthyotoxic compounds. Vast amounts of research exist on opisthobranch mollusks and the antimicrobial, anti-inflammatory, and anti-cancerous properties of compounds found in their secretions (Teeyapant et al, 1993). It is generally agreed that secondary metabolites found in these organisms are of dietary origin (Cimino et al, 1982). This is especially true in nudibranchs of the suborder Doridacea which feed mainly on sponges of the class Desmospongia (Berquist and Wells, 1983).

In contrast, few studies have examined nudibranch feeding biology in terms of ecological interactions within a trophic web. Trophic interactions help define niches and community structure, providing an in-depth understanding of how organisms interact with their surroundings. Too often researchers fail to take into account how animals encounter their habitat; many studies are done with humans in mind to further our knowledge concerning chemicals that may be useful to us. Considering nudibranch feeding from an ecological standpoint may provide insights that help biologists understand community structure as a whole.

This ecological perspective may be especially important in understanding tropical reef systems. Coral reefs are characterized biodiversity hotspots containing an abundance of unique organisms, and due to human influence reef health is deteriorating rapidly. Sponges are sessile filter feeders, often with symbionts, and are subject to their surroundings in much the same way that corals are. Factors such as light, nutrient levels, competition for space, sediment, and salinity all directly or indirectly affect sponge and coral health. Thus, abundance and distribution of an organism dependent on a species of sponge for survival is a potential indicator of reef health.

This study focuses on the feeding habits of two closely related species of nudibranchs, *Glossodoris hikuerensis* (Pruvot- Fol, 1954) and *G. cincta* (Bergh, 1888), and seeks to characterize their feeding strategies of each by comparing food selection to food availability. The possibility of preferential feeding is examined to assess dependence on one sponge of the suborder Desmospongia, *Hyrtios erecta*, and to establish whether these nudibranchs are obligate specialists or opportunistic feeders. The central hypothesis is that while both species prefer *H. erecta* they exhibit an opportunistic feeding strategy and will eat other food items, including algae. Both organisms are abundant at the study site, and a similar feeding strategies may indicate competition for resources between two species occupying the same niche. The data provides interesting insights on the feeding biology and ecology of *G. hikuerensis* and *G. cincta*, and open up the possibility of previously unexamined feeding strategies for dorid nudibranchs as omnivores rather than specialized benthic carnivores.

### *Natural History*

*Glossodoris hikuerensis* and *G. cincta* are very common at the study site, with a slightly larger population of *G. cincta*. The larger *G. hikuerensis* reaches 10 cm in length and 5 cm in width, while G. *cincta* reaches lengths of 7 cm and widths of 3.5 cm. Both *G. hikuerensis* and *G. cincta* are found throughout Indo-pacific. Color varies with geographical location but is consistent within a single locale. Tan *G. hikuerensis* has lavender speckles and a large, frilly purple mantle border, and possesses elaborate double-treed gills (see figure 1). *G. Hikuerensis* attaches itself more firmly to substrate and releases copious amounts of white mucous from the mantle border into the water column when distressed. *G. cincta* is more pink in color with light colored speckles and a thinner, dark blue mantle border, and has less elaborate gills (see figure 2). *G. cincta* was rarely distressed, but released a barely visible mucous when irritated. *G. cincta* survived better in captivity, with only one mortality compared to 8 for *G. hikuerensis*.

**Figure 1.** *Glossodoris hikuerensis*

**Figure 2.** *Glossodoris cincta*

This study was conducted on the fringing reef in front of the University of California at Berkeley Richard B. Gump Field Research Station located at S 17° 24.4' W 149° 33.0' on the west side of Cook's Bay, Moorea, French Polynesia (see figure 3). Moorea is a volcanic island in surrounded by a barrier reef with fringing reefs along much of the shoreline. The study site reef at the Gump station extends approximately 35 meters from the shore and has a depth of 2–4m. An area approximately 20 meters wide and 150 meters long was surveyed. The reef is dominated by coral of the genus *Porites*, and has a large amount of algal cover due to the eutrophication of the bay. Because the site is on station property it is protected from recreational/commercial use. A wide variety of marine invertebrates can be found here, including at least 3 additional species of nudibranchs.

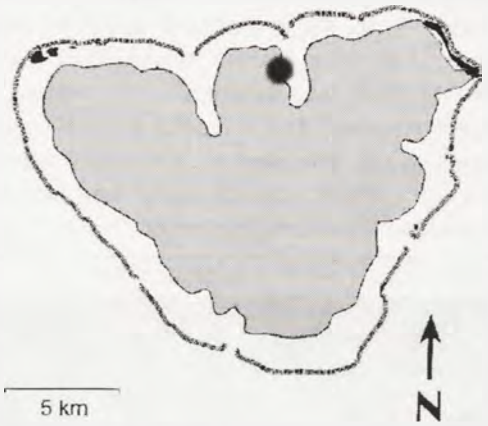


**Figure 3.** The black dot indicates the location of study site in Cook's Bay on Moorea, French Polynesia.

## Materials and Methods

### *2.1 Field Observations*

*Glossodoris cincta* and *G. hikuerensis* were located and observed between Sept. 20, 2003 and Nov 14, 2003 within the study site. Feeding behavior was noted and feeding substrate was recorded.

### *2.2 Nudibranch collection*

Between September 20, 2003 and September 27, 2003, collection occurred at 5am, 1pm, and 9pm on the fringing reef in front of the Gump station. Most individuals were observed feeding in the afternoon indicating that these species of nudibranchs are daytime feeders. When found in the field, their substrate and whether they were feeding was noted. They were then removed from the substrate and placed in a plastic bag with sea-water and, when possible, the substrate they were found on. Multiple nudibranchs of both species were placed in the same bag, and later in the same tank, as they do not appear to be territorial or exhibit adverse interactions between species. To simulate field feeding conditions in the lab, examples of all potential food items found near the collected individuals were included in the tank. Food items included *Hyrtios erecta*, *Halimeda*, *Padina*, *Dictyota*, *Jania*, *Sargassum*, *Turbinaria ornata*, algal turf on rubble, and others.

### *2.3 Survey of fringing reef*

Using a 2m by 2m quadrat, the area of the fringing reef where nudibranchs were most likely to be found was surveyed. This area is approximately 10 m from the edge of the reef, where the water is slightly deeper (3-4m) and diversity is higher. This survey quantified the abundance of food in the field for later comparison with the feeding trial results. Percent coverage was estimated for the food items included in the feeding trials (*Dictyota*, *Halimeda*, *Padina*, *Hyrtios erecta*, algal turf) as well as live coral, sediment, and other algae that nudibranchs were not observed feeding on. I surveyed 160 quadrats, or 640m$^2$, and extrapolated the results to the rest of the study site.

### *2.4 Feeding trials*

Four individuals of the same species were isolated in beakers, secured with a fine mesh covering, and placed in a tank with adequate water flow for 24 hours to starve them. The individuals were then removed and each one placed in the center of a tank .2m by .5m equidistant from 4 food choices, each facing a different direction. Four trials were run simultaneously. Three of the items were chosen because in the field observations nudibranchs were feeding on these most often, and these remained constant in every feeding trial. The fourth choice in the feeding trials was split between *Padina* and *Dictyota*, with two trials each. These were chosen because they were equally prevalent in the range where most of the nudibranchs were found, and the nudibranchs were equally likely to be found on either. The individuals were monitored for 3 hours and their location was noted every half hour. Nudibranchs have been shown to use chemosensory cues and mucous trails to locate one another, and these cues can remain for up to 4 hours. Interspecific cues are not as strong as intraspecific ones, but these two species are closely related and thus precautions were taken. After each feeding trial the nudibranchs were removed and the tank was drained, wiped out by hand and refilled to prevent the previous trial from influencing the results of the next trial. If more than one trial was run on the same day different food items were used.

### *2.5 Fecal collection and analysis*

Each individual was isolated for 24 hours both before and after each feeding trial in a 400ml beaker with a fine mesh covering held in place by a rubber band. The fecal matter along with sediment deposited by water flow was collected via a pipette and placed into a vial. Pre-feeding trial and post-feeding trial samples were compared. Control samples of sediment, collected by placing similar (empty) beakers near to those containing a nudibranch, were also taken. This allowed for the differentiation between the material that was excreted by the organism and that which settled out of the water column in the tank. The fecal samples were then examined under a dissecting scope under 4.5X magnification for the presence of sponge spicules, the structural components of sponges. Spicules, composed of either silica or calcium carbonate, cannot be digested by nudibranchs and their presence indicates that sponge is being eaten in the field and in feeding trials.

*2.6 Statistical analysis*

Feeding trial results were analyzed with a binomial test to determine significant preference or avoidance of a food choice. Field observations were analyzed with Poisson's test, which took into account food abundance in the field to determine significant preference or avoidance. P values equal to or less than 0.05 are significant.

*2.7 Observation at other locations*

Four other locations were searched twice for *G. cincta* and *G. hikeurensis* in order to observe their feeding habits. These included 1) the area towards the mouth of the Paopao river, 2) the area directly across the bay from the station near the Bali High Club, 3) the northeast corner of the bay (north of top dive) 4) the fringing reef directly west of the mouth of Cook's bay, and 5) the lagoon to the reef crest west of the pass leading in to the bay (see figure 4).

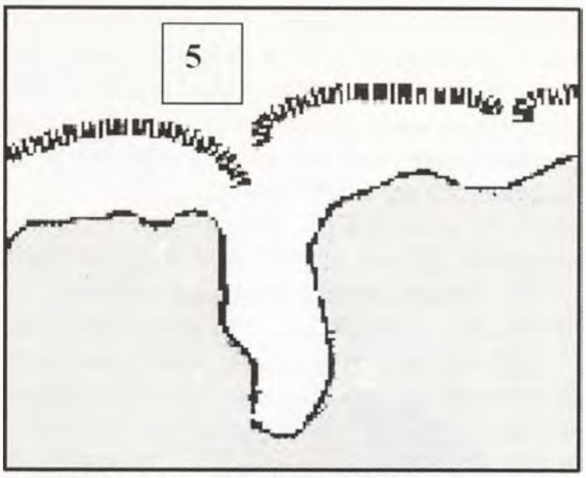


**Figure 4.** This map of Cook's Bay shows the 5 site where population densities of G. cincta and G. hikuerensis were examined.

**Results**

*3.1 Survey results*

I surveyed 640 $m^2$. The percent coverage of each item is shown in figure 5. The most prevalent item on the reef was the algal turf, which was estimated at 51%. This is a conservative estimate as the algal turf partially covering other items in the survey, such as sponge or *Halimeda*, was not estimated. *H. erecta* was the least abundant, accounting for only 0.5% of the possible food available.

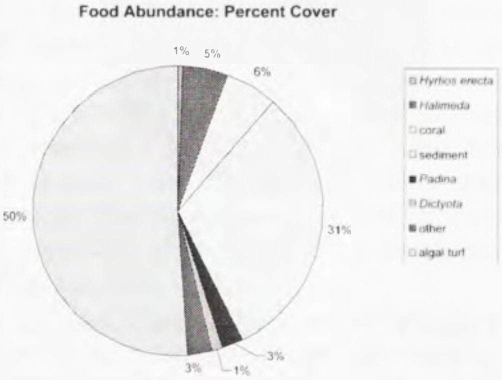
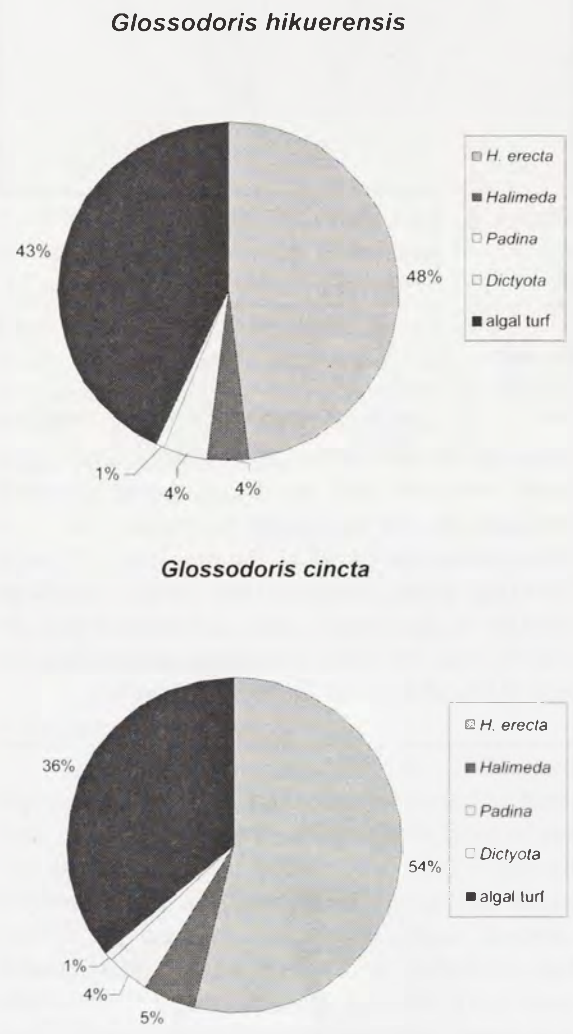


**Figure 5.** Percent coverage of all substrates Nudibranchs were observed feeding on in field.

*3.2 Field observation results*

Figure 6 shows the results of the field observations. Both species were found to be feeding on sponge more than anything else, followed by algal turf. Poisson's test compared the food selected with the food available, yielding a p value of 9.86E-18 for *G. hikeurensis* and 1.35E-26 for *G. cincta*. This demonstrates a statistical preference for black sponge and indicates both species of nudibranchs are targeting sponge as a food source. Poisson's test also showed that *G. Cincta* statistically avoided algal turf (p value equals 0.035). There was no statistical preference or avoidance for any other food item.


Glossodoris hikuerensis

Glossodoris cincta

**Figure 6.** Percentages of food selection by each species. Note the difference between percent of *H. erecta* available in figure 5 and percent of *H. erecta* selected in figure 6.

*3.3 Feeding trial results*

Figure 7 shows the feeding trial results for both species. A binomial test was run to determine significance in the laboratory feeding trials. Trials with *Padina* yielded a p value of $\leq$.0025 for sponge for *G. hikeurensis*, and $\leq$.0005 for *G. cincta*. Trials with *Dictyota* yielded a p value of $\leq$.0005 for sponge for *G. hikeurensis*, and $\leq$.0005 for *G. cincta*. Both species statistically preferred sponge. In trials with *Dictyota*, *Halimeda* yielded a p value of $\leq$.05 for *G. cincta*, indicating that they significantly avoided *Halimeda*.

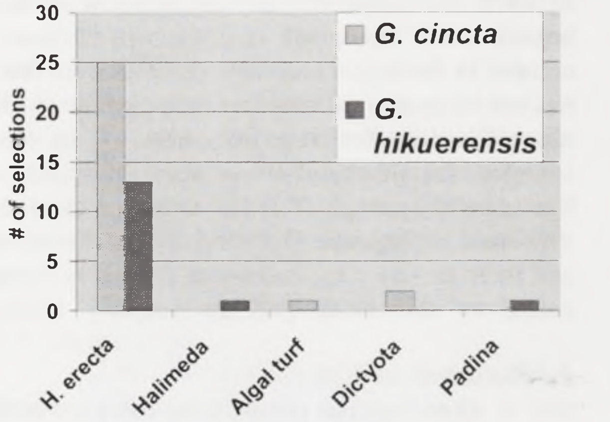


**Figure 7.** Feeding trial results. Both *G. cincta* and *G. hikuerensis* selected *H. erecta* far more than any other option.

*3.4 Fecal sample observations*

Fecal samples after both field feeding and lab feeding trials were examined. No differences were noted between the two. Spicules were the only feeding indicator that could be positively identified. These spicules were identified as belonging to the calcareous sponge *Leucetta chagosensis* (see figure 8). This species was not included in the feeding trial. No algal matter was seen and no organic material could be identified. White pellets were found consistently in the fecal matter of *G. Cincta*, but these could not be identified.

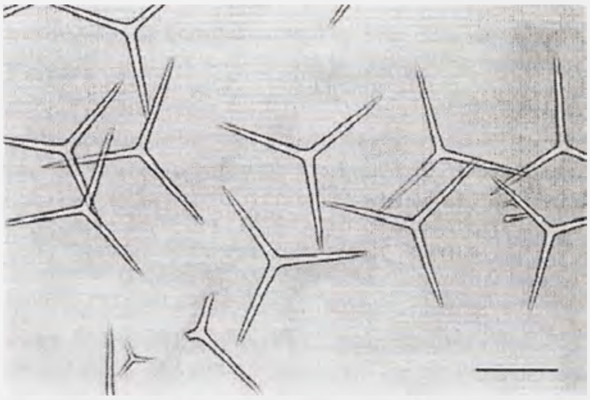


**Figure 8.** The spicules found in the fecal matter analysis looked like these spicules belonging to *Leucetta chagosensis*

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### *3.5 Nudibranch observations at other locations*

Two nudibranchs of each species were found at site 2, and 1 *G. hikuerensis* was found at site 5. Site 1 had murky water due to it's proximity to the Paopao river. A substantial amount of *Halimeda* grew there, as did a purple sponge. Site 2 was very similar to the primary study site, but had less *H. erecta* and less algal turf. Site 3 was very rocky, with very little algae other than *Halimeda* growing there and no *H. erecta*. Site 4 was similar to site 3, with lots of coral rubble and minimal algae growth. However, at site 4 *H. erecta* was sighted. Site 5 has high levels of algae but low levels of algal turf. There was lots of live coral and very little H. erecta.

### *3.6 Food selection observations*

The method of food selection of both species was observed in both the field and the lab.

## Discussion

Though the sponge *Hyrtios erecta* makes up 0.5% of the available food options in Moorea, both *Glossodoris cincta* and *G. hikuerensis* prefer it to all other sources, both in lab and in the field. These results are supported by the work of Rogers and Paul (1991) in Guam, which found a preference for *H. erecta* over the closely related *H. altum* in both *G. cincta* and *G. hikuerensis*. Rogers and Paul focused on the chemistry behind nudibranch defenses and determined that they sequester the compound heteronemin from *H. erecta* to deter predators, specifically reef fish. Interestingly, this study also found episcalaradial, a compound that is not a major metabolite in *H. erecta*, in both species. It is possible that nudibranchs alter the chemical structures of compounds once they are ingested, but these results may also suggest another possible food source for *G. hikuerensis* and *G. cincta*. Rogers and Paul did not investigate this possibility, as their study focused on another nudibranch, *Glossodoris pallida*, and its association with *H. erecta*.

Much of the literature characterizes dorid nudibranchs as obligate specialist benthic predators, often dependent on a specific sponge for both food and defense (Megina et al, 2002). Other possible food items are not mentioned, implying that the nudibranchs were not seen feeding on other food items. This conflicts with the field observation results which indicate that, while *H. erecta* was preferred, nudibranchs of both species were commonly observed feeding on what appeared to be algal matter, specifically algal turf. Rudman (2003, pers. comm.) suggests these nudibranchs are not equipped to digest algal matter, and it is possible that *G. cincta* and *G. hikuerensis* are feeding instead on an encrusting sponge beneath the turf. If this is the case then these nudibranchs are feeding on something other than *H. erecta*, because *H. erecta* does not encrust coral rubble, which was the substrate for much of the algal turf. In an organism as small as nudibranchs, it is very difficult to know which nutrients are being assimilated by the animal, especially the origin of these nutrients, even when gut content is examined.

This is illustrated by *Tylodina perversa*, an opisthobranch in the Mediterranean, which has been described as an obligate specialist preying on two closely related sponges, *Aplysina aerophoba* and *A. cavernicola*. *T. perversa* sequesters metabolic compounds from these sponges (Ebel et al, 1999, Teeyapant et al, 1993a), which have been shown to have strong antibacterial properties (Teeyapant et al, 1993b). But Becerro et al (2002) found a preference in *T. perversa* for sponges with higher levels of cyanobacterial symbionts, which indicates this opisthobranch may be assimilating herbivorous as well as sponge material. Omnivores are fairly rare in nature, but it is possible that if an organism evolved from an herbivore it may have retained the ability to digest plant matter despite its more specialized dietary strategies. Thus it is possible that *G. hikuerensis* and *G. cincta* may be supplementing their sponge diet with algal matter, especially since it makes up more than 50% of the available food.

As mentioned in the results of the fecal matter analysis, there was no discernable difference between post field feeding fecal matter and post feeding trial fecal matter, indicating that what was chosen in the feeding trials was not *radically* different from what was eaten in the field. It is unknown how long it takes ingested material to pass through the gut—it may be longer or shorter than 24 hours, and this introduces a possible source of error. The spicules were identified as being from the sponge *Leucetta chagosensis*, a calcareous, encrusting sponge prevalent in the Indopacific (Nichols, 2003, pers. comm.). *Hyrtios erecta* is unspiculated. Spicules litter the benthos and it is possible that these spicules settled out of the water column in the flow-through tank. However, no spicules were found in the control samples. They may have been incorporated into *H. erecta*, picked up by the nudibranch's mucousy body, or they could indicate another possible food source for *G. cincta* and *G. hikuerensis*.

The population density studies reveal higher densities for both species at the study site than at any of the other sites surveyed. This corresponds with the observation that the availability of *H. erecta* was higher there as well, despite making up less than 1% of the reef cover. *H. erecta* was found at sites 2, 4, and 5. *G. cincta* and *G. hikuerensis* (2 of each) were found at site 2. Both *G. hikuerensis* were observed eating *H. erecta*, as was one *G. cincta*. The sponge being consumed had been grazed down, with the black outer surface completely gone and only the tan inner matrix visible. This indicates that competition among nudibranchs for this resource was high at this site. Competition did not appear to be a problem at the primary study site. One *G. hikuerensis* was observed at site 5, where only one *H. erecta* colony was sighted approximately 20 m from the individual. There may be another food source at this site. Algal turf was also lower at all sites, and was completely absent at sites 3 and 4. Algal turf is high at the study site, most likely due to eutrophication from Rotui Juice Factory effluent, which is released approximately 100 m north of the study site.

Observations of food selection made during feeding trials and in the field raise interesting questions concerning how these species of nudibranchs sense their food. Nudibranchs were spotted in the field approximately .25m from *H. erecta*, their preferred food source, feeding on what appeared to be algal turf. In the feeding trials, nudibranchs were placed approximately .15 meters from each food choice, but would invariably begin moving in the direction they were facing when placed in the tank. Both *G. cincta* and *G. hikuerensis* seemed to only locate *H. erecta* in the tank after encountering it or coming very close to it (>5 cm). If placed facing away from *H. erecta*, the nudibranchs would crawl all over the tank, including over all possible food options in their path. These observations suggest that *G. cincta* and *G. hikuerensis* can not sense their preferred food choice at great distances and raises questions about how they locate their food. An opportunistic feeding strategy rather than a specialized one would be beneficial to an organism that cannot sense their food at a distance because that organism can feed on a greater number of the things they are likely to find themselves near. More work is needed in this area to determine how *G. cincta* and *G. hikuerensis* locate *H. erecta* in the field.

While this study has demonstrated a preference for *Hyrtios erecta* in both *Glossodoris cincta* and *G. hikuerensis*, many questions remain concerning the ecological implications of their feeding biology. Moreover, an effort should be made to resolve the conflicting information regarding the feeding strategies of these organisms and their possible association with an algal food source. Further work is needed to conclusively assess the relationship between *G. cincta* and *G. hikuerensis*, and determine whether these organisms exhibit omnivorous behaviors. The effects on nutrition and defense of removing *H. erecta* from their diet should be examined. It would also be interesting to determine which factors are structuring the distribution of *G. hikuerensis* and *G. cincta* in and around Cook's Bay.

## Conclusion

This study determined that, while the black sponge *Hyrtios erecta* makes up less than 1% of the available food at the study site, 2 species of nudibranchs common at the study site, *Glossodoris cincta* and *Glossodoris hikuerensis*, prefer *H. erecta* to the other available food sources. This was supported by both lab and field data. Both nudibranchs were observed consuming algal material as well, suggesting that these nudibranchs may not be obligate specialists. Population densities are higher at the primary study site than other places in Cook's Bay, possibly due to higher levels of *H. erecta* at this site.

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## LITERATURE CITED

Avila C (1995) Natural products from Opisthobranch mollusks: a biological review. *Oceanography* and Marine Biology Annual Review 33:487-559

Avila C, Paul VJ(1997) Chemical ecology of the nudibranch *Glossodoris pallida*: is the location of diet derived metabolites important for defense? Marine Ecology-Progress Series 150:171-180

Becerro MA, Turon X, Uriz MJ, Templado J (2002) Can a sponge feeder be an herbivore? *Tylodina perversa* (Gastropoda) feeding on *Aplysina aerophoba* (Demospongiae). Biological J. of the Linnean Society 78: 429-438

Becerro MA, Paul VJ, Starmer J (1998) Intracolonial variation in chemical defenses of the sponge cacospongia sp. and its consequences on generalist fish predators and the specialist nudibranch *Glossodoris pallida*. Marine Ecology-Progress Series 168:187-196.

Ebel R, Marin A, Proksch P (1999) Organspecific distribution of dietary alkaloids in the marine opisthobranch *Tylodina perversa*. Biochemical Systematics and Ecology 27: 769

Megina C, Carball JL, Cervera JL, Garcia-Gomez JC (2002) The diet of *Platydoris argo* (Gastropoda; Nudibranchia) and the dietary specialization of sponge eating dorids. J. of Molluscan Studies 68:173-179

Rogers SD, Paul VJ (1991) Chemical defenses of three *Glossodoris* nudibranchs and their dietary *Hyrtios* sponges. Marine Ecology-Progress Series 77(2-3):221-232.

Teeyapant R, Kreis P, Wray V, Witte L, Proksch, P (1993) Brominated secondary compounds from the marine sponge *Verongia aerophoba* and the sponge feeding gastropod *Tylodina perversa*. Zeitschrift für Naturforschung 48c:640

Teeyapant R, Woerdenbag H J, Kreis P, Hacker J, Wray V, Witte L, Proksch P (1993) Antibiotic and cytotoxic activity of brominated compounds from the marine sponge Verongia aerophoba. Zeitschrift für Naturforschung, 48c: 939

Todd CD (1981) Ecology of nudibranch mollusks. Oceanography and Marine Biology Annual Review 19:141-190.

# The Aftermath of a Boring Date: the Facilitative Role, Habitat and Coral Hosts of the Infaunal Date Mussel *Lithophaga sp.*

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ABSTRACT. The ability of a bivalve to bore into and inhabit live coral is rare. Several species within the bivalve genus *Lithophaga* have this unique ability. Some of these biocorroding bivalves are restricted to certain coral species and forms, while others can inhabit multiple species of different forms. Coral hosts and bivalve densities were determined through a series of transects. All species of *Porites* were infested, including the columnar form *P. Rus* and the branched form *P. Nigrescens*. All irregular and encrusting forms of *Montipora spp.* were infested. The minimum thickness of branches that were infested with juveniles was 3.05cm. There were two species of coral present that were not infested: *Acropora cytherea* and *Pocillopora verrucosa*. Both of these corals had average branch thicknesses less than 1.7cm. Surveys of geographical distribution indicate the highest densities of bivalves within bays and extremely low populations within most lagoons and forereefs. This distribution may be due to higher productivity within bays associated with elevated levels of nutrient input.

Several pieces of coral with abandoned boreholes were examined to determine the bivalve's role in the succession of the community. A variety of organisms, including larvae, algae and many juvenile crustaceans and mollusks occupied the burrows. The community was highly uneven, with the majority of occupants being juvenile hermit crabs and snails. The boreholes provide protection for these vulnerable developing organisms.

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## Introduction

Bivalves living within coral are faced with two obstacles; first, they must avoid being consumed by carnivorous polyps and then they must avoid being buried alive by coral overgrowth. Due to these impediments, the ability of a bivalve to bore into and inhabit live coral is rare. Most boring bivalves inhabit dead substrata including: dead coral, rock, limestone, and the shells of various molluscs (Kleemann 1996).

Most live coral boring bivalves belong to the genus *Lithophaga*. These bivalves, commonly referred to as date mussels, are biocorroders; they burrow by secreting chemicals that dissolve certain substrata. Unlike the bioabraders, bivalves that mechanically bore by rasping the substratum with their shell, biocorroders are restricted to calcareous substrata (Kleemann 1980).

Biocorroders have an important role in the destruction of reef and the creation of sediment (Kleemann 1996). Bioeroders, like boring bivalves play an important role in the maintenance of the balance between construction and destruction of the coral reef; especially in the Eastern Pacific, where reef is destroyed just as quickly as it is created.

Productivity and upwelling influence the extent of bioerosion (Risk et al. 1995). As filter feeders, bioeroding bivalves thrive in areas with high productivity. The United States Environmental Protection Agency (EPA), in a description of biological criteria required for assessing coral reef ecosystems, found that bivalves "provide a sensitive assessment of increasing eutrophication on reefs" (Jameson et al. 1998). The EPA has identified boring bivalves as potential bioindicators of water quality and reef health. More information needs to be obtained about these organisms before they will formally be identified as bioindicators in coral reef assessments.

Boring bivalves have a facilitative role within their community. Once the bivalve dies, its borehole is a potential hatching site or dwelling for cryptofauna (Kleemann 1996). Empty boreholes also provide new substratum for coral recruitment. Highsmith (1980) proposed that larvae of the host coral *Montipora berryi* colonize abandoned boreholes of *Lithophaga curta* on dead *Montipora berryi*.

The objective of this study was to determine the geographical distribution of *Lithophaga* around Mo'orea, to identify preferred habitats and hosts, to determine if the bivalve was capable of living on dead coral, and to look at the facilitative role of the bivalve within its community.

## Materials and Methods

*Species Identification*

All of the bivalves examined belonged to the same species, possibly *Lithophaga laevigata*. In a study of macroborers on Mo'orea, Peyrot-Clausade et al. (1992) identified *Lithophaga laevigata*, as the only live coral boring bivalve present. Descriptions of this species provided by Kleemann (1980) accurately describe the species under investigation.

*Study Area and Site Characteristics*

The study was conducted at three primary sites (fig. 1) located in different regions of the coral reef in Mo'orea, French Polynesia (17°30'S and 149°50"W). To avoid variation due to geographical distribution, sites were chosen along a line extending from the northwest region of Cook's Bay to the reef front.

The primary study site was the fringing reef adjacent to the Richard B. Gump Biological Research Station (17°24.4'S, 149°33.0'W). *Porites* was the dominant genus of coral. Massive coral morphologies were prevalent. The reef appeared to be in poor health, with over 50% dead coral and only 2.3% live coral. Algal cover was high, at 50%. Prevalent species of algae include: *Halimeda*, *Dictyota bartayresiana*, *Dasya pilosa*, and *Padina dictyota*, an algae associated with high levels of nutrients. Turbid waters indicated high rates of sedimentation.

The other two sites were situated near the barrier reef on the northwest rim of the bay. The first of these sites was located on the reef flat. Species of *Porites* and *Montipora*, a morphologically irregular coral, were abundant. *Porites rus*, a branching coral, was the prevalent species. Algal cover was 17 %. Abundant species of algae were *Padina dictyota*, *Turbinaria sp.*, and *Halimeda sp.* The reef was bordered by a deep pass to the south and the reef crest to the north.

The second of these sites was situated on the upper reef slope, just beyond the reef crest. The prevailing species of coral was *Pocillopora verrucosa*. Other genera present include *Porites*, *Acropora* and *Montipora*. Unlike the previous sites, only encrusting forms of algae were present. The reef crest to the south and Avaroa pass to the north bordered the site.

*Geographical Distribution*

In addition to the sites aforementioned, population assessments were performed at several bay and lagoon sites around the island (fig. 1). At each site, areas of approximately 500 m$^2$ were surveyed. The presence or absence of the bivalves, as well as a rough estimation of abundance was recorded. A 1m$^2$ quadrant was used to do an in-depth survey of the population within the lagoon at Pt. Aroa in Temae. The

**Figure 1**: Sites and geographical distribution

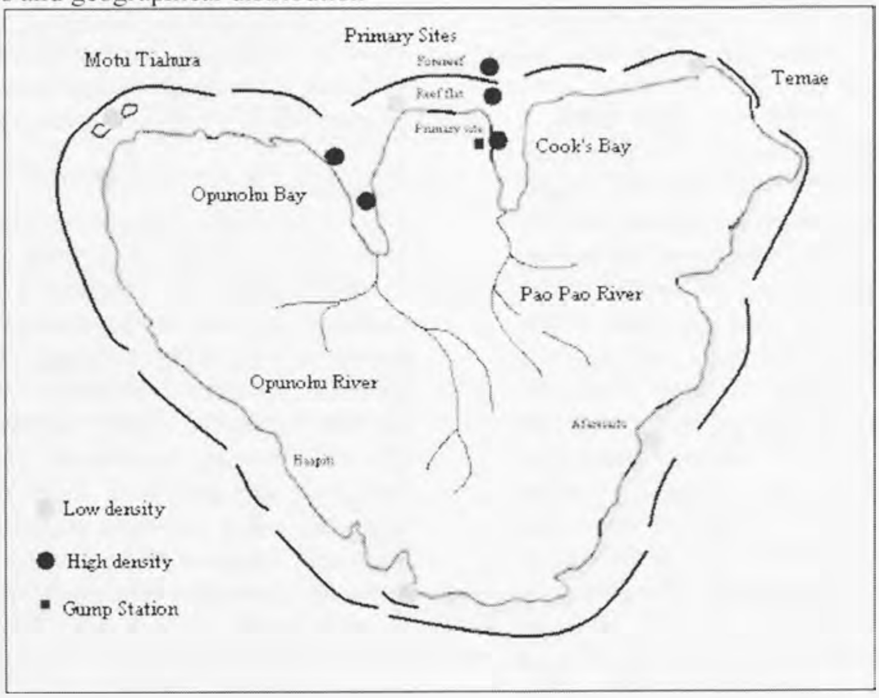

**Figure 2a**: Bivalves in their boreholes. **2b**: Typical specimen. Size ~8.5mm

number of bivalves and the percentage and composition of coral was recorded for 100m$^2$ of contiguous area.

*Substrate Preference*

In order to determine if *Lithophaga laevigata* inhabits dead coral, several coral fragments were collected from the Cook's Bay site. These pieces, all approximately the same size, were examined and the following measurements were recorded for both live and dead coral: estimated percent coverage and the quantity of adult and juvenile bivalves. For the purpose of this study, adult bivalves have been defined as bivalves with a dumbbell shaped aperture. Apertures of juveniles are too small (~1mm) to discern a dumbbell shape, so they appear as black specs on the light coral surface. Some juveniles may have been overlooked, given that they were only visible when they had their dark siphons extended for feeding.

In order to determine coral hosts, a square meter quadrant was used to survey each of the three study sites. One hundred square meters were surveyed within the primary site. At the other two sites, 100m$^2$ was measured and ten randomly selected quadrants were surveyed. The following measurements were recorded within each quadrant: number of adult and juvenile bivalves and the species of their host, the percentage of each species of live coral, the percentage of dead coral, the percentage and species composition of algae. Species identification of massive forms of the coral genus *Porites*, proved difficult due to the similar appearance of several species. Therefore, all massive forms of *Porites* present: *P. lutea*, *P. lobata*, *P. solida* and *P. australensis*, have been combined into one group, referred to here as: massive *Porites*. Based upon observations in the field this distinction should not affect the results, given that all of these species had similar forms and attributes, making them equally infested with bivalves. The binomial test was applied to determine statistical significance.

*Dimensions of Bivalves and Branches*

Several small samples of each species of coral were collected. Thirty random holes were selected for each species. The size of the aperture, width and depth of the hole and the length and width of the bivalve were measured for each borehole and its occupant. For the branched corals, several measurements were made of infested branches to determine the minimum thickness required for occupation. Samples were also collected from two uninfested corals, *Pocillopora verrucosa* and *Acropora cytherea*. Several measurements of branch thickness were made in order to determine the average thickness of their branches.

*Facilitative Role*

Several coral fragments of predominantly dead coral were collected at the Cook's bay site. The contents of boreholes were recorded, as well as the erosional state of the borehole. Four different levels of erosion were defined: elliptical borehole still enclosed, circular borehole mainly enclosed, open and cluster of opened boreholes. The diameter of each hole was measured. Over 150 holes were inspected using tweezers and a brush. Visible biota was removed and recorded for each hole. After all accessible biota had been removed; a hammer and chisel were used to break open the enclosed holes, in search of smaller and more cryptic organisms. A dissecting microscope was used to identify various mollusks and larvae. Measures of species diversity were quantified with both the Shannon and the Simpson indices of diversity.

## Results

### *Geographical Distribution*

*Lithophaga laevigata* was absent or present in extremely low densities (0.2 bivales/m$^2$) at all sites except those located within or on the outskirts of bays (fig 1). Out of Temae and the three main sites, the highest density was recorded in Cook's bay, at 75 bivales/m$^2$. At this site over 650 bivalves could be found on a coral head that occupied only 0.04m$^2$ of the quadrant. Some of this discrepancy may be due to differences in the amount and composition of coral; however, all sites had similar coral compositions and densities.

### *Substrate Preference*

A total of 2750 bivalves were counted on the coral fragments. Of these, 98% of the bivalves were found on live coral, which constituted only 34% of the examined surface area. Dead coral made up 66% of the surface area, but was inhabited with only 2% of the bivalves. No juveniles were found on the dead coral. Apertures of the boreholes of bivalves inhabiting dead coral eroded from their characteristic dumbbell shape, to an elliptical shape.

Preferred coral hosts within the bay were massive forms of *Porites* and several forms of encrusting *Montipora*, including *M. efflorescens*. These were the dominant species on the reef. The preferred coral hosts on the reef flat were again, massive forms of *Porites* and *Montipora*, and a new species, *P. Rus*. Bivalves infested every type of coral encountered at these sites.

The forereef contained three new species of coral. Two of these: *Pocillopora verrucosa* and *Acropora cytherea* were not inhabited by *L. laevigata*. Adult bivalves were present on, but did not statistically prefer the other new species, *P. nigrescens*. Massive forms of *Porites*, and Montipora were present and preferred.

Table 1 shows all p values obtained for each species of coral. Values <0.05 indicate statistical significance. Highlighted corals are preferred hosts, while underlined corals are uninhabited.

### *Dimensions of Bivalves and Branches*

The average size of *L. laevigata* was different for each coral host. Bivalves occupying massive forms of *Porites*, were the largest at 7.6mm. The bivalves inhabiting *P. rus*, were the next largest at 6.4mm. Occupants of *P. nigrescens* and *Montipora* were the smallest at 5.8mm and 5.7mm. All of the bivalves were of the same species. Statistical significance was shown with ANOVA.

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**Table 1**: Results of Binomial Test, p values <0.05 are statistically significant

| | Fringing Reef | | Reef Flat | | Forereef | |
|---|---|---|---|---|---|---|
| | Adult | Juv. | Adult | Juv. | Adult | Juv |
| Massive *Porites* | 0 | 0 | 0 | 0 | 0 | 0 |
| *P. Rus* | | | 0 | 0 | 0 | 0 |
| *P. Nigrescens** | | | | | 0.2 | 0 |
| *Montipora sp.* | 0 | 0.0004 | $4.2x10^{-15}$ | $2.4x10^{-10}$ | | |
| *M. efflorescens* | 0 | 0 | | | | |
| *Pocillopora verrucosa* | | | | | $8.5x10^{-139}$ | $2.22x10^{-237}$ |
| *Acropora cytherea* | | | | | 0 | 0 |

*Refer to discussion

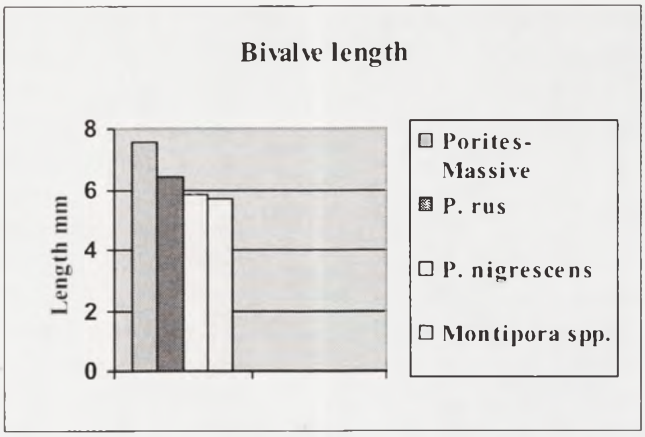

**Figure 3**: Average bivalve size within each coral host

The minimum branch thickness inhabited by *Lithophaga* was approximately 3 cm. The two unaffected species of coral, *Pocillopora verrucosa* and *Acropora cytherea* have average branch thicknesses of 1.7 and 1.5cm.

*Facilitative Role*

Species diversity within the microhabitats created by empty boreholes of *L. laevigata* was low. A total of 26 different species were present. The majority of occupants were juvenile hermit crabs, which clustered together within the holes. On average groups contained three crabs, but could contain as many as 15. *Littorina scabra*, a snail that has a juvenile marine stage and that moves into the littoral zone as it matures, was also prevalent. *Halimeda sp.*, a common alga in this region, anchored itself inside the boreholes. A number of different larvae, especially that of *Crustacea*, and a number of juvenile crabs and snails were found inside the microhabitats.

The rank-abundance diagram (fig.4), ranks organisms based upon their proportional abundance. Species of high rank dominate the community. A complete list of organisms within this microcommunity is located within this diagram. Indices of diversity (table 2) indicate that the community is highly uneven, with low species diversity.

## Discussion

*Geographical Distribution*

Heterotrophic macroinvertebrates, like species of the genus *Lithophaga*, thrive in areas with high nutrient loads. Elevated primary productivity associated with upwelling has led to an extremely high abundance of *Lithophaga* (hundreds of individuals per 0.01m$^2$) on the reefs of Isla del Caño in Costa Rica (Scott & Rish 1988).

Upwelling is a natural input of nutrients into a system; however, unnatural and excessive inputs can lead to the deterioration of water quality and eutrophication. This eutrophication, often combined with sedimentation, dramatically increases the abundance of bioeroding bivalves on the reef (Jameson et al 1998).

High amounts of algae, low water visibility, abundant boring bivalves, and fine substrate, are characteristics of the fringing reef adjacent to the Gump Station that indicate that eutrophication has occurred. Located within Cook's Bay, this site is exposed to abnormal nutrient input from several sources. Jus de Fruits de Mo'orea, a juice factory located directly north of the station, empties its waste directly into the bay. As the most developed bay on the island, input of urban runoff and untreated human excrement is typical. Pao Pao River empties agricultural runoff from Pao Pao valley directly into the head of the bay.

**Table 2**: Indices of Diversity

| Total Species | 26 | | |
|---|---|---|---|
| Simpson | | Shannon | |
| D | 2.308 | H | 1.459 |
| E | 0.089 | J | 0.453 |

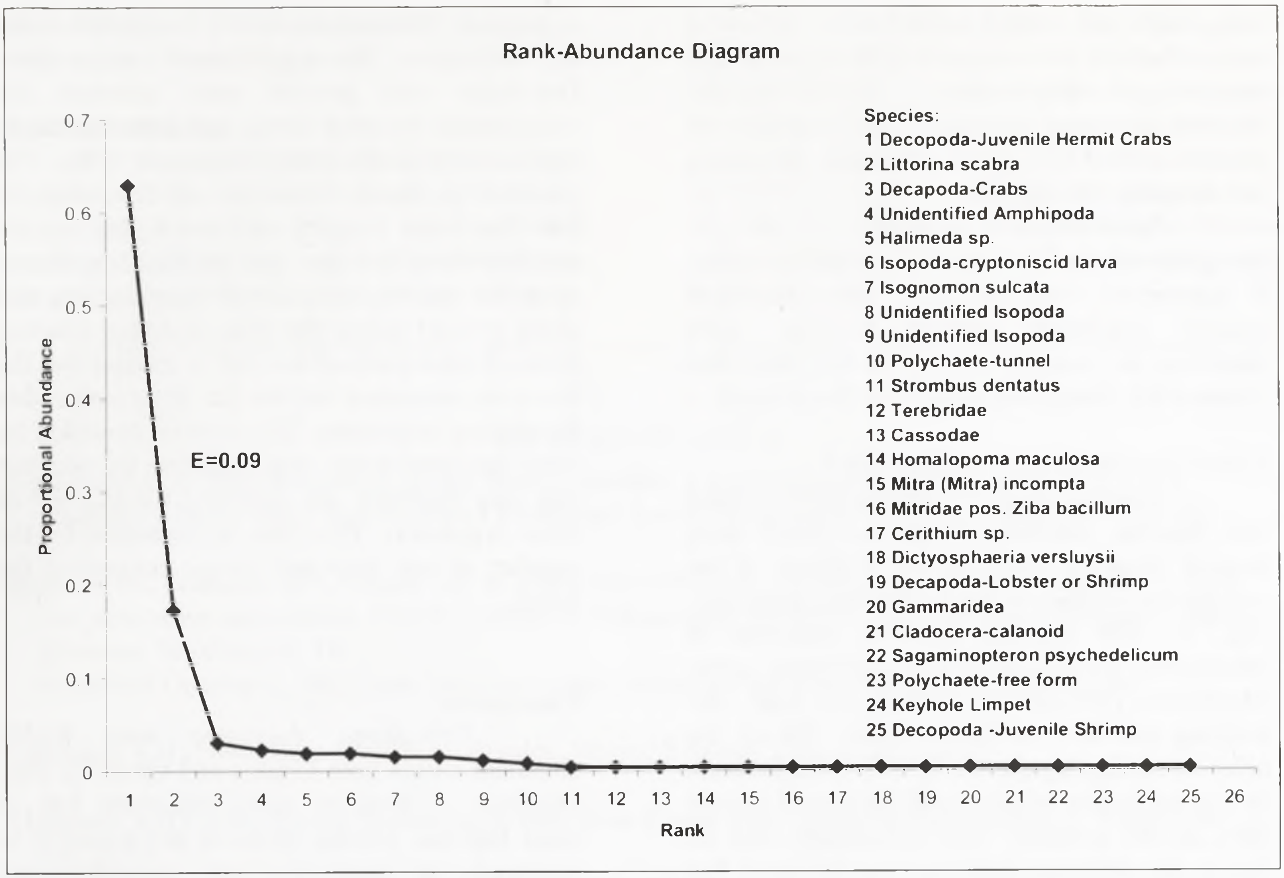

**Figure 4**: Rank-Abundance Diagram of Secondary Inhabitants

Densities were also elevated at the two sites surveyed within Opunohu Bay. This bay is less developed; however, the Opunohu River empties runoff from the agricultural land within Opunohu valley, directly into the head of the bay.

The abundance of bivalves was significantly lower at sites within lagoons. Several of the sites, especially Temae and Motu Tiahura, were continually flushed by currents bringing in fresh, nutrient poor water, typical of the E. Pacific. Water clarity was higher at these sites, indicating lower productivity and less suspended sediment. Based upon these observations and findings, it is plausible that elevated nutrient levels are the cause of the high abundance of bivalves within Mo'orea's bays; however, there are many possible factors involved, such as: temperature, substratum availability, water circulation, structure and age of the coral reef, presence of other bioeroders, etc.

*Substratum Preference*

Specialized live coral boring bivalves are only capable of colonizing live coral (Kleemann 1980). This agrees with the observation that no juveniles were found on dead coral. Almost all of the bivalves (98%) inhabited live coral. Several bivalves were found inhabiting dead coral that had undergone minimal erosion. The only erosion that had taken place was that of the borehole's aperture, making it more elliptical in shape. This indicates that the bivalve, though its veligers cannot settle on dead coral, can live within it, as long as erosion is minimal and the hole remains intact. The bivalve must also compete with algal overgrowth.

The coral fragments examined were typically dead pieces of coral that had recently been recolonized. It is possible that some of the adult bivalves found on the thin layer of new coral, were occupying the dead coral when new coral larvae settled and began to grow over the hole. Since this bivalve is equipped with siphons that secrete acid, it prevented overgrowth, giving the bivalve new protection against a premature death due to erosion or outcompetition by algae.

Each species of *Lithophaga* has its own host-specificity. Bivalves can be restricted to one host or have multiple (Kleemann 1980). Results of the binomial test (Table 1) indicate that *Lithophaga laevigata* has a clear preference for various substrata and clearly avoids others.

*Lithophaga* can inhabit hosts with a variety of forms. Each of the hosts identified had a unique morphology. Represented forms include: massive (*Porites*), columnar and laminar (*P. Rus*), branched (*P. nigrescens*), and encrusting and irregular (*Montipora*).

Non-random distributions of *L. laevigata* were present on all coral hosts, except *P. nigrescens*. Data may have been skewed if stunted (explained below) bivalves were identified as juveniles. If this is the case, data obtained for *Montipora* would also be affected.

*Dimensions of Bivalves and Branches*

Moretzsohn and Tsuchiya (1992) found that bivalves inhabiting branched coral were stunted. Stunting results in the variation of the average size of the bivalve within each coral host (fig. 3). The smallest bivalves occurred in *Montipora*, an extremely thin encrusting coral. *Montipora efflorescens*, occurs on both the fringing reef and on the forereef. Of all the bivalves occupying this coral, 99% were juvenile or stunted on the fringing reef, compared to only 66% on the forereef. This incongruity may be due to the different substrata that the coral has colonized. *Montipora* typically grows on highly eroded dead coral within the fringing reef. Once bivalves bore through this thin coral, they most likely cannot continue to grow through the highly eroded underlying substratum, hence they are stunted. However, on the forereef, *M. efflorescens*, grows on top of the solid limestone coralithion that forms the reef crest. Once the bivalve grows through *Montipora*, it may continue to grow through the coralthion. Due to the presence of adults at both locations, it is assumed that this dissimilarity is not due to age differences of the populations.

The thickness of the branches of the uninhabited corals, *P. verrucosa* and *A. cytherea* was significantly smaller than the minimum branch thickness of inhabited corals. This may be one reason why the bivalve's veligers do not colonize this coral. Other possible reasons include skeleton density and polyp size. Kleemann (1980) believes that veligers choose a host based on their ability to penetrate the coral unharmed, not on the basis of the coral's density. The only effect of density identified by Kleemann was on the rate of boring and therefore, on the growth rate of the bivalve.

*Facilitation*

The microhabitats created by *Lithophaga* alter the successional stage of the community (Kleemann 1996). Empty boreholes are habitations for cryptofaunal communities. Boreholes also provide new substrate for colonization by coral larvae and other sedentary species (Highsmith 1980; Kleemann 1996). The community found within the microhabitats of Pao Pao Bay's fringing reef was highly uneven and therefore, had low species diversity. Based upon the quantity of juvenile hermit crabs and snails present within the holes and their absence from all other parts of the reef, it appears that the holes are important habitat for these vulnerable developing organisms. The security provided by these enclosed holes, may increase the survival rate and therefore, the reproductive success of these organisms. This idea is supported by the number of egg sacs and larvae occupying the holes.

## Conclusion

*Lithophaga laevigata* was highly abundant within both Cook's and Opunohu Bay. Densities of bivalves were extremely low in most lagoons. Boring bivalves are sensitive to increases in nutrients and eutrophication. Excessive input of nutrients from agricultural runoff and human waste into the bays, may account for their high densities within these regions.

This species of boring bivalve inhabits several species of coral: massive forms of *Porites*, including: *P. lutea, P. solida, P. lobata* and *P. australensis, Montipora efflorescens, Montipora spp., P. rus,* and *P. nigrescens.* Stunting occurs on thin encrusting forms of *Montipora*, and on branching forms like *P. nigrescens*.. This bivalve is capable of inhabiting, but not colonizing, dead coral; as long as algal overgrowth and significant erosion do not occur.

The boreholes that *L. laevigata* creates provide security for developing eggs, larvae and juveniles, a hiding place for cryptic fauna, and new substrata for colonization by sedentary organisms. Within this community, boreholes are especially important in the reproductive success of juvenile hermit crabs and snails.

Future research focusing on the relationship between bivalve abundance and nutrient load, would reveal the viability of bioeroding bivalves as bioindicators. A biological assessment of the fringing reef adjacent to the Gump Research Station should be performed to determine the extent and cause of degradation. Based on this assessment, measures should be taken to restore this reef and similar reefs within French Polynesia.

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## *LITERATURE CITED*

Highsmith RC (1980) Burrowing by the Bivalve Mollusc *Lithophaga curta* in the Living Reef Coral *Montipora berryi* and a Hypothesis of Reciprocal Larval Recruitment. Marine Biology 56: 155-162

Jameson SC, Erdmann MV, Gibson GR Jr, Potts KW (1998) Development of biological criteria for coral reef ecosystem assessment. USEPA, Office of Science and Technology, Health and Ecological Criteria Division, Washington, DC.
Retrieved October 2, 2003 from http://www.epa.gov/owow/oceans/coral/biocrit/chap3.4.html

Kleemann KH (1996) Biocorrosion by Bivales. Marine Ecology 17(1-3): 145-158

Kleemann KH (1980) Boring Bivalves and their Host Corals from the Great Barrier Reef. J. Moll. Stud. 46: 13-54

Risk MJ, Sammarco PW, Edinger EN (1995) Bioerosion in *Acropora* across the continental shelf of the Great Barrier Reef. Coral Reefs 14: 79-86

Scott JB, Rish MJ (1988) The effect of *Lithophaga* (Bivalvia:Mytilidae) boreholes on the Strength of the coral *Porites lobata*. Coral Reefs 7:145-153

# The secret identity of an infaunal holothurian, *Chiridota hawaiiensis:* A close look at anatomy and burrowing behaviors

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**ABSTRACT.** An infaunal holothurian was found at three intertidal to shallow subtidal locations in Moorea, French Polynesia. Dissection of the organism revealed that respiratory trees and tube feet are absent. Examination of papillae found along body wall revealed wheel spicules consisting of six spokes. This is characteristic of the order Apodida, family Chiridotidae (Smirnov 1998). Further observations regarding anatomy and morphology demonstrate that the species in question is likely *Chiridota hawaiiensis*. This classification is based primarily on the presence of wheel and rod spicules, reduction of papillae along the ventral surface, as well as the number of digits (6-10) found on each of the oral tentacles (Fisher, 1907). This classification is not yet confirmed due to ambiguities differentiating the anatomy of *C. hawaiiensis* from *Chiridota rigida*.

Extensive observations were made in respect to burrowing behavior and population distribution. *C. hawaiiensis* was found in high density at the Motu Tiahura. Transecting at this location was performed to determine the population distribution and abundance. Transects revealed that there were several areas of particularly high abundance. It was observed that abundance and distribution might be correlated with sediment-grain size. Sediment samples were taken along transects to determine whether grain size affects burrowing behaviors. Sediment samples were separated into five grain sizes and burrowing trials were performed. A wide range of behaviors were noted during the trails. Most notably, burrows in coarser sediment occurred earlier than burrows in smaller sediment. Burrows in coarser sediment were also greater in depth, and once burrowed, specimens did not resurface.

## Introduction

Holothurians play an integral role in benthic marine environments, constituting over 90% of the biomass in deep waters. They are found in tropical, polar, and hydrothermal regions, thus, within the class, there is large variance in morphology and anatomy (Kerr 2000). The typical holothurian body type is symmetrical and elongate along the oral-aboral axis. Unlike other echinoderms, the dermal spicules have been reduced, and as a result, a majority of holothurians are soft-bodied. Holothurians also characteristically possess a calcareous ring and circum-oral tentacles (Hickman 2001). The variations of each of these characteristics, particularly variations in spicule structure, are used in classification determine phylogeny.

Divisions within the order Apodida are almost entirely based on variations in spicule morphology. Members of the order Apodida, family Chiridotidae, are unique in that the spicules are wheel shaped. The family is further divided into two subfamilies based on the presence or absence of sigmoid hooks (Smirnov 1998). Further classifications are dependent upon the structure of the calcareous ring and morphology of oral tentacles. In this study, each of these anatomical features is examined in attempt to identify an organism that appears to be most closely related to *Chiridota hawaiiensis*

*Chiridota cf. C. hawaiiensis* was found in three locations in Moorea, FP. This species is a poorly studied infaunal holothurian. Although this organism was initially described in 1907 by W. Fisher, there are no subsequent studies of its morphology, ecology, and behavior. As a deposit feeder, this species is essential in recycling organic matter within the ecosystem. However, like small many infaunal species, its presence has often goes unnoted.

Because so little research has been performed on this species and it has proven difficult to definitively identify the species at hand. Problems identifying *Chiridota hawaiiensis* stem from ambiguities differentiating its morphology and anatomy with that of its relative, *Chiridota rigida*. Proper documentation indicating the unique characteristics of each of these species needs to be performed.

It is the aim of this study to identify the species found in Moorea while noting several of its key characteristics. Anatomy and morphology are closely examined along with basic behaviors and habitat. The distribution and abundance of *C. hawaiiensis* is assessed at one site in Moorea, providing insight into the poorly understood population dynamics of this species. Furthermore, the effect of grain size on burrowing is examined to determine whether a preference exists.

## Materials and Methods

### *Study Site*

*Chiridota hawaiiensis* was found within intertidal zones at several locations in Moorea, FP: The eastern shore of Motu Tiahura, the beach rock outcrops in Maharepa, and the lagoon between Cooks and Opunuhu Bays. Motu Tiahura, (S 17° 29,179, W 149° 54,739) was chosen as the study site because of its low nutrient, shallow water. This allowed *C. hawaiiensis* to be found easily within the sandy intertidal.

**Figure 1.** Map of Moorea, French Polynesia. *C. hawaiiensis* was found at each of the sites indicated. Transecting and collecting took place at the Motu Tiahura.

### *Collection and Observations*

Specimens of *C. hawaiiensis* were collected at the Motu Tiahura in order to perform dissections and observe burrowing and feeding behaviors in the laboratory. Specimens were kept at the research station in buckets with sediment from the collection site and an inflow of running seawater. Burrowing and feeding behaviors, as well as external anatomy, were observed using glass bowls and dissecting scopes.

### *Internal anatomy*

Dissection of two organisms was performed using a dissecting kit and dissecting scope. Organisms were placed in 90% ethanol before dissection. Internal structures were identified using Hickman 2001, and were recorded with a digital camera.

In order to classify family and species, three *C. hawaiiensis* were dissolved in a solution of water and house bleach to obtain spicules from within, and along the body wall. Spicules were used to classify the family and species of the organism. The solution was viewed under a dissecting scope where particulates were removed. Particulates were then placed on slide and viewed under a compound microscope. Digital images were taken.

### *Population distribution and abundance*

Eight transects were sampled at 10 meter intervals at Motu Tiahura to determine the distribution of *C. hawaiiensis* at this site, along with abundance. Preliminary observations were used to approximate the parameters of the population. From these observations, it was decided that transecting would begin near the center of the population distribution. Transecting was also performed to the north and south of the center starting point (See Figure 2).

Transects began at the high tide mark and ran perpendicular to the shore for 100 meters seaward. A quadrat size of .25 meters squared was used. Quadrats, made from PVC pipes, were placed 10 meters apart. In each quadrant, *C. hawaiiensis* was found by overturning the top five inches of sediment. Algae and rock pieces found within the quadrant were displaced to increase visibility. Necessary time was spent at each quadrant to ensure that all organisms had been found. Once found, organisms were removed and held in a cup so as

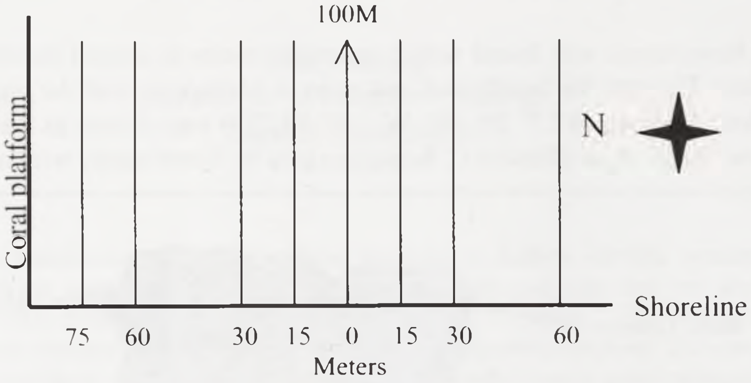

**Figure 2.** Eight transects were performed along the eastern shore of Motu Tiahura. Transecting began at the center of the distribution (0 meters) and ran 75 meters north and 60 meters south. The center of the population distribution was determined by preliminary observations.

not to be counted twice. Organisms were later replaced. Data was then used to construct a contour map illustrating the abundance at each quadrant along all eight transects.

*Burrowing Trial*

Sediment samples were taken along transects. Samples were separated using sieves of sizes 2mm, 500µm, 250µm, 125µm, <125µm. Wet sediment samples were poured through sieves. Sieved sediment was collected in jars and dried in an oven at 60 degrees Fahrenheit for 24 hours. Samples were then collected and placed in respective cups marked 2mm, 500µm, 250µm, 125µm, <125µm. Approximately one inch of sediment was placed in each of the clear, plastic, labeled cups. The cups were then filled with water and allowed to sit until the sediment had completely settled and water was clear. Four specimens were simultaneously dropped into each cup. The time of drop was recorded. The burrowing time for each specimen was also recorded, along with observations regarding whether the specimen re-surfaced, where in the cup the burrow was located, and the depth and orientation of burrow.

*Voucher Specimens*

Voucher specimens of *C. hawaiiensis* are deposited in the University of California Museum of Paleontology.

**Results**

*Systematics*

Phylum ECHINODERMATA
Class HOLOTHUROIDEA
Order APODIDA Brandt, 1835
Suborder Synaptina
Family CHIRIDOTIDAE Ostergren, 1898
Subfamily CHIRIDOTINAE Ostergren, 1898
Genus *Chiridota* Eschacholtz, 1829

Type species. ***Chiridota hawaiiensis*** Fisher, 1907

*Internal anatomy*

Dissection of *C. hawaiiensis* revealed the presence of 12 digitate tentacles attached to a calcareous ring. Five longitudinal muscles were also attached to calcareous ring and ran along the body to

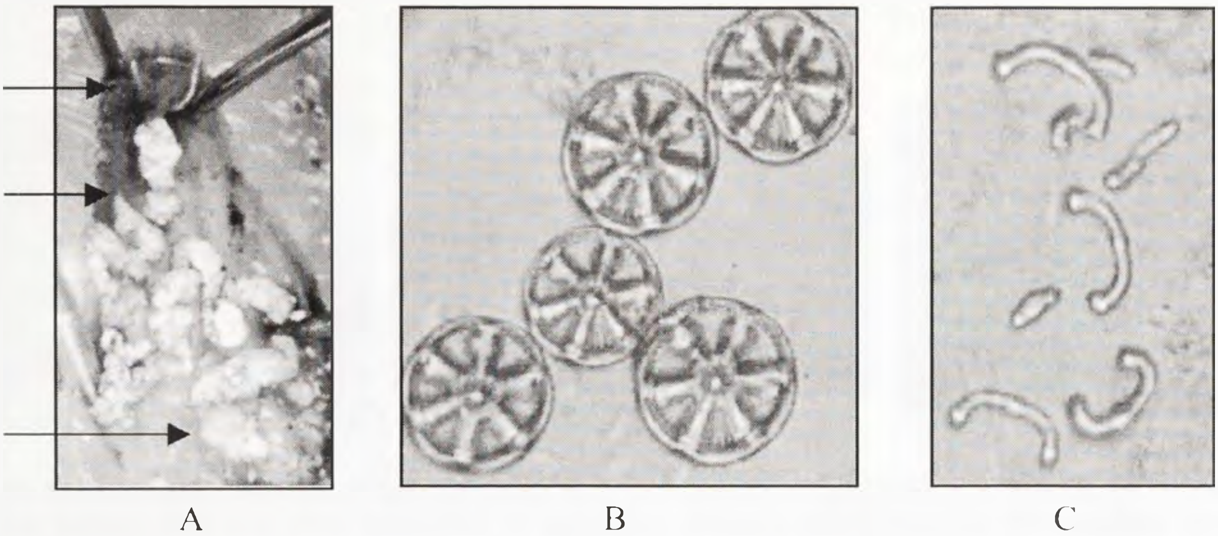

**Figure 3.** Digital images taken during dissection. **A.** (From top to bottom) Calcareous ring, stomach, and intestine. **B.** Wheel spicules obtained from *C. hawaiiensis*. Wheel spicules have 6-spokes and teeth along the inner rim. **C.** Rod spicules of oval and C-shape, knobbed at the ends.

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the anus. The complete digestive system was present, comprised of the mouth, pharynx, esophagus, stomach, intestine, cloaca, and anus. The body is unsegmented. There was no evidence of respiratory trees. Polian vesicles, gonads, and the madreporite may have been present but were difficult to see and were not confirmed.

Both rod and wheel spicules were found. Wheel spicules are comprised of 6-spokes with teeth along the inner rim. Aggregated wheel spicules make up papillae along body wall. The number of wheel spicules present, greatly outnumbers the rod spicules.

The ability to eviscerate was also observed in the lab. Visceral organs were discarded in stressful environments (Byrne 2001). This appeared as yellow tissue extending outside the body along the body wall or from the anus.

*External Anatomy*

*C. hawaiiensis* possesses a soft, worm-like body with an oral and aboral end. Size ranges from ~0.5cm to 7.0cm. Body coloration ranges from red to light pink, often with darker coloration near the oral end, and increasing translucency near the aboral end. On occasion, red coloring stains hands. Tentacles are white or clear.

The body wall has a warty appearance with large white papillae. Papillae were of variable sizes. When turgid, papillae align and form rows parallel to oral-aboral axis, and when elongated, papillae appear randomly distributed. A reduced number occur along the ventral side. It was observed that papillae are occasionally shed.

Tube feet are absent. Instead, locomotion occurs through hydrostatic movement. This is created by longitudinal and circular muscles. Longitudinal muscles are also used for retraction of tentacles. In this action, the body wall is pulled completely over tentacles. Both longitudinal and circular muscles are visible along the body wall.

Twelve digitate tentacles, encircling the mouth, also aid locomotion. Tentacles are covered with a sticky mucous and are used for locomotion, burrowing, and feeding. Tentacles are always active, except when retracted inside of body wall. Tentacles move in an alternating fashion, bringing food in towards mouth or pushing sediment grains away from body. Six to 10 digits were found per tentacle with the number of digits consistent for an individual. Two sizes of digits were present per tentacle, with 2 large terminal digits, surrounded by 2-4 small digits at the sides.

**Figure 4**. Images of *C. hawaiiensis* **A.** Calcareous ring visible through body wall. Also pictured are digitate tentacles with sediment grains attached **B.** Image of translucent body wall with papillae and looped intestine. **C.** *C. hawaiiensis* traversing substrate in search of sediment.

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*Burrowing Behaviors*

*C. hawaiiensis* was found burrowing into coral sand in tropical, shallow reef waters. When burrowed, aboral end is often found inflated. Burrows are generally oriented vertically with oral end down into sediment. This was common when the top inch or two of sediment were gently swept away without disturbing the burrow. This behavior was less common in laboratory conditions. Burrows observed in the laboratory were often shallow and U-shaped, with the aboral end horizontally oriented within sediment. In both the laboratory and the field, *C. hawaiiensis* was often found burrowing in close proximity of 2-6 individuals. Burrowing depths ranged from 1cm to 10cm.

Burrows were created using tentacles. All twelve tentacles move in an alternating fashion, pushing the sediment grains away from body. A sticky mucous was secreted from tentacles.

In the field, *C. hawaiiensis* did not immediately re-establish itself within the sediment once it was exposed. The time taken to re-burrow is unknown. When exposed in the laboratory, however, specimens burrowed immediately underneath any object present (ruler, sediment, rock, other specimens). If nothing was present, specimens would move around dish, eventually reaching a side. At this point, the specimen would travel up along side of the dish and orient its mouth (tentacles active) at water surface. It would remain in this position for some time before crawling

*Population distribution and abundance*

Transecting revealed densities ranging from zero to 55 individuals per quadrat. Distribution and abundance are illustrated using a contour map (See Figure 5). Three areas are marked with particularly high density.

*Burrowing Trial*

Burrowing behaviors were markedly different in smaller grain sizes (125, <125μm) versus larger grain sizes (2mm, 500μm). When *C. hawaiiensis CF* was placed in cups of 125 and <125 μm burrowing was slow. Specimens often moved across the top of sediment before burrowing. It took 15 minutes or longer before burrowing occurred in the <125μm. When burrowing did occur it was shallow, mainly at surface-water interface, and U-shaped. Similar behavior was observed in the 125μm cup. However, burrowing occurred earlier (first burrow occurred at seven minutes, average occurred at 13 minutes). In both cups, continuous burrowing and resurfacing occurred. This behavior was observed for hour and was rare in other cups of larger grain sizes.

Body elongation was also observed in 125 and <125 μm cups. In this behavior, the anterior portion of the trunk would elongate, becoming narrow. This would double or triple the typical body length. During elongation, the oral end reached towards the sides of the cup, or up into the water column. This would occur without movement of the posterior trunk. This was also noted in the 250μm cup but not in the 500μm or 2mm cup.

**Figure 5.** Contour map illustrating the abundance and distribution of *C. hawaiiensis* at the eastern shore of Motu Tiahura. The map indicates particular areas, approximately 50-70 meters off shore, where abundance was greatest. These areas, marked light and dark gray, contain 45-50, and 55-60 organisms, respectively. The overall range for abundance was 0-55 organisms found per quadrat.

Burrowing in the 2mm and 500μm cups was immediate and usually occurred in the location *C. hawaiiensis* was dropped. Therefore, most of these burrows started in the middle of the cup. Burrows were noted to reach the bottom of cup, however many burrows were not visible so their depth and direction was unknown. Once burrowed, *C. hawaiiensis* rarely resurfaced. Only one specimen in the 500μm cup resurfaced during the first and second trial.

Behaviors in the 250μm cup were a combination from all cups. Body elongation did occur, but in fewer specimens. Burrowing times occurred earlier than in the 125μm and <125μm cups. Burrows were shallow, U-shaped, and resurfacing did occur. Burrows also occurred less frequently in the middle of the cup.

Specimens were left in cups for a twenty-four hour period. At the end of this period, all specimens were burrowed.

Feeding behaviors were difficult to observe in larger sediment since these often occurred in the middle of cup. However, it was noted that tentacles, in all cups, were always active.

## Discussion.

### *Systematics*

From the presence of 6-spoked wheel spicules, it was determined that the species at hand is of the family Chiridotidae. Furthermore, the absence of sigmoid hooks indicates the species is within the subfamily Chiridotinae (Ostergren, 1898 and Smirnov 1998). Members of this subfamily characteristically display rod spicules as opposed to anchors or sigmoid hooks, and wheel spicules are aggregated into papillae.

The rod spicules found in this study were oval and curved. This is similar to observations made by Fisher, 1907, in which he describes rod spicules from *C. hawaiiensis* as oval and C-shaped with knobbed ends. Branched rods were also found by Fisher but were not observed in this study. Rod spicules were found in much lower quantities as compared to wheel spicules. This was also noted by Fisher, and, according to his study, contrasts with the number of rod spicules found in *C. rigida*, which are estimated to be greater. Taking these observations into account, it seems that the spicule structures found in this study are consistent with spicules from *C. hawaiiensis.*

It was observed that the species in this study has a marked reduction of papillae along the ventral surface as compared to the dorsal surface. Similarly, Fisher notes that the number of aggregated wheel papillae is greatly reduced in *C. hawaiiensis* as compared to *C. rigida*. He does not, however, make clear the degree of reduction. It is unknown whether *C. rigida* also displays fewer papillae along the ventral versus dorsal surface. Since we do not know the number of papillae typical for *C. rigida* we cannot infer that the papillae from this study are similar or dissimilar.

Perhaps the most distinct variation noted between *C. rigida* and *C. hawaiiensis* is the number of digits on the oral tentacles. Members of Chiridotinae possess 12 or 18 peltato-digitate tentacles with the number of digits per tentacle varied (Smirnov 1998). *C. hawaiiensis* possesses 8-10 digits, while *C. rigida* has 13 digits per tentacle (Fisher 1907). In this study, 6-10 digits were observed. Individually, the number of digits found per tentacle was the same. This is further evidence that the species in question is, in fact, *C. hawaiiensis*.

### *Anatomy and Behavior*

*C. hawaiiensis* is a unique holothurian in that it is highly divergent from most of the class in its morphology and anatomy. Typical of an island species, it body size is dramatically decreased as compared to many of its holothurian relatives. Sizes ranged from ~0.5cm to ~7.0cm. Body length was difficult to measure due to the elasticity of the body wall. An average specimen measuring 2 cm when burrowing could shrink to <1cm or stretch to >7cm.

Specimens dramatically increased in length when placed in certain sediment types. It appeared that body elongation occurred for the purpose of finding more adequate sediment for burrowing. This occurred when sediment was too compact for burrowing or when sediment was below a certain grain size. While elongation appeared to be related to sediment preference, it is likely not confined to this behavior and may be connected to feeding, respiration, or reproduction. This behavior was never observed at Tiahura.

Body length can also be greatly decreased. In this behavior, muscle contraction would pull the tentacles underneath the body wall and the oral and aboral ends became indecipherable. As the body length decreased, papillae aligned into rows parallel the oral-aboral axis, and the body became firm. This occurred when prodded and/or lifted out of water. The specimen typically did not remain in this state for longer that 30 seconds before it uncovered the tentacles. This behavior likely occurs to provide protection of the tentacles and the soft body wall, and to prevent damage from objects in the sediment or water column. This may be also be used for protection from predators, however, no predators were observed.

Predation on these organisms may be rare due to possible aposematic coloration. It was observed that their red coloring occasionally stained when the specimen was picked up and held. This coloring may be a noxious secretion. It would seem that aposematic coloration is likely since re-establishment into the burrow was not immediate. This suggests that *C. hawaiiensis* does not have many predators, since its bright red body wall would give itself away immediately when on top of the white coral sediment.

Although re-establishment into a burrow was not immediate in the field, it was immediate in the laboratory. If sediment was not present, specimens in the lab would attempt to burrow underneath any object present, particularly when observed underneath a lamp. When placed directly under light, the specimen would immediately begin to burrow or traverse the bowl in which it was being held. This may indicate that *C. hawaiiensis*, like many Holothurians, actively feeds at night and remains burrowed throughout the day. However, in the lab, feeding did not appear to increase at night.

*C. hawaiiensis* appeared to actively feed both day and night. Feeding was observed throughout the day in the lab. In the field, specimens also appeared to feed during the day. This assumption was based on the gut content seen through the transparent body wall. It was observed that as the specimen fed, ingested sediment was proportionally excreted out the anus. In the field, the gut content was almost always full and individuals with no sediment in the gut were rarely seen.

It was also noted that there was no obvious preference for sediment type. Specimens were fed numerous types of sediment from locations where *C. hawaiiensis* was absent. In most cases, specimens actively fed and burrowed in sediment. The only sediment that specimens would not ingest was black sand collected in Tahiti.

*Population distribution and abundance*

*C. hawaiiensis* was found in high abundance at Tiahura. Referring to figure 5, we can see that there is a marked increase in abundance at approximately 60 to 80 meters from the shoreline. In several areas, *C. hawaiiensis* was found in remarkably high densities considering the sediment depth ranged from 0 to 15cm. In these areas, individuals were often found burrowed in groups of 2-6. These areas were predominantly sandy with little to no algae and some coral rubble present. Individuals were often found burrowing underneath rocks/coral rubble. However, areas that had a high rock cover (>50%) generally did not have an abundance over five individuals. Similarly, areas with significant algae cover (>35%) contained few individuals.

A discernible gradient of grain size was observed along the entire shore of Tiahura. This gradient ranged from very fine sand with no rock or algae, to courser sediment with a high content of both algae and rock. The population in both of these extremes was nearly non-existent. Based on these observations, we can infer that density is related to grain size. However, it is more likely that grain size is a secondary determinant, and density is instead dictated by organic carbon content. Further sediment analysis needs to be performed in order to determine the biotic or abiotic factors that dictate the distribution of *C. hawaiiensis*.

*Burrowing Trials*

A wide range of behaviors was observed during burrowing trails. However, because burrowing occurred in each of the five sediment-grain sizes, it is difficult to determine whether there was a preference for large or small sediment size.

Based on preliminary laboratory observations, it was expected that *C. hawaiiensis* would not burrow into certain sediment types. This type of behavior was observed when specimens were placed in an aquarium with highly compact sediment. Specimens initially made shallow burrows but over time re-surfaced. Once re-surfacing occurred, there were no more attempts to burrow. Therefore, it was expected that once sediment was established as undesirable, specimens would stay above sediment. However, burrowing occurred in each of the five grain-sizes.

The most notable difference between the small and large grain size was the speed at which burrowing occurred. Burrows in the larger sediment occurred much earlier. Burrows were also deeper. In contrast, burrows in small sediment sizes occurred later and were shallow. When comparing these behaviors to those seen in the field, behaviors from the larger grain sediment are similar. This may indicate that there is grain preference for larger sediment. At the very least, this is an indication of the grain-size most familiar to *C. hawaiiensis.*

It was difficult to determine whether feeding occurred in any of the grain sizes since burrows were usually not visible. Feeding activity may have been a good indication of grain preference. It is possible when considering the 2mm grain, which is not ingestible due to its size that specimens burrowed deeper in search of smaller, more edible sediment. However, if this were true, different burrowing behaviors would be expected for the 500µm grain. This was not observed, and in fact, identical behaviors were observed in the 2mm and 500µm grain. It is important to note, that 500µm is the dominant grain size found at Tiahura, therefore, burrowing behaviors in this grain are likely most similar to burrowing that occurs in the field, and is likely preferred by *C. hawaiiensis.*

## Conclusion.

The species at hand may indeed be *Chiridota hawaiiensis*. This identification is based on several characteristics; the presence of six-spoke wheel spicules, rod spicules, digits per tentacle (6-10), and a reduced number of papillae along the ventral body surface. However, in order to confirm this identification further investigation is necessary. It is recommended that examination of *Chiridota rigida* is carried out in order to provide a detailed account of variations between these two species.

It was also found that *C. hawaiiensis* lives in high density. The factors which dictate abundance as well as distribution are unclear. While sediment grain size did have an affect on burrowing behaviors, it is not necessarily correlated with distribution and abundance. It is recommended that research is performed regarding organic carbon content of sediment in which this species inhabits.

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## LITERATURE CITED

Byrne, M (2001) The morphology of autotomy structures in the sea cucumber *Eupentacta quinquesemita* before and during evisceration. J Exp Bio 204:849-863

Fisher, W (1907) The Holothurians of the Hawaiian Islands. Proc U.S. Nat Mus 32:637-744

Hickman C, Roberts L, Larson A (2001) Integrated Principles of Zoology. McGraw-Hill. 11/e

Kerr A, Junhyong K (2001) Phylogeny of holothuroidea (echinodermata) inferred from morphology. Zoo J Linnean Soc 133:63-81

Smirnov, A (1998) On the classification of the apodid holothurians. Echinoderms: San Francisco. Balkema Publishers:517-522

# Transportation of Foraminifera in *Turbinaria ornata* and *Sargassum mangarevense* Rafts in Cook's Bay, Moorea, French Polynesia

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ABSTRACT. *Sargassum mangarevense* and *Turbinaria ornata* are major contributors to floating vegetation rafts in Cook's Bay, Moorea. *S. mangarevense* and *T. ornata* foliage were sampled in order to characterize their foraminiferal species composition. A live *T. ornata* sample and a sediment sample were collected from the mouth of Cook's Bay to compare the Foraminifera present in the rafts with those in a live algal sample and in a sediment sample. The algae was washed to remove all sediment and Foraminifera, after which all samples were preserved, stained with rose bengal, and examined to remove both recently living Foraminifera and empty tests. The foraminiferal assemblage in the sediment, live *T. ornata*, and *T. ornata* and *S. mangarevense* rafts were examined for differences in species composition. The sediment sample contains the most species, including a large number that are not present in the algal rafts. The rafts contain more species than the live algae. There is species overlap between all three samples, some of which may be explained by the hydrodynamic action needed to form algal rafts. The species present in the rafting algae were almost all alive at the time of collection, which indicates that these species may be able to use algal rafts as a means of increasing their biogeographic distribution.

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## Introduction

Foraminifera are major producers of sediment and calcareous fossils in marine carbonate environments (Venec-Peyre, 1991). They extract calcium carbonate from the oceanic environment or use small sand grains to assemble protective tests, and upon death the tests are deposited in sediment (Thurman, 1975). The abundance and diversity of Foraminifera makes their tests well suited to biostratigraphic analysis of sediment layers (Phleger, 1960). Because biostratigraphy depends on the species distribution of Foraminifera fossils, the biogeographic location of species is important to analyzing the age of sediment layers. Most previous Foraminifera studies in Moorea focused on the geographical distribution of Foraminifera in sediment samples from locations around the island (Venec-Peyre, 1991; Faller, 2001).

*Turbinaria ornata* and *Sargassum mangarevense* rafts, which appear to form when their thalli are displaced from the reef by wave action (Payri, 1999), have been shown to transport invertebrates within their thalli (Shapland, 1997). While algal rafts are important in marine ecosystems as habitat for many invertebrates (Koop and Griffiths, 1982), no studies have been conducted on the presence of Foraminifera in the rafts. Because they are capable of drifting long distances (Payri, 1999), the transport of Foraminifera by these rafts has the potential to impact the geographical distribution of both deceased specimens and viable Foraminifera populations.

The aims of this study are to describe the foraminiferal assemblages in *T. ornata* and *S. mangarevense* rafts in Cook's Bay and to determine whether the assemblage consists of living Foraminifera, empty tests, or both. Finally, the species composition in the rafts will be compared to that of live *T. ornata* samples and sediment samples to determine which Foraminifera species, if any, are transported in the floating rafts.

## Methods and Materials:

### *Study Site*

Moorea (GPS location: S 17°30', W 149°54') is a high volcanic island surrounded by a barrier reef that encloses a shallow back-reef area. The barrier reef is broken by twelve passes, including two in front of the deep bays, Cook's bay and Opunohu bay. This study was conducted in Cook's bay (see figure 1).

A kayak was used to collect *T. ornata* and *S. mangarevense* raft vegetation from the center of Cook's Bay. The rafts were located on a transect running from a channel marker (GPS location: S 17°29.051', W 149°49.045') on the eastern shore to the Richard B. Gump Station (GPS location: S 17°29.052', W 149°49.042') on the western shore (see figure 2). This transect was chosen because rafts moved along it naturally due to wind and current action. Because the rafts were mobile, GPS coordinates were not recorded. The rafts were composed of approximately 80% *T. ornata* and 20% *S. mangarevense*, so rafting algae was collected in roughly these proportions.

Sediment and live *T. ornata* samples were collected from the back-reef area on the eastern shore of Cook's bay. Sampling was conducted on a transect that began at the channel marker described above and formed a 90° angle with the shore (see figure 3). The sample was taken approximately 3 meters inshore from the channel marker using a kayak and snorkeling equipment. This location was chosen because of the high density of *T. ornata* and because it is an exposed point with relatively high hydrodynamic action. It is likely that *T. ornata* removed from this area and from the channel to the east due to swell forms the algal rafts in Cook's bay, as observations did not indicate the presence of floating algae entering the bay from outside the barrier reef.

*Sampling Procedure*

Sediment samples were collected along the transect at a depth of 2 m by skin diving. A 10 cc sample was collected from the top sediment layer and stored in a plastic container filled with seawater. The sample was then washed with seawater over No. 40 and No. 230 sieves. The sediment fraction retained in the No. 230 sieve was preserved in 95% ethanol and stained with rose bengal dye for 48 hours to differentiate between living (stained) and dead (unstained) Foraminifera. After staining, the sample was placed on filter paper and dried for 12 hours in a Fisher Scientific Isotemp Oven© set at 60° C.

Live algae samples were obtained at the channel marker (see fig. 3) by skin diving. 70 L of *T. ornata* were collected in 110 L garbage bags. The holdfasts of the algae were collected along with the thalli. The algae was manually scrubbed in a clean bucket with seawater to remove any attached sediment and Foraminifera. The resulting fraction was decanted to remove all organic matter. The sediment obtained after decanting was preserved in 95% ethanol, stained with rose bengal, and dried identically to the sediment sample described above.

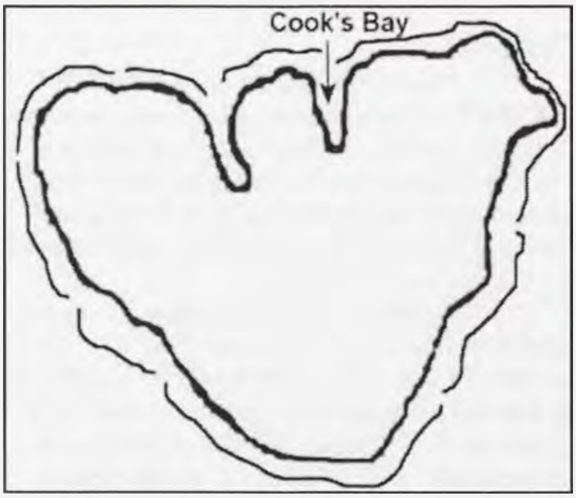

**Fig. 1.** The island of Moorea with the study site, Cook's bay, indicated

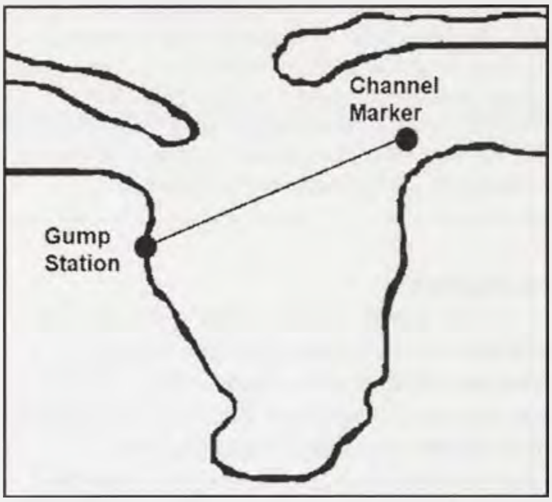

**Fig. 2.** Map of Cook's bay. The transect upon which vegetation rafts were collected is indicated

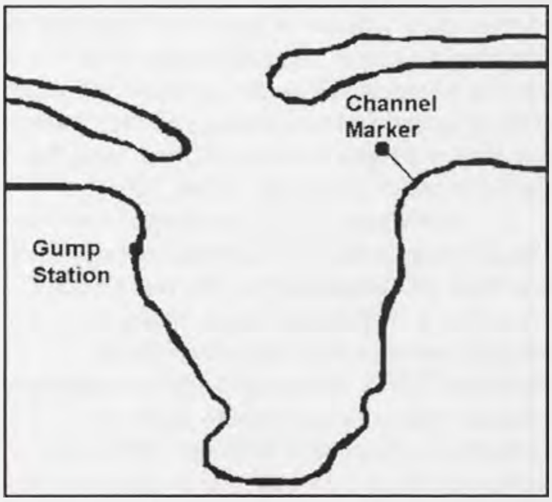

**Fig. 3.** Map of Cook's bay. The transect upon which sediment and live *Turbinaria* samples were taken is indicated.

Rafts composed of *T. ornata* and *S. mangarevense* were collected from Cook's Bay with a kayak. Approximately 90 L of vegetation was collected in 110 L garbage bags. The raft algae was manually scrubbed in the same way as the live algae and was preserved identically to the other two samples.

### *Laboratory Sorting Procedure*

The dried samples were examined using a Leica GZ6E dissecting microscope. All observed Foraminifera, both stained and unstained, were removed from the samples and placed on slides. The Foraminifera were separated by species using a dissecting microscope. The number of each species and whether each individual was living (stained) or dead (unstained) at the time of collection was recorded.

### *Data Analysis*

Presence/absence analysis was performed to determine which Foraminifera were present in the sediment, raft, and growing vegetation samples. The number of each species in every sample was recorded. The number of live specimens and dead specimens in the raft sample was also recorded. Finally, a calculation was made of the % chance that every Foraminifera species in each of the samples was collected (see appendix for details).

## Results

| **Species** | Raft | Live Algae | Sediment |
|---|---|---|---|
| *Sorites orbiculus* | 119 | 102 | 3 |
| *Planorbulinoides retiniculatus* | 144 | 55 | |
| *Sorites orbitolitoides* | 9 | 66 | 1 |
| *Planorbulina acervalis* | 6 | 32 | 3 |
| *Miliolinella baragwanthi* | 4 | 76 | 4 |
| *Pyrgo denticulata* | 7 | 39 | 1 |
| *Millettiana millettii* | 75 | 6 | |
| *Planorbulina* sp. 1 | 1 | | |
| *Amphistegina* sp. 1 | 2 | | 1 |
| *Amphistegina* sp. 2 | 19 | 3 | |
| *Planorbulina* sp. 2 | 6 | | |
| *Triloculina* sp. 1 | 4 | 44 | |
| *Quinqueloculina Sulcata* | 1 | | |
| *Siphonaperta* sp. 1 | 6 | 100 | 8 |
| *Poroeponides* sp. 1 | 13 | | |
| *Poroeponides* sp. 2 | 2 | | |
| *Pyropilus* sp.1 | 1 | | |
| *Pyropilus* sp. 2 | 1 | | |
| *Caribeanella* sp. 1 | 15 | 3 | |
| *Planorbulina* sp. 3 | 51 | | |
| *Planorbulinopsis* sp. 1 | 5 | 47 | |
| W | 1 | | |
| X | 1 | | |
| Y | 4 | 2 | 6 |
| Z | 1 | | 1 |
| AA | 12 | 27 | 1 |
| AB | 13 | 5 | 1 |
| AC | 2 | | |
| AD | 1 | 4 | 3 |
| AE | 1 | | 2 |
| AF | 10 | | 1 |
| AG | 6 | | |
| AH | 10 | 24 | |
| AI | 1 | | |
| AJ | 1 | | |
| AK | 1 | | |
| AL | 2 | | |
| *Vertebralina* sp. 1 | 1 | | |
| AN | 2 | 69 | 3 |
| AO | 9 | | 1 |
| *Poroeponides* sp. 3 | 4 | 8 | 1 |
| AQ | 2 | 45 | |
| AR | 1 | | |
| AS | 7 | 31 | 2 |
| AT | 1 | | |
| *Pyrgo* sp. 1 | 1 | | |
| *Pseudohauerina* sp.1 | 2 | 5 | |
| AW | 1 | | |
| AX | 2 | | 1 |
| AY | 4 | 1 | 1 |
| AZ | 1 | | |

| | | | |
|---|---|---|---|
| BA | 2 | | |
| *Elphidium* sp. 1 | 9 | 6 | 9 |
| BC | 2 | | |
| BD | 2 | | |
| BE | 2 | | |
| BF | 1 | | |
| BG | 1 | | 30 |
| BH | 2 | | 6 |
| BI | 1 | | |
| BJ | 1 | | |
| BK | 2 | | |
| BL | 1 | | |
| BM | 1 | | |
| BN | 2 | | |
| BO | 1 | | |
| BP | 1 | | 1 |
| *Spiroloculina* sp. 1 | 1 | | |
| BR | 1 | | |
| BS | 1 | | |
| BT | 1 | | |
| BU | 1 | | |
| BV | 2 | | 15 |
| BW | 2 | | 40 |
| BX | 1 | 2 | 7 |
| BY | 1 | | 3 |
| BZ | 1 | | |
| CA | 2 | 1 | |
| CB | 2 | 1 | 5 |
| CC | 2 | | 6 |
| CD | 3 | | |
| CE | 1 | 2 | |
| CF | 1 | | |
| CG | 2 | | |
| CH | 1 | | |
| CJ | 1 | | 2 |
| CK | | 1 | |
| CL | | 1 | |
| CM | | 4 | |
| CN | | 1 | |
| CO | | 1 | |
| CP | | 48 | |
| CQ | | 1 | |
| CR | | 1 | |
| CS | | 3 | |
| CT | | 1 | |
| CU | | 2 | |
| CV | | 12 | |
| CW | | 90 | 16 |
| CX | | 1 | |
| CY | | 1 | |
| CZ | | 35 | |
| DA | | 1 | |
| DB | | 11 | 6 |
| DC | | 50 | 35 |
| DE | | 2 | |
| DF | | 1 | |
| DG | | 1 | |
| DH | | 1 | |
| DI | | 1 | |
| DJ | | 9 | |
| DK | | 7 | |
| DL | | 1 | |
| DM | | 1 | |
| DN | | 1 | |
| DO | | 1 | |
| DP | | 1 | |
| DQ | | | 8 |
| DR | | | 1 |
| DS | | | 26 |
| DT | | | 1 |
| DU | | | 1 |
| DW | | | 1 |
| DX | | | 1 |
| DY | | | 5 |
| DZ | | | 1 |
| EA | | | 4 |
| EB | | | 6 |
| EC | | | 9 |
| ED | | | 3 |
| EE | | | 10 |
| EF | | | 5 |
| EG | | | 1 |
| EH | | | 1 |
| EI | | | 1 |
| EJ | | | 5 |
| EK | | | 1 |
| EL | | | 1 |
| EM | | | 10 |
| *Spiroloculina* sp. 2 | | | 2 |
| EO | | | 1 |

| | | | |
|---|---|---|---|
| EP | | | 5 |
| EQ | | | 1 |
| ER | | | 2 |
| ES | | | 1 |
| ET | | | 6 |
| EU | | | 3 |
| EV | | | 1 |
| EW | | | 4 |
| EX | | | 5 |
| EY | | | 1 |
| EZ | | | 1 |
| FA | | | 3 |
| *Cymbaloporetta bulloides* | | | 5 |
| FC | | | 1 |
| *Tretomphalus bulloides* | | | 1 |
| FE | | | 1 |
| FF | | | 1 |
| FG | | | 1 |
| FH | | | 3 |
| FI | | | 1 |
| FJ | | | 1 |
| FK | | | 1 |
| *Eponides* sp. 1 | | | 3 |
| FM | | | 1 |
| FN | | | 1 |
| FO | | | 1 |
| FP | | | 2 |
| FQ | | | 1 |
| *Spiroloculina* sp. 3 | | | 1 |
| FS | | | 1 |
| FT | | | 1 |
| FU | | | 1 |
| FV | | | 2 |
| FW | | | 1 |
| FX | | | 1 |
| FY | | | 1 |
| FZ | | | 42 |
| GA | | | 5 |
| GB | | | 5 |
| GC | | | 1 |
| GD | | | 7 |
| GE | | | 1 |
| GF | | | 7 |
| GG | | | 1 |
| GH | | | 1 |
| GI | | | 1 |
| GJ | | | 1 |
| GK | | | 9 |
| GL | | | 5 |
| GM | | | 6 |
| GN | | | 2 |
| GO | | | 4 |
| GP | | | 3 |
| GQ | | | 1 |
| GR | | | 4 |
| GS | | | 1 |
| GT | | | 3 |
| GU | | | 16 |
| GV | | | 2 |
| GW | | | 8 |
| GX | | | 1 |
| GY | | | 2 |
| GZ | | | 2 |
| HA | | | 2 |
| HB | | | 1 |
| HC | | | 1 |
| HD | | | 1 |
| HE | | | 3 |

**Fig.** 4. Total number of each Foraminifera species found in rafting algae, live algae, and sediment sample.

| **Species** | Number live | Number dead |
|---|---|---|
| *Sorites orbiculus* | 119 | 0 |
| *Planorbulinoides retiniculatus* | 139 | 5 |
| *Sorites orbitolitoides* | 9 | 0 |
| *Planorbulina acervalis* | 3 | 3 |
| *Miliolinella baragwanthi* | 2 | 2 |
| *Pyrgo denticulata* | 5 | 2 |
| *Millettiana millettii* | 75 | 0 |
| *Planorbulina* sp. 1 | 1 | 0 |
| *Amphistegina* sp. 1 | 2 | 0 |
| *Amphistegina* sp. 2 | 17 | 2 |
| *Planorbulina* sp. 2 | 6 | 0 |
| *Triloculina* sp. 1 | 3 | 1 |
| *Quinqueloculina sulcata* | 1 | 0 |
| *Siphonaperta* sp. 1 | 4 | 2 |

| | | |
|---|---|---|
| *Poroeponides* sp. 1 | 13 | 0 |
| *Poroeponides* sp. 2 | 1 | 0 |
| *Pyropilus* sp.1 | 1 | 0 |
| *Pyropilus* sp. 2 | 1 | 0 |
| *Caribeanella* sp. 1 | 15 | 0 |
| *Planorbulina* sp. 3 | 51 | 0 |
| *Planorbulinopsis* sp. 1 | 5 | 0 |
| W | 1 | 0 |
| X | 0 | 1 |
| Y | 4 | 0 |
| Z | 0 | 1 |
| AA | 12 | 0 |
| AB | 13 | 0 |
| AC | 1 | 1 |
| AD | 1 | 0 |
| AE | 1 | 0 |
| AF | 9 | 1 |
| AG | 5 | 1 |
| AH | 10 | 0 |
| AI | 1 | 0 |
| AJ | 1 | 0 |
| AK | 0 | 1 |
| AL | 2 | 0 |
| *Vertebralina* sp. 1 | 1 | 0 |
| AN | 2 | 0 |
| AO | 8 | 1 |
| *Poroeponides* sp. 3 | 4 | 0 |
| AQ | 2 | 0 |
| AR | 1 | 0 |
| AS | 7 | 0 |
| AT | 1 | 0 |
| Pyrgo sp.1 | 1 | 0 |
| *Pseudohauerina* sp. 1 | 2 | 0 |
| AW | 1 | 0 |
| AX | 2 | 0 |
| AY | 4 | 0 |
| AZ | 1 | 0 |
| BA | 2 | 0 |
| *Elphidium* sp. 1 | 9 | 0 |
| BC | 1 | 1 |
| BD | 2 | 0 |
| BE | 1 | 1 |
| BF | 1 | 0 |
| BG | 1 | 0 |
| BH | 2 | 0 |
| BI | 1 | 0 |
| BJ | 1 | 0 |
| BK | 1 | 1 |
| BL | 1 | 0 |
| BM | 1 | 0 |
| BN | 2 | 0 |
| BO | 1 | 0 |
| BP | 1 | 0 |
| *Spiroloculina* sp. 1 | 1 | 0 |
| BR | 1 | 0 |
| BS | 1 | 0 |
| BT | 0 | 1 |
| BU | 1 | 0 |
| BV | 2 | 0 |
| BW | 2 | 0 |
| BX | 1 | 0 |
| BY | 1 | 0 |
| BZ | 1 | 0 |
| CA | 2 | 0 |
| CB | 2 | 0 |
| CC | 1 | 1 |
| CD | 3 | 0 |
| CE | 1 | 0 |
| CF | 0 | 1 |
| CG | 2 | 0 |
| CH | 1 | 0 |
| CJ | 1 | 0 |

**Fig. 5.** Number of live and dead Foraminifera of each species found in rafting algae

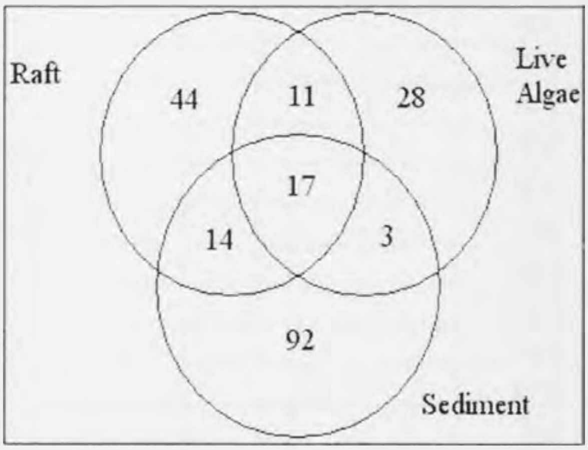

**Fig. 6.** Number of Foraminifera species found in intersections of the three samples

| Sample | Total # of Specimens | % Confidence |
|---|---|---|
| Raft | 654 | 99% |
| Live Algae | 1098 | 99.99% |
| Sediment | 547 | 99% |

Fig. 7. % confidence that all species composing <1% of the total population were collected (Pehl, 2003). See appendix for details.

A total of 209 species were collected. Of these, 86 were in the rafting algae, 59 were in the live algae, and 126 were in the sediment sample. Seventeen species were present in all three samples, 14 were in the raft and sediment samples, 11 were in the raft and live algae sample, and 3 were in the sediment and live algae sample. There were 44, 28, and 92 species found only in the rafting algae, live algae, and sediment respectively (see fig. 4 and fig. 6). There is 99% confidence that all species composing <1% of the total raft and sediment population were collected. There is 99.99% confidence that all species composing <1% of the live algae population were collected (see Fig. 7).

**Discussion**

The hydrodynamic turbulence involved in forming algal rafts (Stiger, 1999) is one potential explanation for some of the observed differences in species composition. Thirty-one species that are found in live algae (28 that are only in live algae and 3 that are also present in sediment) are not present in the rafts. Because they are present in the live algae sample, these species are presumably capable of living attached to algae. It is possible that these species are incapable of clinging to algal matter throughout the turbulence needed to remove algae from the reef and form a raft. The 28 species found in both the live and rafting algae (11 present only in these two samples and 17 found in the sediment as well) are presumably able to cling to algal matter strongly enough to survive the hydrodynamic action necessary to form an algal raft. These species can potentially take advantage of the long-term dispersal opportunities presented by the drifting of the rafts.

Fourteen species are present in the algal rafts and the sediment but are absent from the live algae. These species appear to live in sediment preferentially to algae, but are capable of living in algae, as evidenced by the presence of live specimens in the rafts (see Fig. 5). Their presence in rafting algae is also potentially an effect of the wave action involved in raft formation. The sediment stirred up during heavy wave action contains many species of Foraminifera (see Fig. 4). Potentially some of these species are able to cling to algal matter as it forms rafts. Therefore, these species may also be able to utilize algal raft dispersion as a means of increasing their biogeographic distribution.

There are 92 species that are present only in the sediment sample. These 92 are likely obligate infaunal species, therefore they are not found growing on any type of algal matter. As a result, these species cannot utilize algal raft drift as a means of colonizing new locations. There are 44 species that are found only in the rafting algae, which is potentially due to the fact that no live *S. mangarevense* was collected for examination. Although the rafting *S. mangarevense* made up a smaller percentage of the raft and contained a much lower density of sediment and Foraminifera than the *T. ornata*, there were probably Foraminifera present in the *S. mangarevense*. Future studies should include the collection of live *S. mangarevense* to determine if these 44 species inhabit this algae instead of *T. ornata*.

Of the 653 Foraminifera present in the rafting algae, 95% (623 specimens) were live while 5% (30 specimens) were dead. Because algal rafts travel long distances (Payri 2001) and significant turbulence is probably necessary to form them, dead tests likely cannot cling to algal matter. As a result, the majority of the Foraminifera that the rafts transport are alive and can potentially form viable populations in areas where the algal drift ceases. It is also possible that Foraminifera leave the raft during its drift, so live specimens may be deposited along the entirety of the raft's course of travel. This population movement could strongly influence the biogeographical distribution of both living Foraminifera and empty tests.

There was one main potential source of error in this study. Beds of *S. mangarevense* were not found near the study site, so a live *S. mangarevense* sample was not found. Although *S. mangarevense* made up a smaller percentage of the rafting algae than *T. ornata* and didn't appear to contain many Foraminifera, the lack of a live sample may have affected the observed species composition of live algae.

Further study should include an analysis of raft formation in which foraminiferal species composition is recorded both when pieces of algae are attached to the reef and after the same pieces have formed a raft. The rafts should be analyzed at multiple time intervals to determine if the species number of Foraminifera decreases as the amount of time the raft floats increases. Finally, a study should be done on the mechanisms of attachment used by Foraminifera to cling to algal rafts. Research should be conducted on whether there are morphological or biological characteristics that allow certain species to cling to rafting vegetation, thereby giving them an advantage over species that are unable to increase their biogeographical distribution by using algal rafts for transport.

## Conclusions

This study located 209 Foraminifera species among the sediment, live algae, and rafting algae samples in Cook's bay. The largest species diversity was in the sediment (126 species), followed by the rafting algae with the second highest (86 species) and the live algae with the lowest (59 species). The species in the algal rafts are probably more capable of expanding their biogeographic distribution than the species that are not found in the rafts. There was species overlap between the three samples, some of which is possibly due to the wave action needed to form algal rafts. Most of the Foraminifera present in the algal rafts were alive, which suggests that they can use the rafts as a means of viable population dispersal.

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# LITERATURE CITED

Bicchi, E., Debenay, J-P., Pages, J. (2002) Relationship between benthic foraminiferal assemblages and environmental factors in atoll lagoons. Coral Reefs. 21: 275-290.

Drake, C. et al. (1978) Oceanography. Holt, Rhinehart and Winston.

Faller, M. (2001) Moorea Foraminifera. Geologisches Institut der Albert-Ludwigs-Universitat Freiburg i. Br.

Finger, K. (2003) Conversation on 10 December 2003. University of California, Berkeley.

Koop, K. & Griffiths, C.L. (1982) The relative significance of bacteria, meio- and macrofauna on an exposed sandy beach. *Marine Biology*, 295-300.

Lee, J. *ed.*, Hutner, S. *ed.*, Bovee, E. *ed.* (1985) An Illustrated Guide to the Protozoa. Society of Protozoologists.

Lee, J. *ed.*, Anderson, O. *ed.* (1991) Biology of Foraminifera. Academic Press.

Loeblich, A. R., Tappan, H. (1988) Foraminiferal Genera and Their Classification. Van Nostrand Reinhold Company.

Payri, C.E., Stiger, V. (1999) Spatial and temporal patterns of settlement of the brown macroalgae *Turbinaria ornata* and *Sargassum mangarevense* in a coral reef on Tahiti. Marine Ecology Progress Series. 191: 91-100

Payri, C.E., Stiger, V. (2001) Macroalgal community changes on French Polynesian Reefs, 1980-2000. Phycologia. 40 (4 Supplement): 111.

Pehl, C. (2003) Conversation on 12 December 2003. Paper in preparation. University of California, Berkeley.

Phleger, F. (1960) Ecology and Distribution of Recent Foraminifera. The Johns Hopkins Press.

Rieber, H., Kuhn-Schnyder, E. (1986) Handbook of Paleozoology. The Johns Hopkins University Press

Shapland, R. (1997) Fauna associated with floating vegetation rafts in the lagoon of Paopao Bay, Moorea, French Polynesia. Biology and Geomorphology of Tropical Islands Paper, Student Research Papers. University of California, Berkeley.

Thurman, H. (1975) Oceanography, 2nd Edition. Charles E. Merrill Publishing Company.

Venec-Peyre, M-T. (1987) Boring Foraminifera in French Polynesian coral reefs. Coral Reefs. 5: 205-212.

Venec-Peyre, M-T. (1991) Distribution of living benthic Foraminifera on the back-reef and outer slopes of a high island (Moorea, French Polynesia). Coral Reefs. 9: 193-203.

## Appendix

% Confidence that all species present in each location (raft, live algae, and sediment) were collected (Pehl, 2003):

*Equations:*

$$1-y = (1-x)^n$$

$$\ln(1-y) = n[\ln(1-y)]$$

$x$ = % of the total population that this species represents

$n$ = number of Foraminifera in sample

$1-y$ = chance of collecting a species with % $x$ for a given $n$ = % Confidence

*Table of Values:*

| % of total population | 99 % Confidence | 99.99 % Confidence |
|---|---|---|
| 0.1 | 4602.867 | 6904.301 |
| 0.2 | 2300.282 | 3450.423 |
| 0.4 | 1148.988 | 1723.482 |
| 0.6 | 765.223 | 1147.835 |
| 0.8 | 573.341 | 860.011 |
| 1 | 458.210 | 687.316 |
| 1.2 | 381.457 | 572.185 |
| 1.4 | 326.633 | 489.949 |
| 1.6 | 285.514 | 428.271 |
| 1.8 | 253.533 | 380.300 |
| 2.0 | 227.948 | 341.922 |

Fig. 8. Number of specimens required for 99% and 99.99 % confidence that species composing <2% of the total population were collected

# Influence of Decompositional State on Arthropod Richness and Abundance in Allochthonous wracks of *Turbinaria ornata* in littoral zones of Mo'orea, French Polynesia

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ABSTRACT. Allochthonous inputs can impact food web dynamics of recipient ecosystems. This study focuses on wracks of the macroalgae *Turbinaria ornata* as subsidies to shoreline ecosystems on the island of Mo'orea, French Polynesia. Analysis of variance (ANOVA) tests were run to determine the effect of decomposition on arthropod abundance and richness in the wracks. Decompositional state affects the total number of species in each wrack ($p=0.01$) and species richness ($p=0.04$). The ratio of insects to amphipods differs between wracks of varying decompositional stages ($p=0.05$). Future research could explore the effect of salinity, cover, and distance from freshwater on arthropod composition, as well as compare species composition on floating wracks versus beached wracks.

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**Keywords**
*Turbinaria ornata*, allochthonous, algal wrack, Mo'orea, arthropod

## Introduction

In nature, allochthonous inputs (inputs entering from another habitat) have the potential to impact the patterns and dynamics of recipient systems by influencing populations, food webs, and community dynamics (Huxel and McCann 1998, Nakano et. al 1999, Anderson and Polis 1999, Polis and Hurd 1996, Helfield and Naiman 2002, Rose and Polis 1998, Polis et. al 1997). Polis and Hurd identify four main pathways of subsidization of ecosystems – land to land, land to water, water to water, and water to land (1996). Aeolian ecosystems such as caves, snowfields, and barren deserts can be completely sustained or partially subsidized by land-based windborne detritus (Likens and Bormann 1975, Polis et al. 1997). Transport of nutrients from deep water to shallow water through upwelling is a key determinant of local marine productivity (Polis et al 1997). Leaf litter and organic matter from soil runoff serve as important terrestrial subsidies to marine environments (Minshall 1967). This land to water transport is significant; for instance, Polis et al assert that 75% of market fish in the Amazon receive 50-90% of their diet from terrestrial origin (1997). In another study, terrestrial insect prey subsidized stream fish populations, contributing from 60-100% of fish diet (Nakano and Murakami 2001).

Marine subsidies to terrestrial environments have been the focus of recent attention in the field of ecology (Ricketts et al 1985, Rose and Polis 1998, Polis and Hurd 1996, Anderson and Polis 1999, Nakano et al. 1999). For example, Pacific salmon serve as nitrogen sources to white spruce trees in Alaska through transport by bears (Helfield and Naiman 2002). In the hyperarid islands of the Gulf of California, nutrient input via seabird guano directly increases nitrogen and phosphorus concentrations in inland soils, which influences the concentrations of certain desert shrubs and cacti (Anderson and Polis 1998). High densities of coyotes are achieved along the shore of the Gulf of California relative to adjacent inland areas because of a variety of marine subsidies (Rose and Polis 1998).

Beached algal wrack is another example of a marine subsidy to a terrestrial environment. Polis and Hurd assert that "such flow is often a key feature of the energetics, structure, and dynamics of populations, food webs, and communities" (1994). Sandy beaches support relatively little *in situ* primary production, and beached algal wrack can ameliorate soil and sand characteristics by adding nutrients (Colombini and Chelazzi 2003). In terrestrial food webs with beached algal wrack in the Gulf of California, arthropods are 85-560 times more abundant in the supralittoral zone, or the shore-water interface, than inland (Polis and Hurd 1995). Presence of algal wrack has been shown to determine the distribution and relative abundance of Pygmy grasshoppers in temperate shoreline ecosystems (Bastow et al 2002). Polis and Hurd discovered that marine-derived allochthonous algal wrack supports unusually high densities of spiders on desert islands off the coast of Baja California (1996).

This paper presents the results of a study on the role of allochthonous wracks of the macroalgae *Turbinaria ornata* of varying decompositional states as marine subsidies to terrestrial environments. I have been unable to find any literature discussing the role of *T. ornata* as a subsidy to the littoral zone. This study focuses on arthropod abundance, richness, and evenness in these wracks at different decompositional states in littoral zones on the island of Mo'orea, French Polynesia. Goals of the study include identifying arthropods in the wracks and determining the effect of decompositional state on arthropod richness, abundance, and evenness. It is hypothesized that arthropod composition is influenced by the extent of algal decomposition. Other studies discuss abundance of certain groups of organisms in other species of decomposed algae, including amphipods, isopods, insects, and flies (Colombini et al 2000, Colombini et al 1998, Colombini and Chelazzi 2003, Pennings et al 2000). Accordingly, this study examines these groups in detail. I hypothesize that the ratio of insects to amphipods and the abundance of isopods and flies will change with decompositional state.

## Materials and Methods

### *Natural History of Study System*

This study was conducted on Mo'orea, (17°30'S, 149°50'W), a high volcanic island in French Polynesia surrounded by an extensive coral reef complex (Gabrie et al 1994). The macroalgae *Turbinaria ornata* is native to French Polynesia (Stewart, pers. comm. 2003). Since the mid 1980s, Mo'orean coral reef communities have undergone a shift from a mix of coral and algae to reefs widely dominated by large frondose algae such as *T. ornata* (Payri and Stiger 2001). This shift has been due to a host of reasons. *T. ornata* colonizes dead coral heads, and much coral has died since the 1980's (Payri and Stiger 2001). In 1983, Mo'orean reefs were extensively damaged by prolonged low sea levels and increased cyclonic activity, and while there has been some recovery, many corals died. Between 1978 and 1983, several outbreaks of Crown of thorns starfish (*Acanthaster planci)* occurred, killing many corals, which has increased the amount of macroalgae growth by providing a dead coral substrate for colonization (Hutchings et al 1994). Increase in pesticide use and land clearing has resulted in dead and damaged corals, which has provided a space for *T. ornata* to grow (Hutchings et al 1994). This shift is especially obvious on high islands like Mo'orea where anthropogenic disturbance is greater (Stiger and Payri 1999). Once removed from coral heads by wind, current, or other disturbance, *T. ornata* forms floating vegetation rafts that eventually can wash ashore. This study focuses on beached wracks of *T. ornata.*

### *Study Design*

I kayaked from the Gump Station to the Beachcomber to observe and categorize stages of *T. ornata* decomposition (see Figure 2). Three distinct zones of decomposition (zones 1, 2, and 3) of *T. ornata* were identified based on integrity of algal structures (see Figure 1 at end). Wracks of zone 1 decomposition are newly washed ashore. The algal structures are robust and intact, and air pockets separate individual algal strands. In a zone 2 wrack, algal structures are not entirely intact. Zone 3 is comprised of algae whose structures are indiscernible, and the consistency of the wrack is mushy. Four samples were taken from each zone at different locations on Mo'orea (see Figure 2 below).

**Figure 2**. Map of Mo'orea with sites labeled by decompositional stage

At each site, length, width, and depth of wrack was measured with a 100 meter transect tape; this information, along with decompositional state, was noted on a dive slate (see Table 1). Each wrack was photographed using a Canon digital camera. Samples were taken from the midpoint of the length and the width. Amount of algae sampled was based on a fixed and consistent surface area of *T. ornata* wrack and a variable, measured depth. The surface area of each sample was 484 sq cm (22 cm long, 22 cm wide). The depth sampled was from the algae-air interface to the algae-sand interface in its entirety. Each sample was placed in an enclosed plastic container and immediately taken to the Gump Research Station and relocated to a Berlese funnel (see Figure 3). Six Berlese funnels were constructed, each with a desk lamp, funnel, and a plastic Nalgene container. Berlese funnels function on the premise that arthropods will crawl away from the heat source and get caught in the plastic container at the bottom. The Berlese funnels were covered with fish nets to prevent arthropod escape. Samples remained in these devices for 6 hours, after which time the algae were returned to the shore and the samples were placed in alcohol. Arthropod identification was completed at the Richard Gump Research Station, French Polynesia, and at the University of California, Berkeley, United States. Voucher specimens are held at the Essig Museum of Entomology at the University of California, Berkeley.

### *Statistical Analysis*

Variable *T. ornata* wrack masses were standardized in order to compare arthropod composition among sites by dividing the number of each arthropod found in each sample by wrack depth. Using this information, analysis of variance (ANOVA) tests were run to determine significance of decompositional stage on arthropod richness and abundance as well as on individual species (Amphipod C, Staphylinid A) and individual group (Diptera, Isopoda) abundance. Tukey-Kramer tests were run to determine which treatments (decompositional states) were statistically distinguishable. The data from the significance of decompositional state on ratio of insects to amphipods was in percent; each data point was normalized to fit ANOVA requirements by using a square-root transformation [Square root ratio = square root (ratio + 0.5)].

## Results

The sample from the zone 3 at the Beachcomber site was removed from the analysis due to its possibly unnaturally high numbers of Amphipod Species C.

**Table 1**. Physical Characteristics of Sites

| | **GPS** | **Length (m)** | **Width (m)** | **Depth (cm)** | **Decompositional State** |
|---|---|---|---|---|---|
| **etoai** | S 17°29.525’, W 149°52.229’ | 236.8 | .73 | 28 | 1 |
| **etoai** | S 17°29.525’, W 149°52.229’ | 236.8 | .56 | 38 | 2 |
| **mp** | S 17°24.4’, W 149°33.0’ | 25.6 | .48 | 20 | 3 |
| **varo** | S 17°32.714’, W 149°46.722’ | 48.87 | 1.52 | 29 | 2 |
| **are** | S 17°31.379’, W 149°46.843’ | 200 | .45 | 32 | 1 |
| **are** | S 17°31.379’, W 149°46.843’ | 200 | .72 | 32 | 3 |
| **reaitu Snack** | S 17°33.011’, W 149°47.385’ | 60 | 1.44 | 37 | 1 |
| **reaitu** | S 17°33.25’, W 149°47.47’ | 120.14 | .32 | 20 | 2 |
| **’atea** | S 17°34.333’, W 149°47.195’ | 159.2 | .95 | 23 | 3 |
| **a** | S 17°34.878’, W 149°50.560’ | 391.28 | 1.5 | 27 | 1 |
| **chcomber** | S 17°29.488’, W 149° 53.074’ | 238.03 | .8 | 11 | 2 |

### *Effect of Decompositional State on Richness, Evenness, and Total Number*

***Graph 1**. Effect of Decompositional State on Arthropod Richness*

significance at p< 0.04 noted by different letters

*Graph 2. Effect of Decompositional State on Arthropod Abundance*

significance at p< 0.01 noted by different letters

***Graph 3**. Effect of Decompositional State on Evenness*

p<0.36
Values based on the Simpson's Diversity Index
$1-\sum p_i^2$

### *Effect of Decompositional State on Species Composition*

***Graph 4**. Effect of Decompositional State on the Ratio of Insects to Amphipods*

significance at p< 0.02

***Graph 5**. Effect of Decompositional State on Abundance of Amphipods*

p< 0.058

***Graph 6**. Effect of Decompositional State on Diptera (Species K, K2) Abundance*

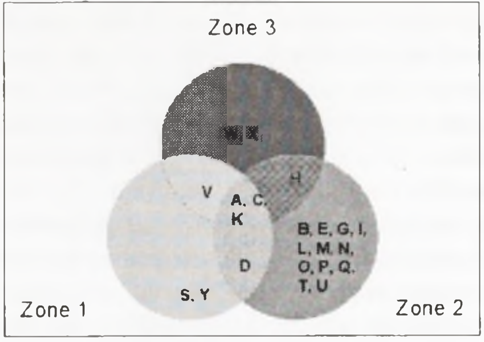
p=0.25

***Graph** 7. Effect of Decompositional State on Staphylinid (Species A) Abundance*

***Graph 8.** Effect of Decompositional State on Isopod (Species H, S, T) Abundance*

p=0.6

***Diagram 1.** Species presence in Decompositional States*



## Discussion

### *Experimental Design*

A preliminary study was conducted at 2 beach wracks of *T. ornata*, one in Cook's Bay and one in Temae. At these sites, I swept for insects with a fish net attached to a wooden rod for 2 minutes; this was completed at 6 am, 12 pm, and 4 pm, and each sweeping was spaced a day apart at each site to allow for recolonization. In addition, a physical sample of each wrack at each of these times was brought to the Richard Gump Research Station and placed in a Berlese funnel to collect arthropods from the samples. Sampling was conducted to determine the temporal fluctuations in species composition and abundance in *T. ornata* wracks. The results from this preliminary study show that in the sweep nets, there existed temporal differences in abundance of arthropod assemblages but not differences in species composition. There was little temporal fluctuation in arthropod abundance in the algal samples that were placed in the funnels, and thus it was determined that for the study, arthropods would be collected using the Berlese apparatus rather than sweep nets.

### *Effect of Decompositional State on Arthropod Abundance, Evenness, and Richness*

The results of the study indicate that zone 2 *T. ornata* wracks support higher total numbers of individuals than newly washed ashore wracks (see Graph 2). Similarly, zone 2 wracks have higher species richness than zone 1 and statistically similar species richness as zone 3 (see Graph 1). There is a trend that zone 2 is higher in richness and total number of species than either zone 1 or zone 3. Three species (A, K, C) are generalists, with the majority of taxa specializing in one zone, primarily zone 2 (see Diagram 1). Decompositional state has no significant effect on evenness (see Graph 3). The change in community composition is due to even change among the different species at each decompositional state meaning that changes in abundance are due to addition of species, not a change in the representation of those species in the community (Graph 3).

Current literature supports the finding that arthropod abundance and composition change as algae undergoes decomposition (Colombini et al 1998, Colombini et al 2000, Pennings et al 2000, Colombini and Chelazzi 2003).

One explanation for these results is that zone 2 supports a wider variety of habitats due to it being an ecotone, or a transition zone between adjacent ecological systems (Samways and Stewart 1997). Zone 2 can be defined as an ecotone because it exhibits algal structure qualities that are a mixture of zone 1 and zone 3. Because of this variation in integrity of algal structures and air pockets, more habitats are created, and thus a wider range of organisms can be supported. It is for this reason that Zone 2 is richer in taxa (see Graph 1, Diagram 1). For example, organisms that inhabit zone 1 because they are better suited for robust structures and air pockets might still be able to find a habitat similar to this in zone 2, like organism D (see Diagram 1).

Newer wrack and more decomposed wrack likely differ in nutritional quality, and arthropod composition in these wracks is due to species' ability to use these nutrients (Pennings et al 2000). For example, decaying seaweeds are colonized by bacteria and fungi that may themselves be more digestible than fresher seaweed tissue to certain organisms (Pennings et al 2000). This could explain a change in arthropod composition as algae decompose and are colonized by bacteria.

### *Effect of Decompositional State on Species Composition*

Colombini and Chelazzi write that "some species have adapted their abundance, spatial distribution, and feeding ecology in relation to the spatial and temporal patterns of wrack deposition" (2003). A closer examination of species composition in the different zones can help explain the abundance and presence of certain groups of organisms in different stages of decomposition.

#### *Effect of Decompositional State on Abundance of Insects and Amphipods*

In congruence with my hypothesis, the results indicate that the ratio of insects to amphipods changes as algae decompose; specifically, there are more insects in newly washed ashore wrack than the most decomposed wrack (see Graph 4). This study finds that insects as a group are primary colonizers, with the ratio of insects to amphipods statistically lower in the most decomposed wrack. There is a trend (with significance) that amphipod abundance increases as the wrack undergoes decomposition (see Graph 5).

The results from other research on species composition in different stages of decomposition vary in terms of the effects of decomposition on the abundance of insects and amphipods. Two studies found that amphipods are usually primary colonizers of newly deposited wracks because they have a tendency to forage on freshly stranded material (Colombini et al 2000, Colombini and Chelazzi 2003). This could mean that increase in amphipod abundance and presence as *T. ornata* decomposes is related to factors other than decomposition. However, both of these studies took place in San Uanle, Somalia, at sites near arid dunes without nearby vegetation; the Mo'orea sites were all near vegetative stands. The difference in nearby vegetation and the climate might have affected the feeding ecologies. Also, the Somalian sites might have been subject to different tidal fluctuation than Mo'orean sites, which might have an impact on amphipod abundance. Also, the results of the Somalian study were based on the preference of one genus of amphipod, *Talorchestia* (Colombini et al 2000). Perhaps *Talorchestia*'s feeding ecology differs from the amphipods found in Mo'orean wracks.

The results of another study indicate that amphipods are more abundant in wracks that are more decomposed because more decomposed wracks have decreased toughness of algal structures, which increases its palatability to amphipods (Pennings et al 2000). In Mo'orean wracks, amphipod abundance increases as algae decomposes. While feeding ecology studies were not conducted on amphipods in Mo'orean wracks, I think these amphipods are feeding on the algae much like in other studies (Colombini et al 2000, Colombini et al 1998, Pennings et al 2000, Colombini and Chelazzi 2003).

#### *The Effect of Decompositional State on Staphylinid and Diptera Abundance*

While the results of the ANOVA test show that there is no significant effect of decompositional state on abundance of staphylinids or diptera, there is a trend that staphylinids and diptera primarily inhabit newly washed ashore *T. ornata*, with abundance decreasing as wracks undergo decomposition (see Graphs 6 and 7). Other studies have found that staphylinids and diptera are early wrack invaders, and use the wrack for feeding (Colombini et al 2000, Colombini and Chelazzi 2003). While feeding ecology studies were not conducted, I think that the staphylinids and diptera in Mo'orean wracks probably use algae for feeding as well.

*Effect of Decompositional State on Isopod Abundance*

There is a trend that isopods are primarily found in the middle zone of decomposition, although statistically there is no effect of decomposition on isopod abundance (see Graph 8). These results are congruent to results found in other studies; in algal wracks in British Colombia, the isopod *Ligia* is found in algal wrack that is medium decomposed (Pennings et al 2000). In other research, isopods are early colonizers and use the wrack for refuge and as a food source (Colombini and Chelazzi 2003). Isopods probably use Mo'orean wrack for the same purposes. Behavioral studies would need to be conducted to determine if this is actually the case.

***Other factors influencing arthropod composition***

Other factors could be influencing arthropod composition in wracks of *T. ornata*. As algae decompose, interstitial ammonium concentrations and salinity change (Pregnall and Miller 1988). Different organisms might be able to tolerate different concentrations of ammonium or salt. It is unknown how interstitial ammonium concentration or salinity change as decomposition takes place in wracks of *T. ornata*, however, this change could impact arthropod composition. For example, perhaps amphipods that live in wracks of *T. ornata* are better adapted to salt or ammonium concentrations that are indicative of more decomposed wracks. Perhaps salinity and/or ammonium concentrations are the determining factor(s) in amphipod and other arthropod abundance rather than nutritive value. It is necessary to track the change in salinity and ammonium as decomposition occurs to determine if arthropod composition is affected.

It has been noted that amphipods change their zonation within each stage of decomposition and between the zones according to the semi lunar cycle, which affects tidal inundation of wracks (Colombini et al 2000, Colombini and Chelazzi 2003). During different times in the lunar cycle, temporal separation of the wrack can occur, reducing levels of interspecific interference (Colombini and Chelazzi 2003). I might have sampled during a point of the lunar cycle when the tides were higher, which might have changed the nutrient level. However, this data was not recorded. Diurnal and nocturnal variability can exist at certain stages of the lunar cycle (Colombini et al 1998). While the results of my pilot study indicate no difference between diurnal and nocturnal arthropod assemblages, I might have sampled wracks for my actual study at different stages of the lunar cycle, which might have affected my sampling. Future research could observe behavior patterns over the course of an entire days and nights at different stages of the lunar cycle.

It has been determined that "decomposition of algal organic matter may vary in rate, extent, and manner depending primarily upon the prevailing environmental conditions" (Force and McCarty 1970). Perhaps arthropod composition is determined by microclimatic conditions and is more related to location than decompositional state. It is for this reason that it is important to take into account rainfall, humidity, wind, temperature, and tidal fluctuation at each site. Each location varies in distance from freshwater and type of nearby vegetation, which could impact arthropod assemblages.

Interspecific competition and resource partitioning could be factors influencing arthropod composition in *T. ornata* wracks. Perhaps arthropods in zone 1 are better adapted to consuming newly washed ashore algal wrack. Perhaps arthropods in zone 1 prefer medium decomposed wrack, but the arthropods in zone 2 are better competitors. Behavioral studies need to be conducted before any conclusions can be made on interspecific competition or resource use in these wracks.

***Community Effects***

Temporal separation of arrival at a specific food source may have a number of important implications with regard to subsequent species interaction and community development. It has been documented that early arrival of organisms to wracks can give these organisms a competitive advantage (Colombini and Chelazzi 2003). However, not all organisms that arrive later are at a disadvantage. Often, arthropods can benefit from the earlier arrival of primary colonists (Colombini and Chelazzi 2003). For example, isopods and dipteras arrive early, fragmentize the wrack and accelerate decomposition through burrowing activities (Colombini and Chelazzi 2003). This provides an ideal habitat for amphipod species C which primarily arrives later.

There is species turnover through the successional process, and most taxa found in beached *T. ornata* wracks are specialists (see

Diagram 1). Analysis of succession of species on algal wracks in Sar Uanle, Somalia illustrates that not all species invade wracks at the same time, suggesting resource partitioning according to species' metabolic, habitat and trophic needs (Colombini et al 2000). Staphylinid species A and diptera species K were found in all three wracks (see Diagram 1). I think that these two species can feed on all three stages of wrack and are generalists. Statistically, decompositional state does not affect their abundance. Most species found in *T. ornata* wracks are specialists. Perhaps these specialists can only eat algae of one decompositional state, or perhaps the limiting factors are salinity or ammonium concentrations. Perhaps lunar cycle, tidal inundation, interspecific competition, and microclimactic conditions are the factors most influencing arthropod composition in these wracks. I think that a combination of factors, including decompositional state, impact arthropod abundance and richness in beached *T. ornata* wracks.

### *Sources of Error*

#### *Sampling*

The pilot study showed that temporal fluctuations did not exist when using a Berlese funnel to capture arthropods in algal wracks. Other studies have shown that the semi lunar cycle influences temporal fluctuations (Colombini et al 2000, Colombini et al 2003). I did not sample at the same point in the semi lunar cycle at each site. This might have influenced arthropod abundance and composition.

When sampling, some arthropods might have escaped between the time I placed the algae in plastic containers and the time I put the lid on, although much care was taken to avoid this.

Berlese funnels were chosen as the method of arthropod collection to decrease bias in sampling as discussed in the Methods section. However, the Berlese apparatus might not have trapped all the arthropods in each sample. Perhaps some of the arthropods in *T. ornata* wracks are more heat tolerant and require more than 6 hours to become trapped in the plastic container.

#### *Analysis*

A decision was also made to discard the results from the Beachcomber Zone 3 sample due to seemingly unnaturally high numbers of amphipod species C. I along with my team of statisticians thought this could be an outlier, but there is a possibility that the sample was, in fact, representative of the arthropod abundance of the entire wrack. More sampling from this wrack is needed to determine its representative species composition and abundance.

### Conclusions

The results of this study demonstrate that decompositional state is a key determinant of arthropod abundance, richness, and composition in allochthonous beach wracks of the macroalgae *Turbinaria ornata* along the coast of Mo'orea. Decompositional state does not affect evenness of arthropods in these wracks. It is important to gain insight to the influence of decomposition on arthropod composition to understand the importance of decomposition on nutrient cycling within and between ecosystems. Linkages between marine and terrestrial food webs are becoming clearer although much work remains to be completed on the dynamics of these systems. Future research could focus on the effect of environmental factors such as rainfall on *T. ornata* decomposition, determine arthropod composition in wracks of other algae, or determine the impact of a change in ammonium and salinity concentrations as algal tissues decompose on arthropod composition. Variables such as distance from other vegetation and the effects of arthropod behavior, resource partitioning, and changes in the lunar cycle could also be studied, and future research could test for covariance between these variables.

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## LITERATURE CITED

Anderson Wendy B., Polis Gary A. (1999) Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. Oecologia 118:324-332

Bastow Justin, Sabo John, Power Mary E (2002) A basal aquatic-terrestrial trophic link in rivers: algal subsidies via shore-dwelling grasshoppers. Oecologia 131:261-268

Colombini I, Chelazzi L (2003) Influence of marine allochthonous input on sandy beach communities. Oceanography and Marine Biology: an Annual Review 2003 41:115-159

Colombini I, Aloia A, Fallaci M, Pezzoli G, Chelazzi L (1998) Spatial Use of an Equatorial Coastal System (East Africa) by an Arthropod community in relation to periodically varying environmental conditions. Estuarine, Coastal and Shelf Science 47:633-647

Colombini I, Aloia A, Fallaci M, Pezzoli G, Chelazzi L (2000) Temporal and spatial use of stranded wrack by the macrofauna of a tropical sandy beach. Marine Biology 136:3:531-541

Force Edward, McCarty Perry (1970) Anaerobic Decomposition of Algae. Environmental Science and Technology 14:10

Gabrie C, Planes S, Payri, C (1994) Study of Coral Reefs of Bora Bora (Society Archipelago, French Polynesia) for the development of a conservation management plan. Ocean and Coastal management 25: 189-216.

Hetfield James (2002) Salmon and alder as nitrogen sources to riparian forests in a boreal Alaskan Watershed. Oecologia: 133: 572-582

Hutchings Pat, Payri Claude, Gabrie Catherine (1994) Current Status of Coral Reef Management in French Polynesia. Marine Pollution Bullettin 29: 26-33.

Huxel Gary R, McCann Kevin (1998) Food Web Stability: The Influence of Trophic Flows across Habitats. The American Naturalist 152:3

Lawrence John, Britton EB. (1994) Australian Beetles. Melbourne University Press, New York.

Likens GE and Bormann FH (1975) An experimental approach in New England landscapes. Coupling of Land and Water Systems. Springer-Verlag, New York pp. 7-27

Minshall GW (1967) Role of allochthonous detritus in the tropic structure of a woodland stream. Ecology 48:139-149

Nakano Shigeru (1999) Terrestrial-Aquatic Linkages: Riparian Arthropod Inputs alter Trophic Cascades in a Stream Food Web. Ecology 80:7:2435-2441

Nakano Shigeru, Murakami Masashi (2001) Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. Ecology 98:166-170

Payri C., N'Yeurt AR, Orempüller J (2001) Algae of French Polynesia -Algues de Polynésie Française. Au vent des Iles, Tahiti

Payri C, Stiger V (2001) Macroalgal community changes on French Polynesian reefs 1980-2000. Phycologia 40:4.

Pennings Steven C, Carefoot Thomas H, Zimmer Martin, Danko Jean Paul, Ziegler Andreas (2000) Feeding preferences of supralittoral isopods and amphipods. Canadian Journal of Zoology 78(11):1918-1929

Polis Gary A, Hurd Stephen (1996) Linking Marine and Terrestrial Food Webs: Allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. The American Naturalist 147: 396-423

Polis Gary A, Anderson Wendy B, Holt Robert D (1997) Toward an Integration of Landscape and Food Web Ecology: The Dynamics of Spatially Subsidized Food Webs. Annual Review of Ecological Systems 28:289-316

Pregnall A Marshall, Miller Steven L (1988) Flux of ammonium from surf zone and near shore sediments in Nahant Bay, Massachusetts, USA in relation to free living *Pilayella littoralis*. Marine Ecology Progress Series 50:161-167

Ricketts Edward, Calvin Jack, Hedgpeth Joel (1985) Between Pacific Tides. Stanford University Press, Stanford

Rose Michael, Polis Gary (1998) The Distribution and Abundance of Coyotes: The Effects of Allochthonous Food Subsidies from the Sea. Ecology 79(3): 998-1007

Samways MJ, Stewart DAB (1997) An aquatic ecotone and its significance in conservation. Biodiversity and Conservation 6:1429-1444

Stewart Hannah (2003) Department of Integrative Biology, University of California, Berkeley. Personal communication. 3 December 2003

Stiger V, Payri CE (1999) Spatial and Seasonal variations in the Biological Characteristics of of two invasive brown algae, Turbinaria ornata (Turner) J. Agardh and Sargassum mangarevense (Grunow) Setchell (Sargassaceae, Fucales) spreading on the reefs of Tahiti (French Polynesia). Botanica Marina 42

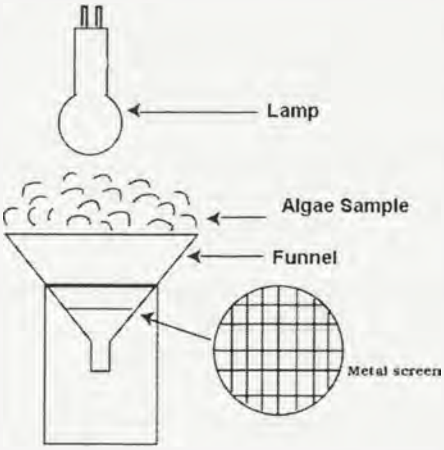
Stiger V, Payri,CE (1999) Spatial and temporal patterns of settlement of the brown macroalgae *Turbinaria ornata* and *Sargassum mangarevense* in a coral reef on Tahiti. Marine Ecology Press Series 191: 91-100

Figure 1

a. Zone 1 b. Zone 2

c. Zone 3

Figure 3 – Berlese Funnel



Appendix 1 – Species List

| Species Type | Taxonomy |
|---|---|
| A | Coleoptera, Staphylinidae |
| B | Orthoptera |
| C | Amphipoda |
| D | Decapoda |
| E | Acari |
| G | Dermaptera, Forficulidae |
| H | Isopoda |
| I | Coleoptera, Ptiilidae |
| K | Diptera |
| K2 | Diptera |
| L | Oligachete |
| M | Isoptera, Kalotermitidae |
| N | Hymenoptera, Formicidae |
| O | Hymenoptera, Formicidae |
| P | Decapoda |
| Q | Oligachete |
| S | Isopoda |
| T | Isopoda |
| U | Diptera, Sphaeroceridae |
| V | Coleoptera, Scolytidae, Scolitinae |
| W | Decapoda |
| X | Orthoptera, Gryllidae |
| Y | Hymenoptera, Formicidae |

# The ecology of rhodoliths from shallow-water back reef environments in Mo'orea, French Polynesia

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ABSTRACT. Few studies have been preformed on the ecology of free-living forms of coralline red algae known as rhodoliths. Rhodoliths, forming beds, support a diversity of invertebrates and macroalgae, and fossil beds serve as evidence for the paleoenvironmental record. Observations were made on the environmental factors influencing rhodolith beds at three sites in Mo'orea, French Polynesia. Three species of Corallines, *Neogoniolithion frutescens*, *Hydrolithion reinboldii*, and a species identified to the subfamily *Lithophyllum*, formed beds in shallow waters from 0-2m deep. Measurements taken from October to November 2003 showed that beds averaged 50m in width and bottom water temperatures ranged from 25-30 °C. Rhodolith shapes, recorded as spherical, ellipsoidal, and discoidal, varied along water motion gradients from shore to the reef. Bottom substrate and water motion controlled plant size and branching density. Water motion was measured comparatively using the Plaster Dissolution Method. Estimates for rhodolith contribution to the $CaCO_3$ budget are included for each site. Results imply that rhodolith morphology and distribution are dependent on a variety of factors and specific to species. Future ecological studies are needed for beds worldwide so that more rigorous interpretation of environmental influences can be made.

Keywords: Coralline algae, morphology, distribution, rhodoliths, French Polynesia

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## Introduction

Rhodoliths are free-living forms of coralline red algae that are non-geniculate (Foster, 2001). Living beds, defined by Marrack (1999) as areas of vegetative substrate are found worldwide over a wide range of latitudes and depths. Rhodolith beds have been described in tropical reefs, temperate fjords and bays and in polar regions, from the shallow intertidal zone to depths over 200m (Marrack, 1999).

Rhodoliths input large amounts of $CaCO_3$ into the marine environment and at depth, are the major producers. On otherwise sandy benthos, rhodoliths provide a structured biogenic habitat for a diversity of marine invertebrates, micro and macroalgae (Steller et. al, 2003). Well preserved as fossils, rhodolith morphology, distribution and infaunal assemblages have been used as evidence for the paleoenvironmental record (Marrack, 1999).

Less than half of the rhodolith beds worldwide have been studied and there is no documented research for the rhodolith beds of Mo'orea, French Polynesia. Little is known of rhodolith bed ecology, however environmental factors such as, depth, temperature, and water motion are considered important influences that determine rhodolith distribution and morphology (Johansen, 1981). With only few studies on the influences of these factors, the use of rhodoliths as indicators for the paleoenvironmental record seems premature.

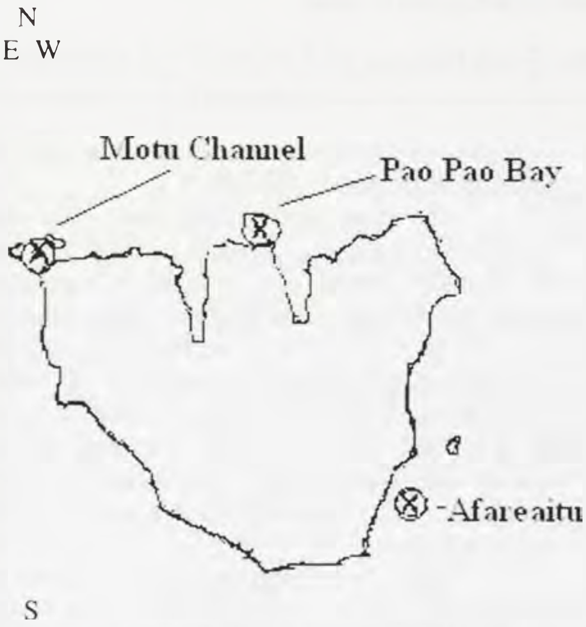
The objectives in this study were to quantify the influence of environmental factors on rhodolith habitat and to examine variation within the rhodolith community at shallow-water beds off the island of Mo'orea, French Polynesia. The specific questions asked were: (1) At what temperatures, depths, and rates of water motion are rhodoliths growing?; (2) Within a bed, which species are present and how dense are the populations?; (3) What are the characteristics of these organisms?

Light and temperature are the primary factors that control species distribution, growth rates and growth forms of coralline algae around the world (Marrack, 1999). In the tropics, calcareous alga are abundant more so than in cold waters, perhaps because warmer waters allow for lower partial pressures of carbon dioxide and supersaturation of calcium carbonate. Water motion prevents fouling of rhodoliths, affects rhodolith shape, and allows light to reach all surfaces. Steneck and Adey found that the largest and most complex branching protuberances occur on rhodoliths in somewhat sheltered areas and that less-branched rhodoliths are found in areas of wave intensity (Johansen, 1981). It is expected that rhodoliths of Mo'orea will follow these trends. This paper will discuss which coralline species and morphologies have adapted to Mo'orean environmental conditions better than others.

### Methods

The locations of shallow water rhodolith beds on Mo'orea were surveyed. Three sites were chosen for their unique environments. Sites were chosen at the channel between motus Fareone and Tiahura (GPS S 17° 29.328', W 149° 54.783'), the reef lagoon outside of Pao Pao Bay (GPS S 17° 28.869', W 149° 49.657'), and behind the fringing reef in the southwestern town of Afareaitu (GPS S 17° 33.239', W 149° 47.416').

Figure 1. A map of the island of Mo'orea, French Polynesia. Three rhodolith beds used as study sites, the Motu Channel, Pao Pao Bay, and Afareaitu, are indicated.



*FieldMethods*

All field work was done during the austral winter of 2003. Bed widths were measured and a 30m x 20m quadrat was distinguished at the inner thirty meters. The quadrat was divided into an upper, middle, and lower margin. Bed width, approximate distance from shore and reef, water depth at low and high tides, water temperature and wave surge, were measured at three buoys in each margin.

The distribution of rhodoliths on Mo'orea is zonal, where shallow beds take the shape of long bands that stretch between reef passes. It became clear that the width of these ~~beds was the important measurement. According~~ to the definition of a rhodolith bed by Marrack (1999), bed width was measured from the shore to the reef wherever vegetative substrate was living. The distance from the rhodolith bed to the shore and to the reef were measured if lengths were shorted than 50m and approximated if longer. Approximations were made by extending a transect tape between two kayaks. Measurements to the shore and reef were taken from the closest two quadrat corners.

Water depth was recorded at high and low tides for each site. Tides are constant on Mo'orea, therefore, each measurement for high tide was taken at noon and measurements for low tide were recorded at 6:00 am or pm. Depth was recorded using a transect tape, four times over the course of this study. Depth data for each site is reported as an average of those four measurements.

Water temperatures were recorded for the Pao Pao Bay and Afareaitu sites every 15 minutes over the same three-day period using ACR Smart Button technology. The temperature readings for the motu site were taken using a glass thermometer because wave conditions were too strong to use Smart Buttons. Readings for the motu waters could only be recorded at two afternoon times, 12:00 pm and 3:45 pm, four times during the study. Water temperatures were taken from the bottom waters, among the rhodolith community.

Water action was quantified using the Plaster Dissolution Method (Doty, 1971). By determining the amount of erosion from a plaster mold after a period of time in the water, comparisons can be made as to how strong the waves surge at each site. Plastic cups 7cm tall and 3cm in diameter were used as molds for the plaster of paris. The molds were weighed, glued to cement blocks and then placed at nine buoys at each site for the duration of two days. The molds were recollected, dried, and the plaster weighed again. The control for this experiment was one mold at each site that was vertically enclosed in an open tin can. The control mold was subject to sea water dissolution but it did not receive any force from wave action. The same weighing methods were applied for the control. To account for dissolution by higher water temperatures and not erosion by wave force, the amount that each plaster mold eroded was adjusted by subtracting the percentage lost by the control. The difference in final and adjusted weights of the molds within and among sites was correlated to the amount of wave force in the water.

The objective was to move from site to site as quickly as possible, placing the plaster molds in the water promptly so that the amount of common time the molds spent in the water was maximized. By doing so, variables such as differences in weather conditions or temperature were minimized.

*Laboratory measurements*

A second series of small-scale measurements were taken to characterize the rhodolith community. The large quadrat was divided into a grid, each meter was numbered one through 20 along width, which paralleled the shore, and one through 30 for the length, perpendicular to the shore. At each site, five transects were performed. They were taken at 1, 5, 1 0, 1 5 and 20m along the width of the large quadrat. Transects were performed perpendicular to the shore. Going along each transect line, $1m^2$ small quadrats were placed at 1, 5, 10, 15, 20, 25 and 30m along the length of the quadrat, to examine individual rhodoliths.

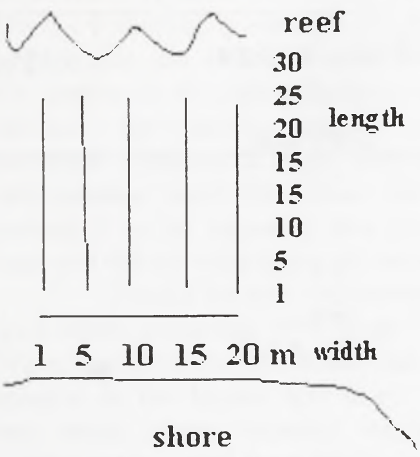


Figure 2. A diagram illustrating the quadrat grid and transect lines.

In each small quadrat, individual rhodoliths were numbered and the species recorded. Using a random numbers table, rhodolith specimens were collected in a random fashion, to be analyzed later in the lab. Weight, volume, circumference, longest, intermediate, and shortest dimensions were measured. Also recorded was the density of coralline protuberances in five haphazardly placed $1cm^2$ quadrats and the lengths of five haphazardly chosen coralline protuberances. Species were identified from descriptions and photographs by Payri et. al (2001), Johansen (1981), and Woelkerling (1998). The longest possible circumference was recorded for each rhodolith, branches were measured from the core of the rhodolith outward, and knobbed protuberances were measured as a surface length. Lab measurements allowed other numbers to be calculated, such as density of rhodoliths per square meter and amount of calcium carbonate produced.

**Results**

Surveys conducted to determine the locations of living rhodolith habitat on Mo'orea revealed that rhodolith beds are widespread off the coast of Mo'orea, but not continuous. Rhodoliths grew on all sides of the island, distributed in beds over shallow sloping beach flats. Beds took the shape of wide bands that extended between reef passes. These bands appeared highly zonal, beginning a certain distance from the beach and ending just before areas of large coral head growth.

At the shallow sites studied, waters were clear light blues. Turbidity was low, allowing for maximum light penetration available for rhodolith photosynthesis. Water movement directly off beach shores, depths less than 20cm, was controlled by wind driven forces. Below 20cm of water, tidal forces dominated.

Water action at rhodolith bed sites did not affect rhodolith movement. It was observed that rhodoliths at these sites grew sedentarily and neither rolled with along bottom substrates, nor rocked in place with water motion forces. In situ, rhodoliths grew partially buried in the substrate. Coloration of rhodolith surface facing the water column ranged from yellow to pink and below the substrate, surface pigments ranged from shades of purple and red. From these colors, the top and bottom rhodolith surfaces could be distinguished.

On sandy bottom substrates, rhodoliths were not the only hard structures. Rhodolith beds were distributed over dense areas of coral rubble, however, these rhodolith structures were more highly colonized. Crevasses, between protuberances, and burrowing through layers of calcium carbonate, a variety of polychaetes, amphipods, bryozoans, hydroids, sponges, micro and macroalga, were found living. It was observed that branched rhodolith morphologies were more densely colonized than those that were knobbed.

Rhodolith species growing in Moorea were identified as *Neogoniolithon frutescens,* *Hydrolithon reinboldii*, and a third species from the subfamily *Lithophyllum*. The morphology of *N. frutescens* is branched. Branching density is frequent and branches end in apical tips.

*Hydrolithon reinboldii* is an applanate crutose, laminar in morphology. Rhodoliths are composed entirely of protuberances that are globular and irregular. Inner cores are nucleated, coral rubble pieces.

Thalli from the subfamily *Lithophyllum* are crutose, spherical, and composed entirely of branched protuberances. Branches are intergrown and lamellate. Rhodoliths are non-nucleated, inner crusts are concentric and closely stacked, which represents successive colonizations and overgrowths of corallines algae. This growth form appears more foliaceous than *N. frutescens*.

*Study sites*

*Motu Channel site description*

Motus Fareone and Tiahura are close neighbors off the Northeastern coast of Mo'orea, approximately 230m from the mainland.

Between these motus, a fast moving water channel extends 70m across. Wind and currents driving this channel originate from the North. The bottom substrate of the channel was composed entirely of rhodolith and shell fragments. This site was visited frequently by snorkelers and boaters, possibly presenting a negative impact on thalli remaining intact.

Two distinct beds inhabit this channel, one on each motu shore. The rhodolith bed studied in this paper was located off the coast of Motu Tiahura. Rhodolith bed size was 40m wide. The 30m x 20m quadrat for this site was centrally placed along the channel side of the island. The quadrat was placed an average of 25m from the shore and 170m from the reef.

Table 1. *Environmental Factors Influencing Rhodolith Habitat*. Depth, Temperature, and Percent Lost are reported as averages from the upper, middle, and lower margins, by site. Percent Lost refers to the percentage of the Plaster of Paris mold eroded, from which water action was compared.

| Site | Depth (cm) High tide/Low tide | Temperature (° C) 3:00 pm | Percent Los |
|---|---|---|---|
| **Motu Channel** | | | |
| upper | 36.00/24.33 | 27.75 | 53 |
| middle | 50.33/48.33 | n/a | 61 |
| lower | 71.67/61.33 | 25.84 | 55 |
| **Pao Pao Bay** | | | |
| upper | 58.00/48.33 | 32.5 | 38 |
| middle | 68.00/53.67 | n/a | 37 |
| lower | 67.33/58.00 | 47.4 | 35 |
| **Afareaitu** | | | |
| upper | 53.67/48.83 | 34.6 | 35 |
| middle | 33.00/18.00 | n/a | 51 |
| lower | 31.00/27.17 | 33.8 | 53 |

Depths increased from the upper to lower margins of the quadrat and from North to

South. Temperatures ranged from 26.17°C to 28.00°C at 12:00 pm and from 25.50°C to 27.50°C at 3:45pm. Temperature decreased from upper to lower margins. Plaster erosion percentages were highest at the middle quadrat margin, ranging from 53 to 61 percent (Table 1).

Within the bed at the motu channel, *Neogoniolithon frutescens* and *Hydrolithion reinboldii* coralline algae species formed rhodoliths, the species from the *Lithophyllum* subfamily was not present. *N. frutescens* and *H. reinboldii* had almost an equal presence at this site, with *H. reinboldii* dominating 56% percent of the population. Most rhodoliths were multispecific and nucleated. There was an average of 55 rhodolith organisms per square meter at this site. $CaCO_3$ added to the ecosystem at this site was approximately 11.2g per square meter.

*Pao Pao Bay site description*

This reef lagoon site was situated 200m from the shore at the end of Pao Pao Bay. Reef break to the east side of the quadrat was approximately 60m and 100m from the West. Depths within the quadrat ranged from 60-75cm at high tide and 43-70cm at low tide. No trend for depths at this site was apparent, possibly because the bottom terrain was variable. Substrate consisted of larger coral rubble pieces and smaller coral bits. This site was rarely visited, if so, by kayakers who fished from the boat and did not step out on the ocean floor.

Toward the reef, temperatures increased with depth, averaging 30°C to 48 °C at 3:00pm. Wave action off the reef break did not reach the quadrat as the lagoon was large. Wave action was wind driven, blowing westward. Plaster erosion rates varied from 35-38 percent, highest in the upper quadrat.

Species present at the Pao Pao site were *Neogoniolithon frutescens* and *Hydrolithon reinboldii*, lacking *Lithophyllum*. *H. reinboldii* was the found at higher concentrations than was *N. frutuescens*, dominating 88% of the rhodolith bed. Rhodoliths were multispecific and nucleated. There was an average of 11 rhodoliths per square meter at this site. $CaCO_3$ added to the ecosystem by rhodoliths was 7.33g per square meter.

*Afareaitu site description*

South of the town of Afareaitu, a large and dense rhodolith bed exists off the backyards of residential homes. This site is often used for kayaking and boogie boarding. An exit for boats was dredged on the North end of the site, making up the North perimeter of the rhodolith bed.

The large quadrat at this site was placed 30m from the shore line. The upper margin of the quadrat begins in the deepest waters, averaging 53.67cm at high tide. Approximately 10m toward the reef, from the quadrat side parallel to the shore, dead coral brommie covers the ocean floor. Rhodoliths grow on the shallow brommie at average high tide depths of 33.00cm for the middle margin and 31.00cm for the lower margin, border-lining the fringing reef. The large quadrat at the Afareaitu site was placed 30m from the shore and at 10m directly behind the fringing reef.

Force from the reef break produced the most water action at the lower and middle margins. At low tides, rhodoliths were almost out of the water on the coral brommie.
Temperatures, reported at 3:00pm were not affected by the low tide. In the upper margin, high tide temperatures average 34.6°C, and in the shallow lower margin, 33.8°C was the average.

At the upper margin, where depths were high, rhodoliths grew 5 or 6 organisms stacked on top of each other. This dense growth was unlike the other two beds which had rhodoliths scattered among the substrate. This site was also unique as it was not inhabitied by *N. frutescens* or *H. reinboldii*. At Afareaitu, the only species of coralline algae present belonged to the subfamily *Lithophyllum*. *Lithophyllum* rhodoliths were larger in diameter and weight (Graphs 5&6), in comparison to the other two sites. Rhodoliths averaged 41 organisms per square meter at this site. The amount of $CaCO_3$ produced per square meter was an average of 30.1g at Afareaitu.

*Graph 1*

Along transect lines at the Motu Channel site, the density of individual rhodoliths is lowest at the upper margin, peaks at the middle margin, and declines in the lower margin. The majority of rhodoliths at the Motu Channel site are monspecific *H. reinboldii* and multispecific *H. reinboldii* and *N. frutescens*. Monospecific *H. reinboldii* are present at higher densities on the southern end of the quadrat more so than any other locality.

*Graph 2*

Monospecific *H. reinboldii* rhodoliths are present at the highest densities at the Pao Pao Bay site. Along transect lines, numbers of *H. reinboldii* organisms vary. There is a dense gathering of *H. reinboldii* rhodolith at the eastern end of the quadrat in the middle margin.

*Graph 3*

The only species present at the Afareaitu site is monospecific *Lithophylum*. The distribution of this species increases in the upper margin, decreases in the middle and lower margins. Higher densities occur on the southern end of the quadrat. There is a dense gathering of *Lithophyllum* rhodoliths at the middle margin of the 5m transect.

*Graph 4*

The branching density of apical protuberances of *N. frutescens* varied by site and by margin within each site. At the Motu Channel, branches were most dense at the middle quadrat, lowest in the upper quadrat, and at an intermediate density in the lower quadrat.

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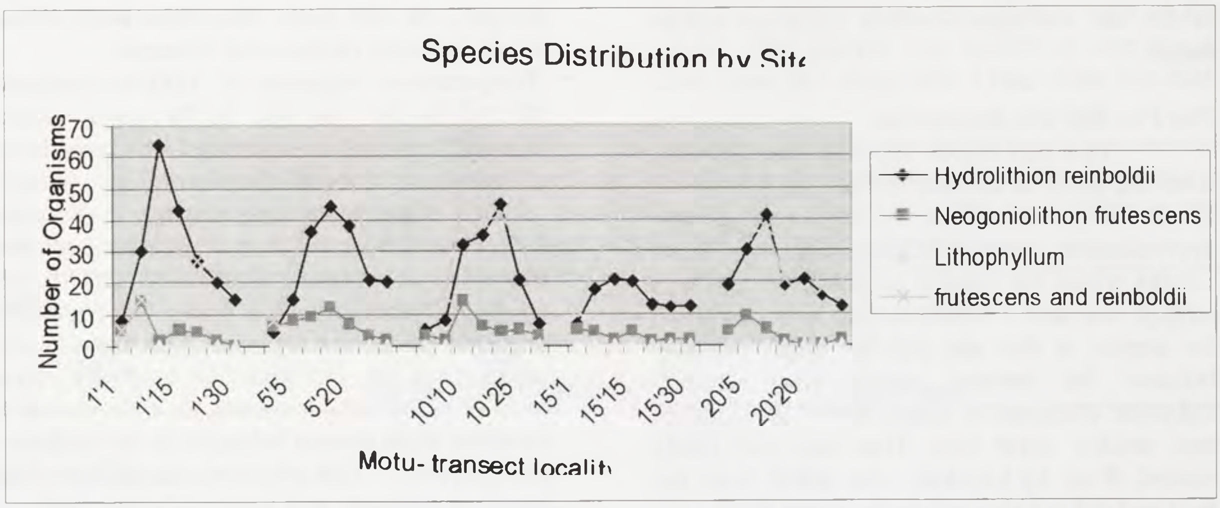
Graphs 1-3. *Species Distribution by Site*. Numbers of monospecific *H. reinboldii*, monspecific *N. frutescens*, multispecific *H. reinboldii* and *N. frutescens*, and *Lithophyllum*, rhodoliths are given for each transect locality. The axis labels, shown on Graph 1, are alike for all graphs 1-3.

Graph 1.



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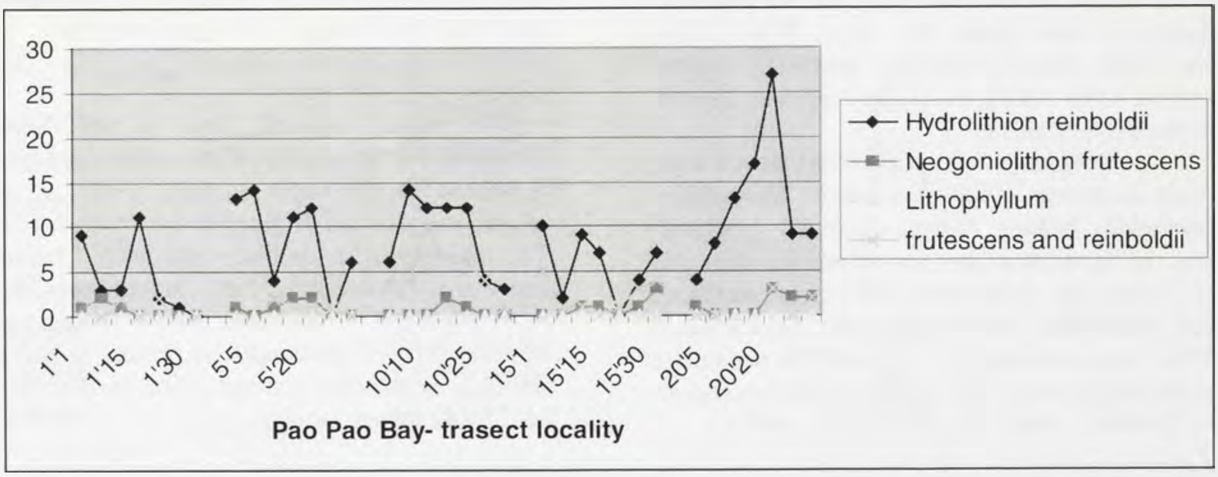
Graph 2.



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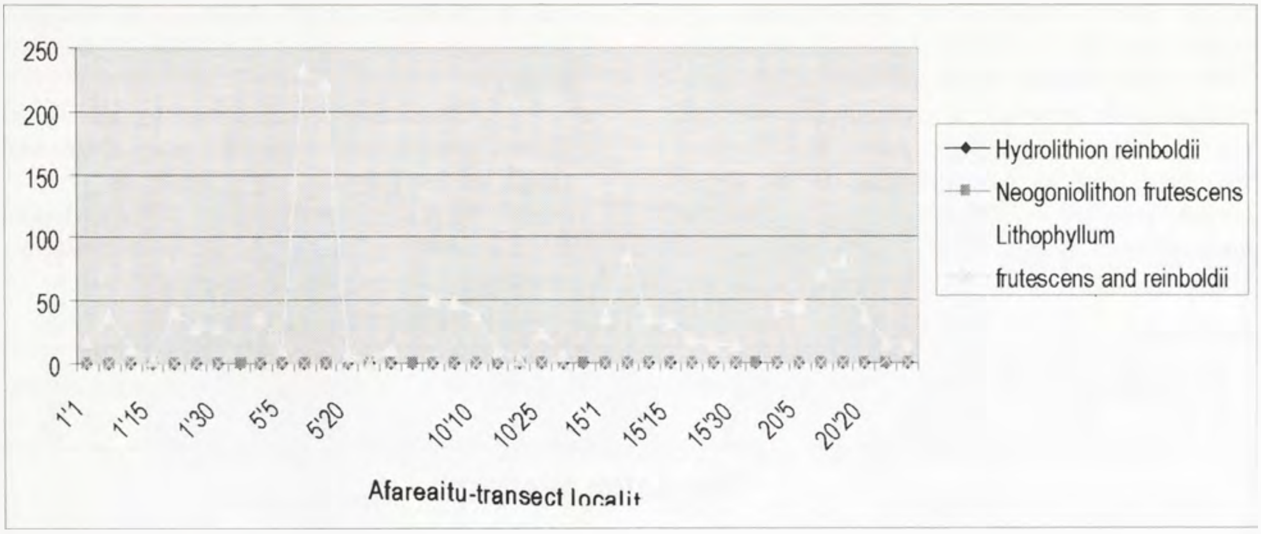
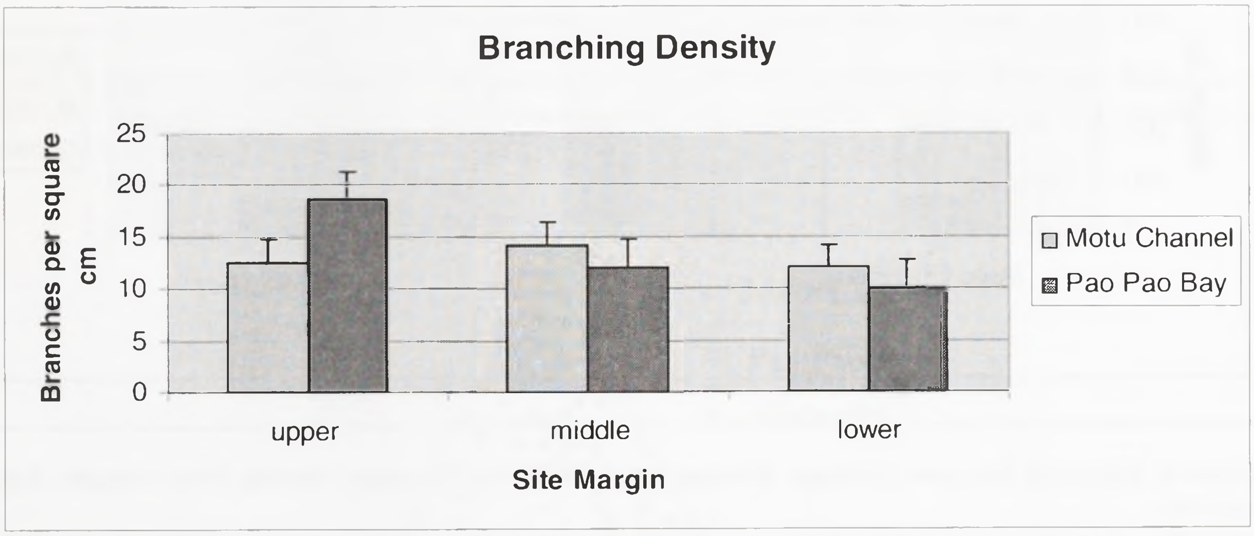
Graph 3.





Graph 4. Branching Density of *N. frutescens*. Branching density of *Neogoniolithi*on *frutescens* at the upper, middle, and lower margins of the Motu Channel and Pao Pao Bay sites.

*Graph 5*

Rhodoliths vary in weight by site and among margins within each site. At the Motu Channel site, rhodoliths were heaviest at the lower margin, of an intermediate weight at the upper margin, and of lightest weight at the middle margin. At the Pao Pao Bay site, rhodoliths were heaviest at the upper margin, of an intermediate weight at the lower margin, and of lightest weight at the middle margin. At the Afareaitu site, rhodoliths were heaviest at the lower margin, of an intermediate weight at the upper margin, and of lightest weight at the middle margin.

*Graph 6*

Rhodolith diameter also varies by site and among margins within each site. At the Motu Channel site, rhodolith diameters were longest at the lower margin, of an intermediate length at the upper margin, and of shortest length at the middle margin. At the Pao Pao Bay site, rhodolith diameters were longest at the lower margin, of an intermediate length at the middle margin, and of shortest length at the upper margin. At the Afareaitu site, rhodolith diameters were longest at the upper margin, of an intermediate length at the lower margin, and of shortest length at the middle margin.

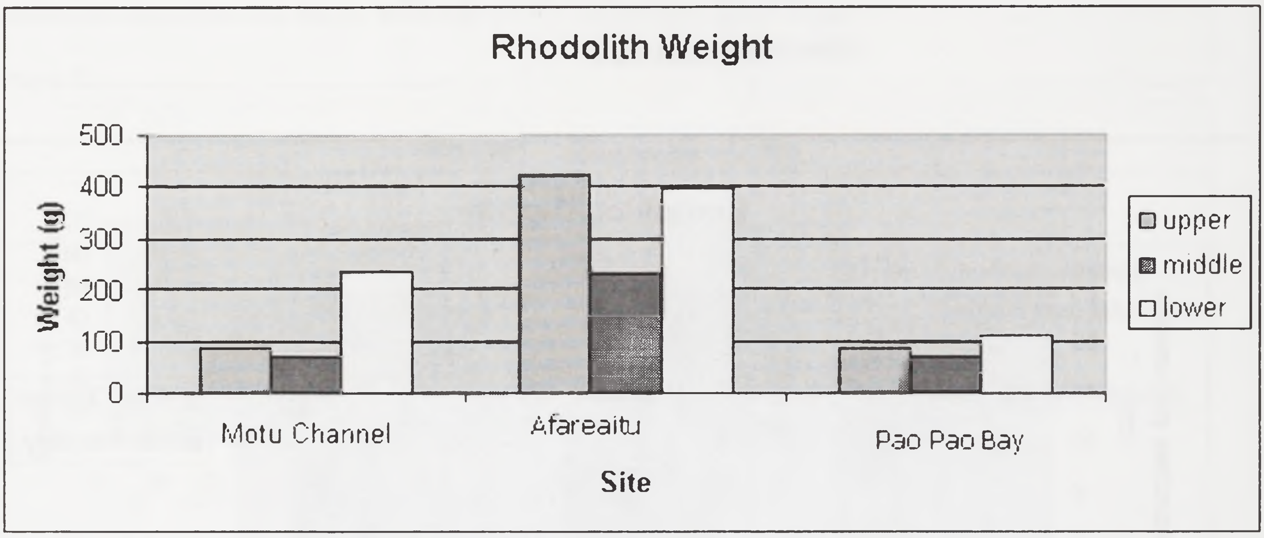
*Graph 7*

Wave action also varies among and within sites. At the Motu Channel site, water motion was strongest at the middle margin, weakest at the upper margin, and an intermediate strength at the lower margin. At the Pao Pao Bay site, water motion was strongest at the upper margin, weakest at the lower margin, and an intermediate strength at the middle margin. At Afareaitu, water motion was strongest at the lower margin, weakest at the upper margin, and an intermediate strength at the middle margin.

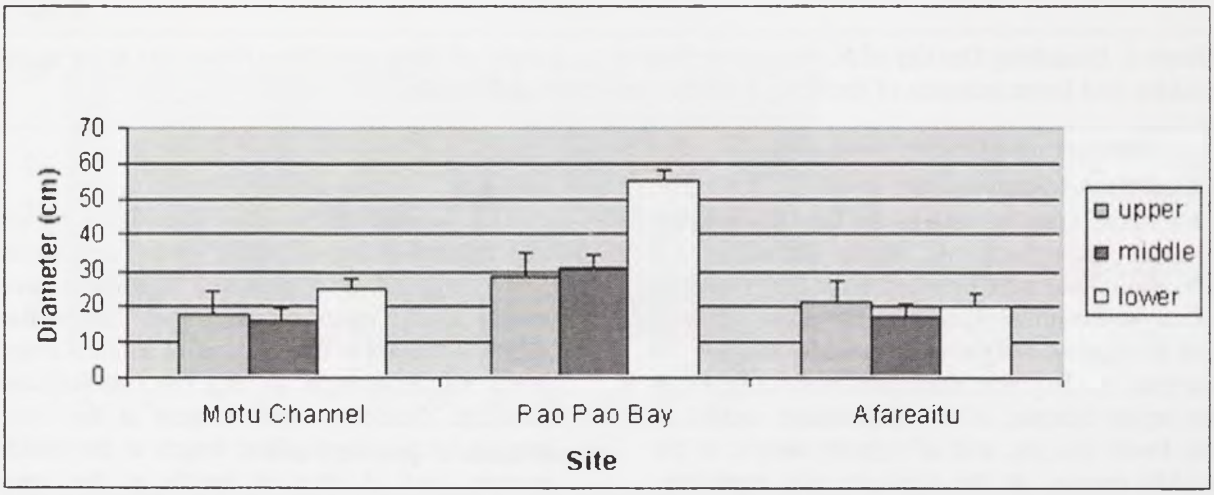
*Graph 8*

Rhodolith shapes at vary by site. At the Motu Channel, rhodoliths take on an ellipsoidal shape. At Pao Pao Bay, the majority of rhodoliths graphed in this triangle gather toward the discoidal side. At Afareaitu, rhodoliths are graphed at the apex of the triangle, corresponding to spherical shapes.

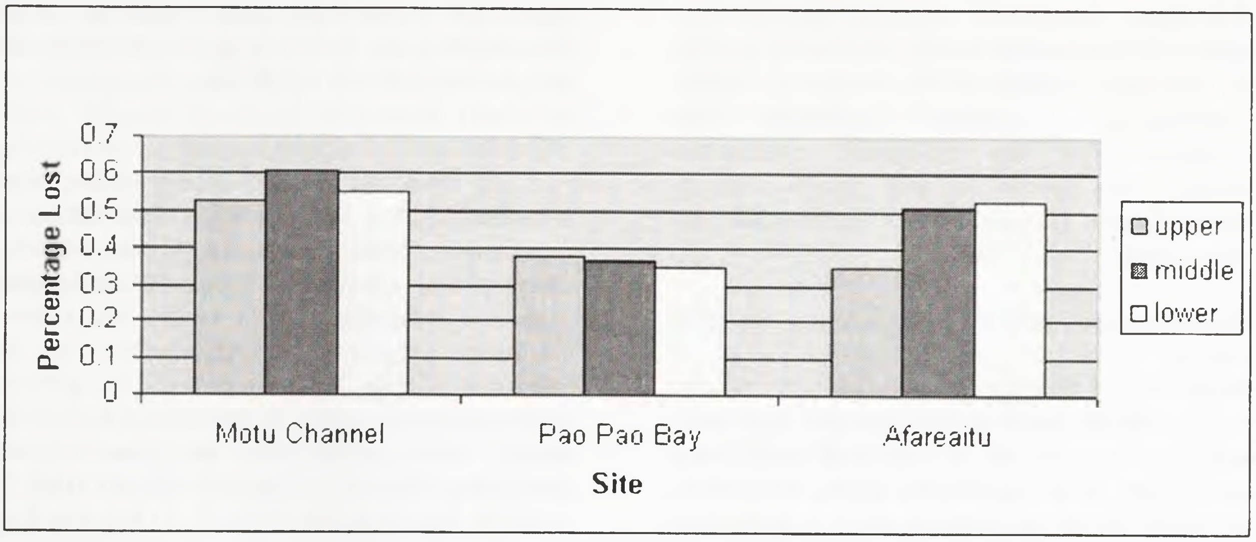
Graph 5. *Rhodolith Weight*. Average weight for rhodoliths at the upper, middle, and lower margins from each site.



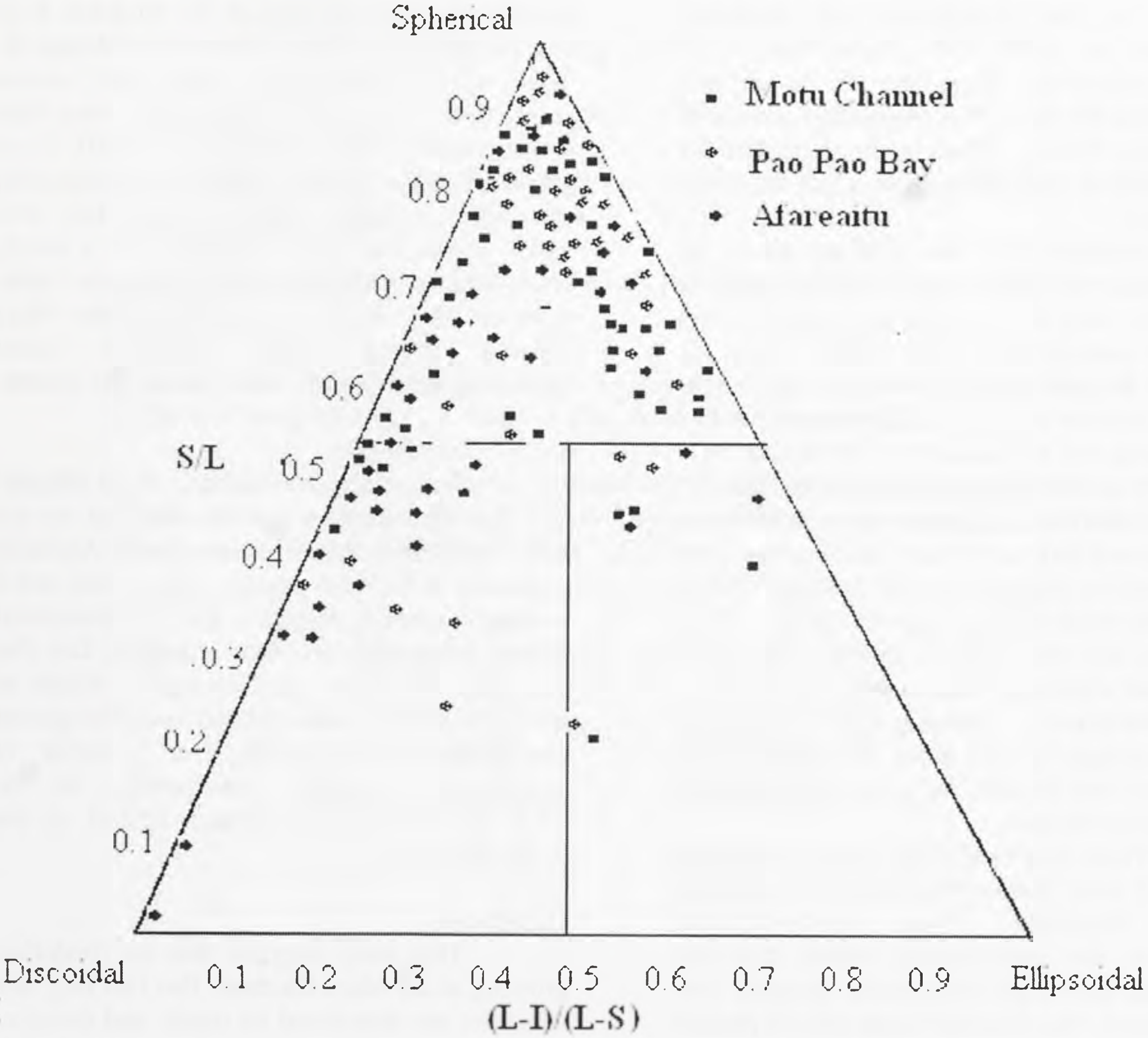
Graph 6. *Rhodolith Diameter*. Average diameter for rhodoliths at the upper, middle, lower margins from each site.



Graph 7. *Water Action.* Wave action compared between sites according the percentage of plaster of paris lost from molds placed in the upper, middle and lower margins.



Graph 8. *Rhodolith Shape Diagram.* Each point is the sphericity of one rhodolith. S, I, and L, correspond to shortest, intermediate, and longest dimensions (cm) of each individual. Equations shown on the axes are used to determine placement within the triangle.



## Discussion

In discussing the results of this experiment, conclusive evidence as to why certain environmental factors influence growth or branching patterns will not be made. Confounding variables prevented the significance of any conclusive correlation. Instead, this discussion will propose trends observed and suggest possible influences for these trends.

### *Environmental factors influencing rhodolith habitat*

*Depth*

Water depth at both low and high tides influences the amount of light that reaches the ocean floor. As photosynthetic plants, the growth and development of coralline algae is dependent on the quantity and quality of light available to the rhodolith community (Johansen, 1981). The quantity of light on the ocean floor decreases with depth, the quality of light can be reduced by such factors as water turbidity.

The influence of depth can be seen in Mo'orea by the distribution of rhodolith organisms in zones. Rhodoliths were not growing where the water met the beach, but meters from the shore, stopping before a zone of coral heads. This distribution was controlled by water depth, or light availability to the rhodolith community.

Evidence for rhodoilith sensitivity to light is observed in the coloration of rhodoliths. Rhodoliths vary in color on the surface facing the water column and on the surface facing the substrate because algal cells have adapted to varying amounts of light. Pink and orange colors representing the top surfaces of rhodolith have evolved with photoprotectant pigments that act as a sunscreen for chlorophyll cells. On bottoms, rhodoliths are dark purples and reds because they lack protecting pigments, these cells are able to capture as much light as possible (Payri et. al, 2001). At sites that are too shallow, light is too intense and algae cells cannot grow. At sites too deep, chlorophyll in rhodolith algal cells do not capture enough light to grow. It is perhaps for this reason that the distrubtion of rhodolith beds was zonal in Mo'orea.

There is evidence for rhodoliths beds at depths of over 200m (Marrack, 1999), where light is diminished. These corallines have adapted to this environment, where they can grow with little light availability, possibly low temperatures. The coralline algae species present in the shallow intertidal zones of Mo'orea are not of this type. Instead, the species present *Hydrolithion reinboldii*, *Neogoniolithion frutescens*, and *Lithophyllum*, at the three sites in this study grow in Mo'orea because they are adapted to Mo'orean conditions.

*Wave Action*

While water motion may be important for discouraging fouling and sedimentation on rhodoliths, wave action is not necessary for bed development (Marrack, 1999). Water motion was not observed in this study, but colored pigments suggest that both surfaces of the rhodolith receive light since both are growing with colored pigments. At the Motu Channel site where wave action was the most intense, rhodoliths formed ellipsoidal shapes due to possible fragmentation of thalli. At Pao Pao Bay, where wave action was least, rhodoliths developed more discoidal shapes as a result of the growth rate of some apical protuberances growing faster than others in *N. frutescens*. At Afareaitu, moderate wave action produced sphereical rhodolith shapes by erosion of protuberances on all sides of the rhodolith from rolling, perhaps on the coral brommie (Graph 8). This shape morphology and wave action correlation was also observed in Baja Conception by Steller and Foster in 2003. From graphs 4 and 7, wave action also controlled branching density. At the Pao Pao Bay site, water action was more constant. As a result, branching densities for *N. frutescens* were constant as well. Water motion at the Motu Channel varied, which produced varied branching densities for the *N. frutescens* species.

*Species Distribution*

It is uncertain why the Motu Channel and Pao Pao Bay were both inhabited by the same coralline algae species and Afareaitu supported a different species. There was not a striking variation between the environmental factors influencing the Motu Channel, Pao Pao Bay, and Afareaitu sites. Therefore, trends of species preference were not obvious. The species distribution could possibly be a factor of colonization, meaning the species in the subfamily *Lithophyllum* hasn't settled at the other two sites.

## Conclusion

This study suggests that the rhodoliths growing at the Motu Channel, Pao Pao Bay, and Afareaitu are distributed by depth, and therefore light availability. The species of coralline algae present, *Hydrolithion reinboldii, Neogoniolithion frutescens*, and *Lithophyllum*, have adapted to areas of high light availability by using photoprotective pigments that minimize damage to chlorophyll cells. High water action at the Motu Channel produced ellipsoidal rhodoliths possibly due to fragmentation.

Low water action at Pao Pao Bay produced discoidal rhodoliths due to individual protuberance growth rates dominating others, possibly as a function of light.

**Acknowledgements**

At Afareaitu, rhodoliths were spherical in shape as water motion was moderate and allowed for even erosional forces. More work needs to be conducted on why the species of coralline algae differed from the Motu Channel and Pao Pao sites to the site at Afareaitu.

I would like to acknowledge Jere Lipps for introducing me to rhodoliths at Motu Tiahura, K. Blake Subtle for advice on my experimental design, and for their continuous support in the field and off, Heather Laederich, Brooke Massa, and Hadas Dimenstein.

## LITERATURE CITED

Doty, MS (1971) Measurement of Water Movement in Reference to Benthic Algal Growth. Botanica Marina 14: 32-35

Foster, MS (2001) Rhodoliths: Betweem Rocks and Soft Places. J. Phycol. 37: 659-667.

Johansen, HW. Coralline, Algae, A First Synthesis. CRC Press, Inc. Boca Raton Florida. 1981.

Marrack, EC (1999) The Relationship Between Water Motion and Living Rhodolith Beds in Southwestern Gulf of California, Mexico. Palios. 14: 159-171

Payri, C. N'Yeurt AR, Orempüller J. Algae of French Polynesia. Edition Au Vent des Iles-Tahiti. 2001. 320 pp.

Steller DL, Foster MS (1995) Environmental factors influencing distribution and morphology of rhodoliths in Bahia Concepcion, B.C.S., Mexico. Exp. Mar. Biol. Ecol. 84: 201-212

Steller DL, Riosmena- Rodiriguez R, Foster MS, Roberts CA (2003) Rhodolith bed diversity in the Gulf of California: the importance of rhodolith structure and consequences of disturbance. Aquatic Conservation: Mar. Freshw. Ecosyst. 13: S5-S20

# Temporal and Spatial Variation in Physical Factors at the Temae Intertidal and Supralittoral Microbial Mats in Moorea, French Polynesia

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**ABSTRACT.** Previous studies of microbial mats have focused on biogeochemistry, hinting at dynamic physical processes without significantly describing the actual conditions. The purpose of this study is to explore, in detail, the temporal and spatial variation in the physical characteristics of microbial mats, and their relation to mat texture zonation. On the island of Moorea, French Polynesia, microbial mats bordered by a marine channel and terrestrial vegetation were selected as the study site. Four parallel transects were established, each with up to 12 sites. Three 48 hour sampling periods were conducted, during which temperature was measured every ten minutes, while salinity and groundwater depth were measured every six hours. Nine microbial mat textures, designated by coloration and morphology, were mapped and divided into three zones based on mat thickness. These zones, which were parallel to the marine channel shore, statistically correlated with and were potentially determined by temperature, salinity, and groundwater depth. These physical factors not only cycled diurnally, but also changed significantly during part of a lunar cycle due to probable seasonal variation. Finally, temperature, salinity, and groundwater depth appear to dynamically interact and play a role in the distribution of the microbial mat zones.

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## Introduction

Microbial mats are laminated sedimentary structures (Krumbein, 1983) formed by microbial communities, usually dominated by cyanobacteria (Stolz, 2000). Also known as algal mats, cyanobacterial mats and potential stromatolites, microbial mats differ from biofilms, which are microbial communities that form on solid surfaces (Stolz, 2000). Microbial mats are literally "an entire ecosystem of organisms" (Golubic, 1992) able to form different specialized mat types and collectively withstand a variety of environments, ranging from hypersaline to freshwater, tropical to polar, and supralittoral to deep sea (Sprachta et al., 2001; Jannasch, 1995). In addition, microbial mats are characterized not only by extreme physical and chemical gradients but also by their stratification into discrete layers (Stolz, 2000). Their versatility is perhaps overshadowed by the knowledge that this community is one of the earliest life forms on Earth, providing a living model for Precambrian microbial communities as old as 3.5 billion years (Golubic, 1992).

Many microbial mats exist in intertidal and supralittoral zones. Fluctuating water and salinity levels provide conditions too extreme for all but a select group of organisms. These conditions also lead to interesting biogeochemical processes and cycles that have been the focus of much study. Examples of major study sites include Hamelin Pool of Shark's Bay, Australia (Golubic, 1992), Laguna Guerrero Negro and Laguna Mormona of Baja California (Horodyski et al., 1977; Javor et al., 1980), and the Gavish Sabkha, Abu Dhabi, and Solar Lake in the Persian Gulf (Golubic, 1991; Gerdes et al., 1985).

Considerable study has been conducted on the biogeochemistry of microbial mats. Research on mat microfabrics, mat growth, and species composition is summarized by Javor et al. (1980). Microfabric studies include detailed structural analysis of the mat in relation to sedimentology, including sediment trapping, binding and precipitation capabilities. Growth studies include field monitoring of mat growth and surveys of different mat community growth structures. Using a range of techniques from transmission electron microscopy of fixed mat samples to isolation and culture of living mat microbes, identification of algal species has also been emphasized. In coastal zones, the cycling of carbon and sulfur has typically been investigated (Mao Che et al., 2001). During 2000, Poetker (2000) conducted a study on the texture variation of intertidal and supralittoral Temae microbial mats of Moorea, French Polynesia. She mapped different texture types, microscopically analyzed the textures, and briefly collected environmental data that allowed her to find that mat thickness had a negative correlation with distance from salt water.

**Figure 1.** Location of Temae microbial mats on the island of Moorea

The purpose of this study is to explore, in detail, the temporal and spatial variation of the physical characteristics of microbial mats, and their relation to mat texture zonation. Well developed and largely undisturbed by humans, the Temae microbial mats are the chosen study site as they are comparable to other studied microbial mats and are able to offer insight into other hypersaline ecosystems around the world. Other studies have hinted at spatial and temporal variation of microbial mat environments, but none have detailed the actual conditions (Golubic, 1991, 1992; Stolz, 2000). The hypotheses being tested are (1) the presence of diurnal variation and variation over part of a lunar cycle in temperature, salinity, and groundwater depth, (2) an effect of the physical conditions of one day onto the next, (3) the correlation of physical factors with distance from the marine channel, tidal cycles, day vs. night, time of the day and mat zonation, and (4) the correlations between and among physical factors with each other.

## Materials and Methods

### *Site description*

The Temae intertidal and supralittoral microbial mats are located near the northeastern tip of Moorea (S 17°28', W 149°46'), French Polynesia (fig. 1). The mats, occupying an area roughly 200 meters wide by 300 meters long (Poetker, 2000) are located on the landmass of Temae. Although connected to the mainland of Moorea at its southern end, Temae is partially separated from the mainland by a marine channel that leads to Lake Temae. Beginning 180 meters north from the southeast end, a reed marsh begins that divides the microbial mats from other vegetation while the eastern border of the mat is lined by coconut trees, hibiscus and *Cassytha* (Poetker, 2000). The remaining perimeter of the mat is bordered by the marine channel.

These microbial mats were chosen for reasons of accessibility, size, similarity to other microbial mats, and borders of both a marine channel as well as terrestrial vegetation. While many microbial mats are remotely located, a road follows the eastern side of the microbial mat. Other microbial mats in Moorea, many often located near stream outlets to the ocean, were too small for the projected scale of this experiment. In contrast, Temae microbial mats were much larger, undisturbed by humans, and well developed. During preliminary literature research, the descriptions of the Temae microbial mats were often similar to other studied microbial mats around the world, allowing for a comparison and contrast of collected data. Finally, the Temae microbial mats present the opportunity to study microbial mats bordered by a marine channel on one side and vegetation on the other. Subsequently, transects were able to span from aquatic to fully terrestrial habitats.

### *Site preparation*

In order to obtain data to spatially characterize the microbial mat, four parallel transects in the direction of 23.5° N NE were established 50 meters apart and designated A, B, C, and D, each. (fig. 2). Within each transect, individual sites were 20 meters apart, numbered from 1 (bordering a marine channel) to a maximum of 13 (bordering a reed marsh). The

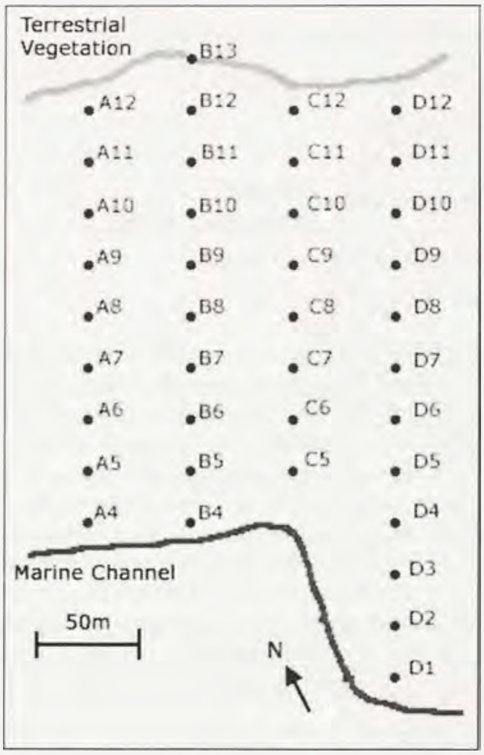

**Figure 2.** Site map

sites were marked by a small portion of the PVC pipe used to measure groundwater depth that remained above the surface. Site A4 is located at S 17°28.798', W 149°46.300' and is at the corner of a total of 39 sites. This section of the mat was chosen for study as preliminary observations showed that it had a relatively shallow water table, allowing for easy access to the groundwater for depth and salinity measurements.

*Measurement program*

In order to obtain data that physically characterized the microbial mat over short-term diurnal fluctuations and over part of a lunar cycle, 48 hour sampling periods were conducted each week for a total of three weeks. The sampling period was longer than a single day to measure correlations between days. Both salinity and groundwater depth were measured every six hours at each site, while temperature was measured more frequently.

To measure groundwater depth, half meter long PVC pipe of 1" outer diameter was placed into the ground at each site. The mud was removed from the interior of each pipe. In addition, holes were drilled along the length of the pipe, which allowed water to freely enter and exit. When measuring groundwater depth, a ruler was lowered into the pipe. The change in the reflection of the water's surface as the ruler hit the water's surface was used to mark and measure the groundwater depth. A small groundwater sample from within the pipe was analyzed using a refractometer to quantify salinity.

Temperature was measured by ACR Smart Button sensors every ten minutes during the sampling period. These sensors are 17mm in diameter and 6mm in height. When attached to a computer, the time between temperature readings can be set and recorded temperatures logged with an accuracy of .5°C. These sensors were installed in seven sites along transect B, buried approximately 6cm below the ground. After the three sampling periods were finished, there was concern that the temperatures recorded in the Poetker study were measured on the surface and were therefore not comparable. In order to quantify the difference between temperatures at different depths in the ground, the sensors were placed on the surface to 15cm below the surface in 3cm increments at site B7 for 1 hour.

*Mat texture & zone designation and mapping*

After the physical characteristics data were obtained, nine different microbial mat textures, defined by surface coloration and morphology, were mapped in the vicinity of the transect lines. The boundaries of the mat textures were noted along the transect lines and then visually estimated for the distance in between the transect lines. Pictures were taken of each texture site. Samples were also obtained of each mat texture for cross-section characterization of stratification and thickness. Zones, not textures, were used for analysis with the environmental data collected in the rest of the study because there were not enough sites of every texture type.

*Data analysis*

Data were analyzed using a variety of methods: mapping, graphing raw data, graphing average values with standard error, analysis of variance, analysis of covariance and linear regression. Maps were used to visualize trends of texture and zone placement. Raw site temperature data for each week was graphed. In most instances, however, data were averaged and graphed with standard error. Analysis of variance was used to determine correlations of each physical factor with the time of day, day vs. night, tides, distance from marine channel, and zonation. Analysis of covariance was used instead to determine correlations between the physical

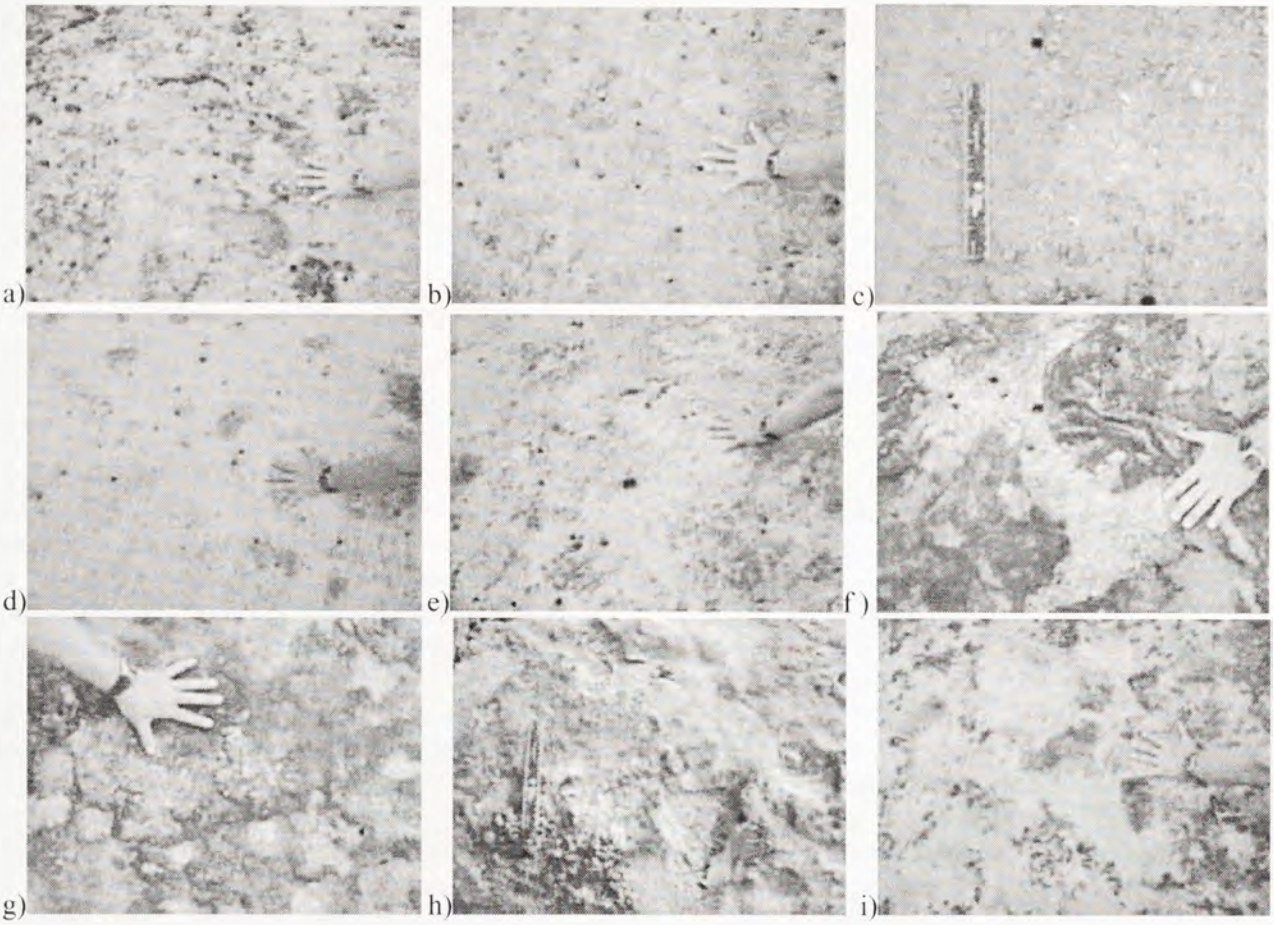

**Figure 3.** Mat texture photos a) brown, b) dark grey, c) matted transition, d) grey, e) black/grey, f) black ripped, g) pink/black, h) pink/grey, i) black mottled

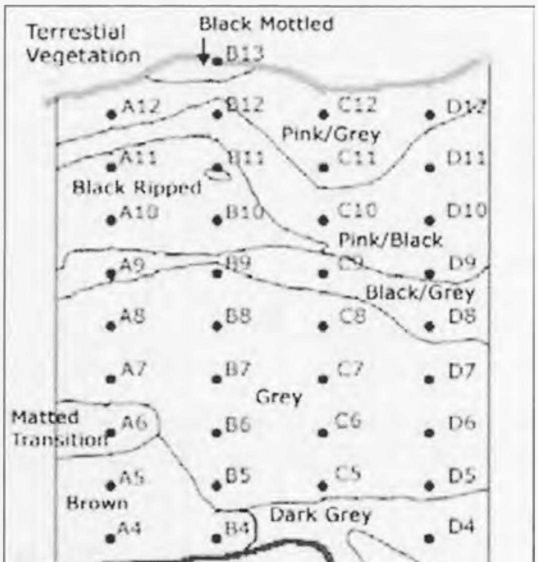

**Figure 4.** Map of mat textures

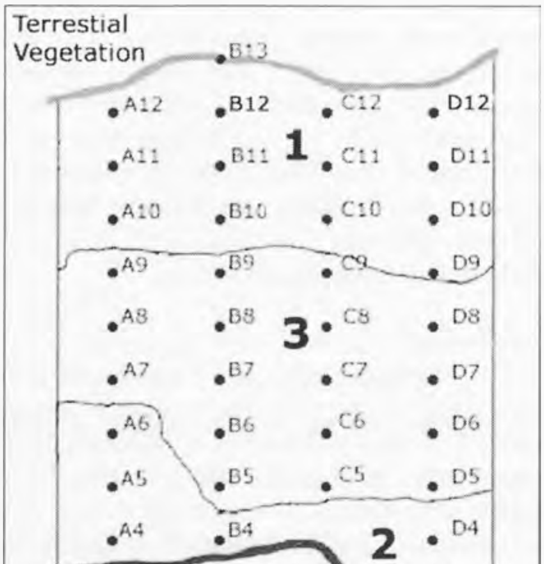

**Figure 5.** Map of mat zonation

**Table 1.** Mat texture type descriptions

| Microbial Mat Texture | Description |
|---|---|
| Brown | Borders marine channel shore, high relief, brown sediment, white sand, few cracks |
| Dark Grey | Moist, no crust, grey sediment, lots of crab holes, extremely soft substratum |
| Matted Transition | grey, sandy sediment, no cracks |
| Grey | dry, sandy sediment, hard surface, infrequent black and grey thin crust |
| Black/Grey | transition texture, black and grey crust with white sediment flecks |
| Black Ripped | black crust on top of grey sediment, prominent rips |
| Pink/Black | continuous black crust with pink splotches, orange layer below crust |
| Pink/Grey | pink, grey and dark grey continuous crust with small rips, orange layer below crust |
| Black Mottled | grey crust, orange and black bumps, orange layer below crust |

factors themselves. Lastly, linear regression was used to determine the extent of correlation of day 1 data on day 2 data, where data from the same time during the two days of the same sampling period were compared.

**Results**

*Mat texture and zones*

Nine microbial mat textures were defined in the study area (fig. 3, table 1). These nine microbial mat texture types, defined by color and morphology, were grouped into three zones based on mat thickness (fig. 4 and 5). Zone 1 has the thickest, most obvious crust and a soft substratum. Stratification exists well below the surface. It includes the black ripped, pink/black, pink/grey, and black mottled mat textures and is found adjacent to the vegetation. Closest to the marine channel, zone 2 includes the brown, dark grey, and matted transition textures of medium thickness. This zone also has a soft substratum, but had a distinctive surface texture with lots of relief. Zone 3 has the thinnest thickness mat textures that include black/grey and grey. The crust, if present at all, is very thin and is based on a hard substratum.

*Temperature*

The data shows that temperature cycles daily (table 2, fig. 6). The temperature peaks around 2 to 4pm and reaches a minimum usually around 6am. In addition, the sites that get the highest temperatures, always in the middle of the mat, seem to have the largest range during their daily cycle. For example, site B7 reached the high temperatures of 38.5°C and 44°C during week 1 and 3 respectively. Both these temperatures were the highest of any site during that week. At the same time, site B7 had a range of 17°C during week 1 and 24°C during week 3, again the highest of any site during that respective week. It is not certain, however, what happened with site B7 during week 2. In addition, the smallest ranges of temperature occur at the edges of transect B, closest to the marine channel or to the vegetation. Generally, the maximum, minimum and range in temperature was specific to site and the week of sampling.

**Table 2.** Weekly temperature minimum, maximum and range at each site

| Week | Site | Mean (°C) | Min (°C) | Max (°C) | Range (°C) |
|---|---|---|---|---|---|
| 1 | B4 | 27.0 | 24.5 | 32.5 | 8 |
| | B5 | 28.8 | 24.5 | 32.5 | 8 |
| | B7 | 29.5 | 21.5 | 38.5 | 17 |
| | B9 | 29.6 | 24.5 | 34.5 | 10 |
| | B10 | 28.8 | 21 | 33.5 | 12.5 |
| | B12 | 29.6 | 20 | 35 | 15 |
| | B13 | 26.4 | 23 | 33.5 | 10.5 |
| 2 | B4 | 27.3 | 23.5 | 29.5 | 6 |
| | B5 | 28.3 | 23 | 34 | 11 |
| | B7 | 28.0 | 24 | 31 | 7 |
| | B9 | 28.2 | 23 | 34 | 11 |
| | B10 | 27.6 | 23.5 | 31 | 7.5 |
| | B12 | 27.7 | 23.5 | 30.5 | 7 |
| | B13 | 27.0 | 24 | 29.5 | 5.5 |
| 3 | B4 | 24.9 | 21 | 29.5 | 8.5 |
| | B5 | 25.3 | 20.5 | 33 | 12.5 |
| | B7 | 28.0 | 20 | 44 | 24 |
| | B9 | 25.1 | 20.5 | 31.5 | 11 |
| | B10 | 24.6 | 20.5 | 29.5 | 9 |
| | B12 | 26.3 | 24 | 28.5 | 4.5 |
| | B13 | 24.2 | 20.5 | 28 | 7.5 |

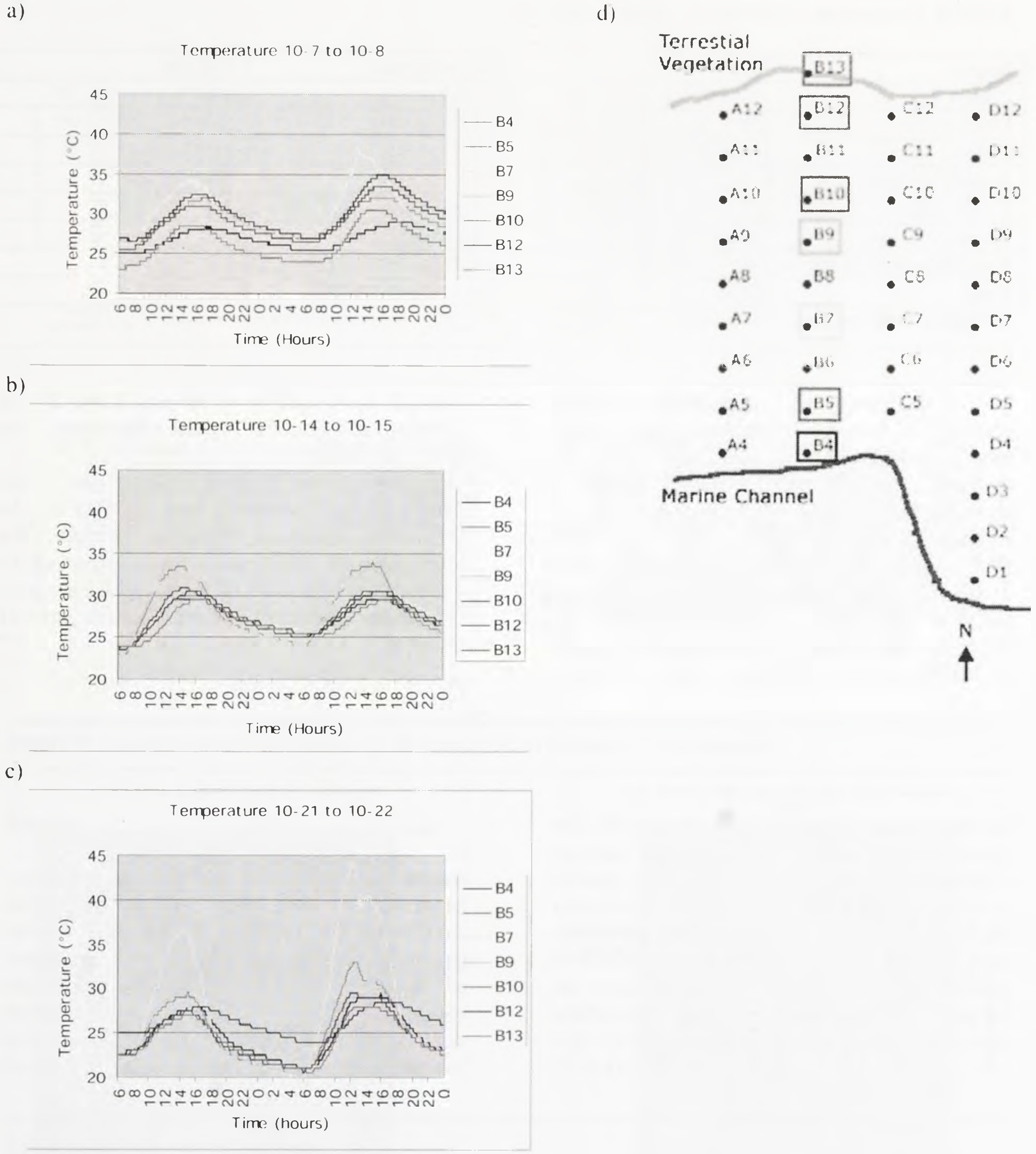

**Figure 6.** Temperature results a) week 1, b) week 2, c) week 3, d) location of each site where temperature was measured in matching colors to the graphs

**Table 3.** Temperature ANOVA results ($R^2$=.541)

| Source | d.f. | Mean Square | F-Ratio |
|---|---|---|---|
| Zone | 2 | 20.63 | 3.6** |
| Daynight | 1 | 557.51 | 98.0* |
| Tide | 1 | 32.40 | 5.7** |
| Zone*Daynight | 2 | 28.17 | 5.0** |
| Zone*Tide | 2 | 13.58 | 2.4 |
| Daynight*Tide | 1 | 14.00 | 2.5 |
| Zone*Daynight*Tide | 2 | 15.71 | 2.8 |
| Error | 156 | 5.68 | - |

*P<0.001, **P<0.05

Analysis of variance revealed correlations between temperature and several other environmental factors (table 3). For example, analysis of variance showed a significant correlation of temperature with the different zones (P<0.05), day vs. night (P<0.001), and low vs. high tides (P<0.05) (table 3). The graphical representation of the average values of temperature for each site at either day vs. night (fig. 7) shows the highest temperature during the day was in the middle of the mat at site B7. In contrast, at night, the highest temperature was found at site B12.

A vertical temperature test was performed on a relatively cold day (fig. 8). As the depth increased from the surface, the temperature first decreased at 3cm. From 6cm to 12cm, however, the temperature increased. Finally, the temperature decreased at the depth of 15cm.

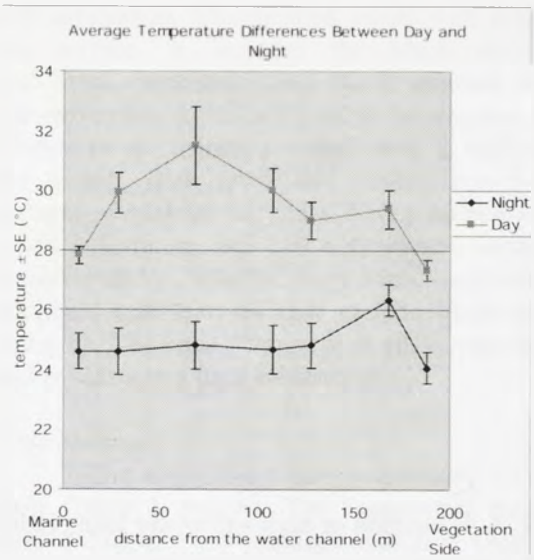

Figure 7. Average temperature differences between day and night

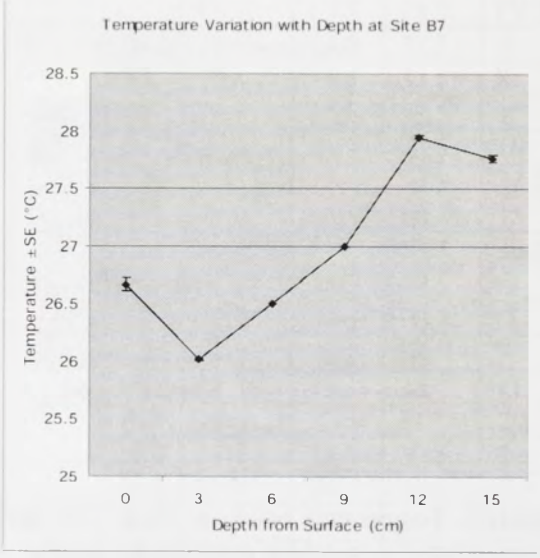

Figure 8. Temperature variation with depth at site B7

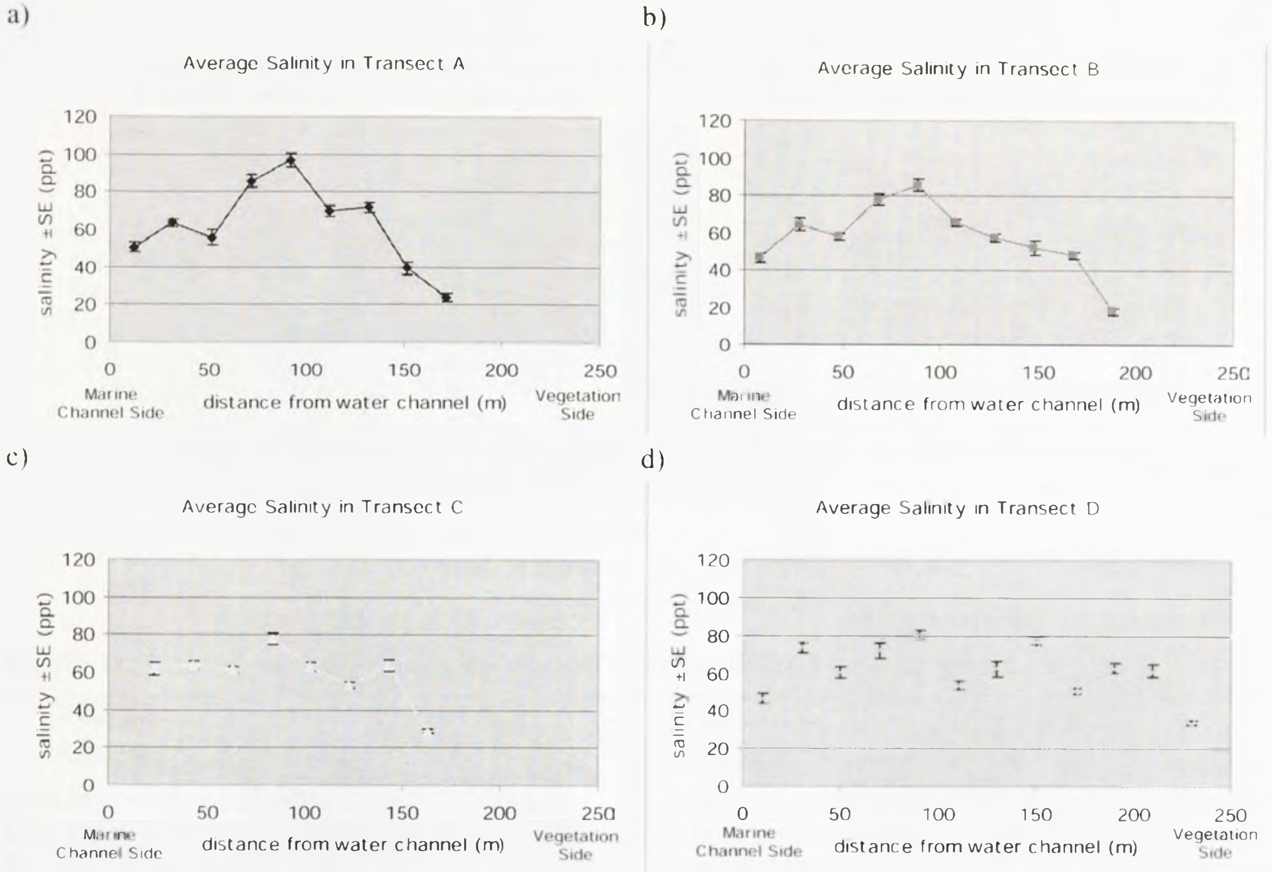

**Figure 9.** Average salinity a) transect A, b) transect B, c) transect C, d) transect D

*Salinity*

Although salinity patterns were not consistent from transect to transect, several inferences can be made from the averaged salinity data (fig. 9). First of all, there is an immediate drop in salinity when reaching vegetation, to around 25ppt. Similarly, on the marine channel side, the salinity is usually around 45ppt. In addition, there is a clear increase in salinity in the middle of each transect with the exception of transect D, which shows an increase and decrease in salinity several times. Salinity values at the same site also showed a variation from week to week. Finally, salinity correlated strongly with time (6,12,18,24) ($P<0.001$), zones ($P<0.001$), and distance from the water channel ($P<0.001$) (table 4). Salinity additionally showed a slight trend with day vs. night ($P=0.1$), but no correlation with tidal cycles ($P>0.1$) (table 4).

**Table 4.** Salinity ANOVA results

| Source | R^2 | d.f. | Mean Square | F-ratio | Error | |
|---|---|---|---|---|---|---|
| | | | | | d.f. | Mean-Square |
| Time | 0.023 | 3 | 3377.11 | 7.43* | 932 | 454.62 |
| Day/Night | 0.003 | 1 | 1258.65 | 2.72 (P=0.1) | 934 | 463.15 |
| Zone | 0.233 | 2 | 50487.60 | 141.51* | 933 | 356.77 |
| WaterDis | 0.598 | 38 | 6832.57 | 35.182* | 897 | 194.21 |
| Tide$ | 0.001 | 1 | 336.720 | 0.73 | 934 | 464.14 |

*P<0.001, **P<0.05

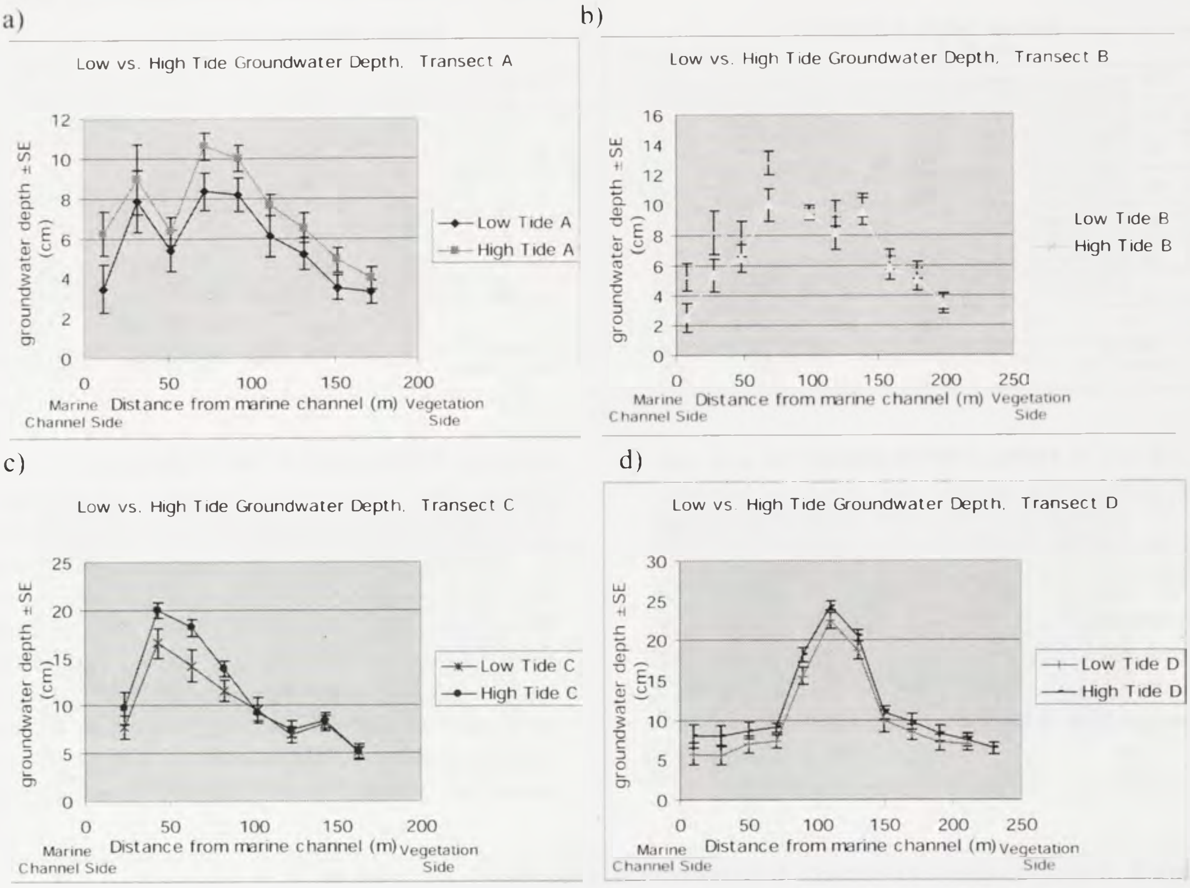

**Figure 10.** Low vs. high tide groundwater depth

*Groundwater depth*

Similar to salinity and temperature data, the graphical representation of groundwater depth data elucidates many trends that can be statistically clarified (fig. 10). For example, although graphs show the odd result that low tide groundwater depth is closer to the surface than high tide groundwater, ANOVA shows no statistical difference between low and high tide for groundwater depth (P>.05) (table 5). However, groundwater depth definitely peaks in the middle of each transect, which is verified by the significant correlation between groundwater depth and distance from the water channel (P<0.001) and zonation (P<0.001) (table 5). The zones that I chose when mapping also seem to correlate well with groundwater depth as does the time of the day (P<0.05) (table 5). In addition, groundwater depth values at the same site showed high variation from week to week.

**Table 5.** Groundwater Depth ANOVA results

| Source | R^2 | d.f. | Mean Square | F-ratio | Error | |
|---|---|---|---|---|---|---|
| | | | | | d.f. | Mean-Square |
| WaterDis | 0.66 | 38 | 498.54 | 43.065* | 858 | 11.58 |
| Tide$ | | 1 | 1.30 | 0.112 | | |
| Waterdis*Tide$ | | 38 | 5.43 | 0.469 | | |
| Zone | 0.25 | 2 | 3603.53 | 153.68* | 933 | 23.45 |
| Time | 0.01 | 3 | 124.64 | 4.046** | 932 | 30.81 |

*P<0.001, **P<0.05

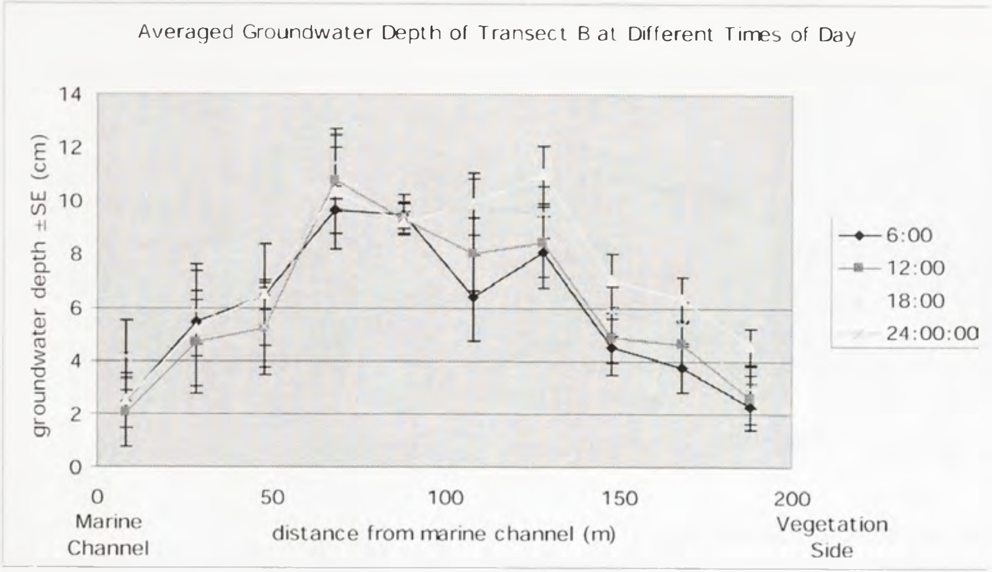

**Figure 11.** Average groundwater depth of transect B during different times of the day

Groundwater depth may have a more complex relationship with the time of the day (fig. 11). Closer to the vegetation side in transect B, the groundwater depth has an ordered relationship with day of the time. Starting at 6am, the groundwater depth increases to 12 noon and then reaches a maximum at 6pm. The groundwater depth then decreases at 12 midnight. Near the marine channel, however, there is no clear trend that describes the effect of time on groundwater depth for several sites. The groundwater data of each site was statistically analyzed using ANOVA with the time of day of each measurement (table 6). No significant correlations were found.

**Table 6.** ANOVA results of Transect B sites with time

| Source | R^2 | Analysis of Variance with Time (Df=3) | | | Error (Df=20) |
|---|---|---|---|---|---|
| | | Mean Square | F-ratio | P | Mean-Square |
| B4 | 0.077 | 6.332 | 0.649 | 0.557 | 11.367 |
| B5 | 0.031 | 3.843 | 0.213 | 0.886 | 18.032 |
| B6 | 0.030 | 2.844 | 0.205 | 0.892 | 13.893 |
| B7 | 0.036 | 3.210 | 0.251 | 0.860 | 12.814 |
| B8 | 0.010 | 0.129 | 0.069 | 0.976 | 1.875 |
| B9 | 0.196 | 16.815 | 1.627 | 0.215 | 10.332 |
| B10 | 0.156 | 10.323 | 1.230 | 0.325 | 8.390 |
| B11 | 0.165 | 7.718 | 1.316 | 0.297 | 5.865 |
| B12 | 0.196 | 7.205 | 1.625 | 0.215 | 4.433 |
| B13 | 0.186 | 6.122 | 1.528 | 0.238 | 4.007 |

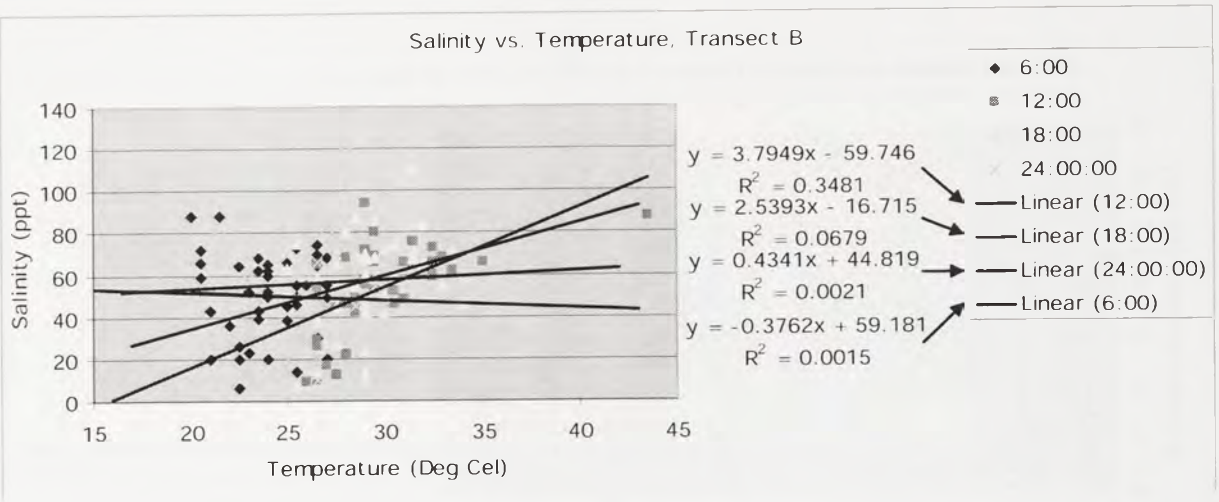

**Figure 12.** Salinity vs. temperature at transect B

### *Temperature, salinity, and groundwater trends*

Salinity vs. temperature data changed depending on the time of the day (figure 12). This was verified using two methods. Linear regression lines of each set of data from the different times of the day showed different slopes and $R^2$ values. The calculated slope was actually negative at 6am, but increased to a positive slope for 12 midnight and further increased for 6pm and then 12 noon. $R^2$ values also increased in the same order, implying that temperature has more significant correlation with salinity, the hotter the time of the day. Therefore, the most significant correlation is at 12 noon. However, analysis of covariance shows that salinity correlated strongly with the temperature ($P=0.002$), but not clearly with the time of the day ($P=0.200$) (table 7).

Groundwater depth correlates with salinity ($P<0.001$), but not with temperature ($P=0.293$) (table 8 and 9).

**Table 7.** Analysis of covariance of salinity and temperature ($R^2$=0.074)

| Source | d.f. | Mean Square | F-ratio |
|---|---|---|---|
| Time | 3 | 678.66 | 1.57 |
| Temp (covariate) | 1 | 4336.60 | 10.01** |
| Error | 160 | 433.22 | - |

*P<0.001, **P<0.05

**Table 8.** Analysis of covariance of groundwater depth and temperature ($R^2$=0.513)

| Source | d.f. | Mean Square | F-ratio |
|---|---|---|---|
| Time | 3 | 28.19 | 2.76** |
| Temp (covariate) | 1 | 11.39 | 1.17 |
| Error | 136 | 10.21 | - |

*P<0.001, **P<0.05

**Table 9.** Analysis of covariance of groundwater depth and salinity ($R^2$=0.289)

| Source | d.f. | Mean Square | F-ratio |
|---|---|---|---|
| Zone | 2 | 2545.66 | 113.45* |
| Time | 3 | 67.69 | 3.02** |
| Zone*Time | 6 | 15.10 | 0.67 |
| Salinity (covariate) | 1 | 317.04 | 14.13* |
| Waterdis | 1 | 410.11 | 18.28* |
| Error | 922 | 22.44 | - |

*P<0.001, **P<0.0

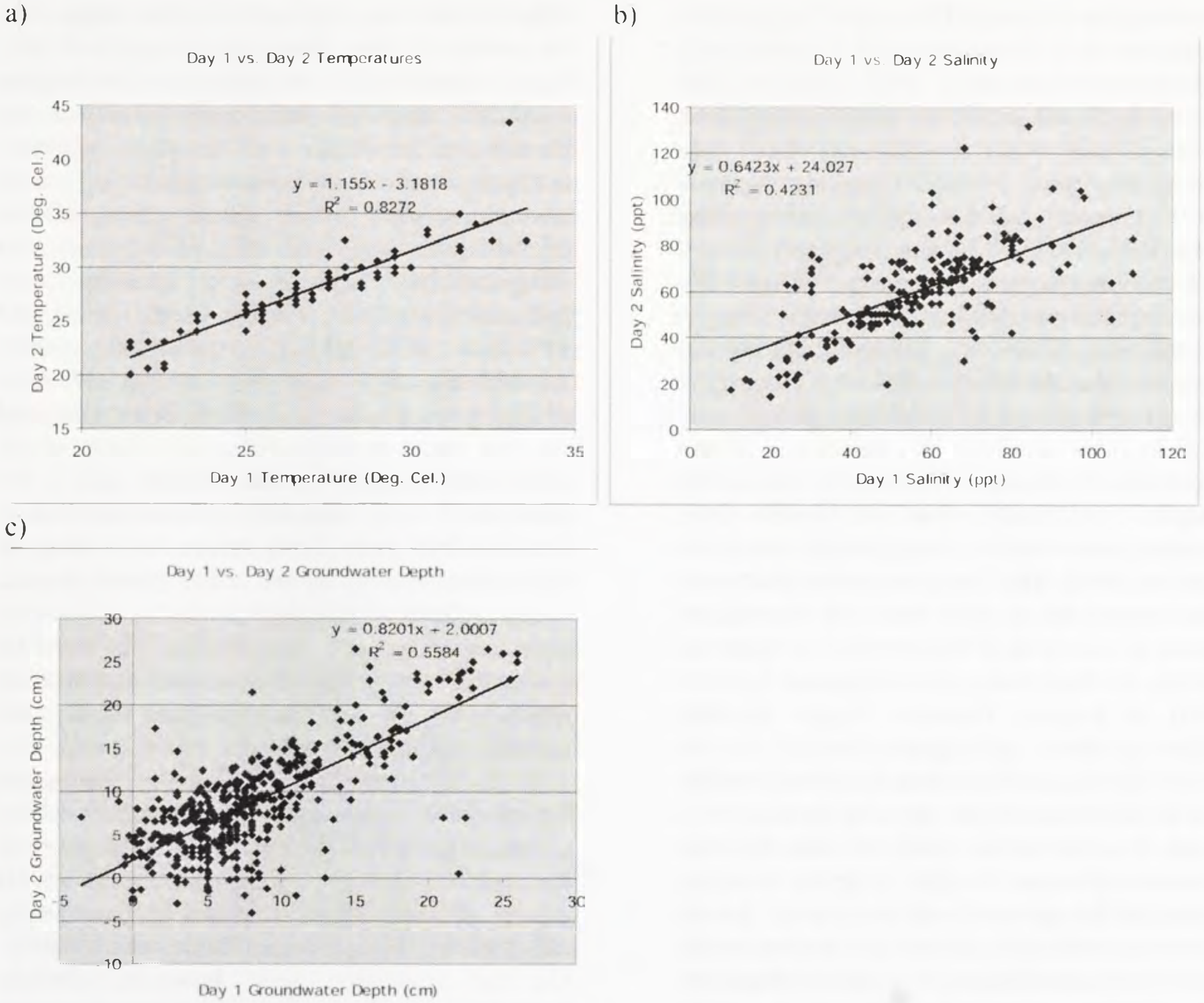

**Figure 13.** Day 1 vs. day 2 physical factor graphs a) temperature, b) salinity, c) groundwater depth

*Day 1 and 2 analysis*

Linear regression analysis shows that the relationship of day 1 vs. day 2 temperatures, groundwater depths and salinities are significant (fig. 13). The relationship between the same time of day between the first and second days of each sampling period is most significant with temperature ($R^2$=0.8272), less significant with groundwater depth ($R^2$=0.5584), and somewhat less with salinity ($R^2$=0.4231).

## Discussion

*Mat Textures and Zones*

The importance of physical and chemical factors accounts for the "spatial variation in microbial community structure" (Rothrock et al., 2002). This study's findings that temperature, salinity and groundwater depth show strong correlations with microbial mat zonation support this statement. In addition, the zones, with boundaries essentially parallel to the shore, clearly correlate with distance from the marine channel as evidenced in figure 5. All these factors—temperature, salinity, groundwater depth and distance from the marine channel—are interconnected and form different habitats that are more suited for certain mat zones. This supports Golubic's suggestion that mat zonation is the result of temperature and water availability gradients (1992). Microbial mats zonation is also based on microscopic factors. Success and failure of a particular species out of the many that form a microbial mat, however, is due to the interaction of physical and chemical factors (Golubic, 1992; Stolz, 2000). These different species distributions and abundances result in the different mat types.

The correlation of microbial mat diversity to the extent of "extremeness" is not clear. Rothrock (2002) believes that both extreme and normal conditions tend to decrease microbial mat diversity. This would suggest that the Temae microbial mats exist in moderately extreme conditions as a wide range of mat textures are found there. In contrast, others have expressed that many distinct microbial mat texture are typical of an extreme environment with high salinity and temperature (Sprachta, 2001). Thus, although it is not perfectly clear if the Temae microbial mats exist in very extreme or moderately extreme conditions, the physical and chemical factors do influence the spatial zonation of the microbial mats.

Other microbial mats around the world also seem to have similar zonation and mat texture types to the microbial mats in Temae. For example, in Hamelin Pool of Shark's Bay, Australia, nine coastal zones parallel the shore (Golubic, 1992). The Temae microbial mat zones are also parallel to the shore of the marine channel as are most of the mat texture types. In addition, the three mat zones designated by Javor (1980) at Laguna Guerrero Negro in Baja California show striking similarities to the Temae mat zones. For instance, Javor's middle zone is the thinnest mat type as is zone 3 in Temae. In addition, the furthest zones from the salt water sources in both Laguna Guerrero Negro and Temae are black and crusty. As salt marshes are all similar in that they have a source of salt water, the zonation of genera and species, and therefore microbial mat zonation, is usually similar (Javor et al., 1980).

Surprisingly, many differences were found when comparing results to the Poetker study of 2000. Poetker (2000) noted that mat growth patterns, texture, and color all changed as the distance from the marine channel increased. Most mat textures boundaries are parallel to the shore in this study, but Poetker's mat texture map shows that many of her zones were perpendicular to the shore (2000). In addition, she seemed to have at least grouped the brown, grey, and dark grey mat textures into one texture type. These textures are easily discernable at the microbial mat. Perhaps, the filling in of marshland north of the airport since the Poetker study changed microbial mat environmental conditions to the point of affecting mat texture distribution. This potentially explains the disparity in results between the two studies.

### *Temperature*

The most obvious observation from the temperature data was its clear daily cycling and variation over a larger time scale. Diurnal patterns at the microbial mats are most likely linked to the changing input of solar energy over the period of a day. These diurnal cycles of light, largely manifested in temperature values ranging from 20°C to 44°C, have profound effects on biochemical processes such as photosynthesis, nitrogen fixation, and methanogenesis, which also show daily cycles (Stolz, 2000). Other microbial mats such as the Gavish Sabkha and in Rangiroa show daily variation in temperature from 24°C to 38°C (Gerdes et al., 1985) and 31°C to 36°C (Mao Che et al., 2001) respectively. The changing amount of solar energy over seasons, as well as other tidal and weather variation, also changes the temperature values and ranges. This was evident even in the small three week sampling period conducted at the microbial mats. Furthermore, the timing of the maximum temperature of the microbial mats being around 2 to 4pm and the minimum temperature at 6am, instead of at the times of maximum and minimum sun exposure respectively, is evidence of the high heat capacity of the microbial mats.

Changing amounts of evaporation across the microbial mat also led to trends along transect B. Temperature was always highest in the middle of the mat. Temperature was lowest on the marine channel side due to the cooling effect of the marine water (Gerdes et al., 1985). On the vegetation side, however, shallow groundwater indicated that water was somehow also being supplied to this area. The additional information that low salinity was present near the vegetation creates a possibility that an aquifer connects the vegetation side of the microbial mat with the nearby mountain, located on the opposite side of the marine channel. This may also be caused by the normal freshwater lens, which forms under motus (McLane et al., 2002) Where water was scarce, a temperature change was unable to be neutralized and led to harsh increases and decreases in temperature over a short period in time. Site B7, located near the middle of the mat, had the highest day temperature and range during week 1 and 3. While, the maximum day temperature remained in the middle of the mat, the interruption of this site B7 trend during week 2 was probably due to the unusual change in tidal height and rainy weather observed.

The maximum temperature across a transect occurs at different sites during the day than at night. The site of maximum temperature during the night was found to be closer to vegetation. Temperature may be equalizing everywhere that water is freely circulating during the night, when evaporation is minimal. This temperature equalization would occur in microbial mats part of the marine water circulation or part of the fresh water circulation near the vegetation. Sections of the mat that are between these two circulations, however, have no way to significantly release their accumulated heat energy from the day, effectively causing them to have higher temperatures. During the day, evaporation of groundwater releases heat energy from the microbial mats. Therefore, microbial mats with limited groundwater to evaporate will have higher temperatures. This location is closer to the marine channel.

In addition, temperature correlates with tidal fluctuations and mat zonation. The greater abundance of water during high tide led to a larger cooling effect over most of the microbial mats. The range of temperatures at the mat, as affected by tides and other environmental factors, can be tolerated by the microbial mats as long at the temperatures allow for the presence of liquid water (Stolz, 2000). The Temae microbial mats showed an interesting correlation of mat zonation with temperature, which was not present in the Gavish Sabkha (Gerdes et al., 1985). This correlation potentially shows how different mat zones with different species compositions prefer different temperature characteristics.

Vertical temperature changes within the mat on a colder day showed that the temperature was higher within the mat than on the surface. Therefore, the mat is likely an insulator, warmer below the surface on a cold day, and cooler below the surface on a hot day. The model of the mat as an insulator is also supported by the higher temperature at midnight than at 6am. Residual energy from the day still remains with the mat at midnight, but is dissipated by 6am. Regardless of the reason, temperature varied by as much as 2°C as depth from the surface increased. On a hot day, temperature variation could increase significantly within the mat. This variation is a source of error because although the sensors were buried at approximately 6cm below the surface, this depth was not measured during the 48 hour sampling periods and could have been off by as much as 3cm.

Other studies, which probably collected their data at the mat surface, showed that the temperature data obtained at the Temae microbial mats was reasonable. For example, the range of temperatures reported by the 2000 Poetker study ranged from 27°C to 48°C. The temperatures measured in this and the Poetker studies were measured during the same month of the year and therefore are highly comparable. The slightly higher temperatures obtained by Poetker are likely caused by her lack of night data and sampling at the surface. If my measurements of hot days were taken on the surface, the temperatures likely would have been recorded as a few degrees higher. Furthermore, if this study has measured temperature where the highest salinity and deepest groundwater depths predicted the most extreme temperature on transects other than transect B, temperatures at least as high as the 48°C from the Poetker study would almost certainly have been recorded. The Temae microbial mats, however, are cooler than other microbial mats such as Solar Lake where temperatures as high as 62°C have been reported. Nonetheless, temperature must be measured at the Temae microbial mats in the summer to be certain.

### *Salinity*

Like temperature, salinity clearly follows a diurnal and seasonal cycle. This daily cycling, supported by statistical correlations of salinity with the time of the day and day vs. night, is probably due to evaporation occurring during the day. After increasing during the day, the salinity at a particular site decreases during the night because of an equilibration with water being input into the system that isn't immediately lost by evaporation. Although tidal cycles theoretically could have a major impact on salinity, the lack of correlation of salinity with high vs. low tides supports the prominent role of evaporation in salinity cycling. Seasonal salinity variation caused by weather and tidal influences, complicates this daily cycle over a longer period of time. This was observed during the three weeks of data collection. During the most saline time of the year, the late summer and fall period, the microbial mats are inactive, but less saline periods allow the growth of cyanobacteria. The lamination of microbial mats is evidence of the differential growth caused by these seasonal salinity changes (Bowen et al., 2001; Friedman et al., 1985; Javor et al., 1980).

Several trends across the transects are apparent such as salinity dropping to near 25ppt near the vegetation, which is not considered hypersaline (Gerdes et al., 1985). This sudden and consistent drop in salinity can be explained by either freshwater input from an aquifer (Gavish et al., 1985), or by plant mechanisms that lower salinity. As the groundwater depth is progressively shallower near the vegetation, freshwater input seems more likely. Therefore, the lower salinity is probably what allows the plants to live in this area.

Next, the salinity is always around 45ppt near the marine channel. This value of salinity is considered metahaline as it is of a higher salinity than sea water without exceeding 70ppt (Gerdes et al., 1985). Adjacent to the marine channel, the microbial mats are constantly inundated with salt water. Therefore, the salinity of the microbial mats is similar to the salt water. Usually, ocean water in French Polynesia is around 36ppt (Sprachta et al., 2001). As the marine channel is subject to intense radiation and is shallower than the open ocean, however, it is more saline (Golubic, 1992).

Ultimately, the highest salinities at the microbial mats are found in the middle of the transects, where the highest temperatures and most evaporation occurs. The salinities are usually metahaline and alpha-hypersaline (70-100ppt). Rarely, values barely gamma-hypersaline (140-300ppt) (Gerdes et al., 1985) were recorded during this study. However, during the hottest and driest times of the year, it is possible that salinities surpass gamma-hypersaline somewhere at the Temae microbial mats. Transect D, however, exhibited more complex behavior, peaking to equal salinity values at several sites at the same point in time. Perhaps this deviation from the single peak in salinity of the other transects is due different groundwater dynamics. Transect D is located near the drier section of the Temae microbial mats and spanned a larger distance, warranting further investigation for full comprehension.

According to other studies, the Temae microbial mats are in the middle of the span of salinities experienced by other microbial mats. At the Gavish Sabkha and Solar Lake, the salinity ranged from 50 to 300ppt (Gerdes et al., 1985). However, these high salinity values were obtained by a special water pump that allowed them to sample water in the mat above the groundwater table (Gavish et al., 1985). Similar techniques at Temae would have also yielded higher salinity values. In contrast, microbial mats in Rangiroa, French Polynesia show exceptionally low salinity ranges from 5 to 7ppt and 20 to 28ppt (Mao Che et al., 2001). Nevertheless, the previous study at the Temae microbial mats reported an average salinity of 68ppt, which is comparable to the results of salinity collected at Temae for this study. Finally, reported salinities for the Laguna Mormona microbial mats range from 30 to 115ppt (Horodyski et al., 1977). This range of salinity is very similar to what was found during this study of the Temae microbial mats. In addition, unicellular green algae were observed growing in salinities between 19 and 30ppt at Laguna Mormona (Horodyski et al., 1977). After significant rain at the Temae microbial mats, salinity was lowered and green algae were also observed colonizing the surface of the microbial mats.

### *Groundwater depth*

Microbial mats were additionally influenced by the daily and seasonal cycling of groundwater depth. A statistical correlation of groundwater depth with the time of the day was found, resulting from the general effect of evaporation and solar energy input. Groundwater depth cycling is actually essential to microbial mat growth because the dropping water level allows air to enter the mat (Golubic, 1992). This air provides enough oxygen to support bacterial aerobic respiration (Golubic, 1992). Although the sampling period of three weeks was not long enough to be completely conclusive, groundwater depth most likely exhibits seasonal cycling that is the cause of tidal and weather changes. At the Gavish Sabkha and Laguna Mormona, for example, the microbial mats are usually flooded in April and desiccated by October (Friedman et al, 1985; Horodyski et al., 1977). The configuration of the shoreline and groundwater level is clearly seen to change with the seasons (Friedman et al, 1985). In addition, the laminations of the mats can also be evidence of differential growth periods of the microbial mats because of cyclic desiccation (Javor et al., 1980).

Significant variation is also present across a transect at the Temae microbial mats. The groundwater depth, first of all, clearly peaks in depth near the middle of the transect. This portion of the microbial mats is furthest away from the salt water source and the assumed freshwater source near the vegetation. In addition, the middle of the microbial mats experiences the highest temperatures and therefore more evaporation. It is also possible that since groundwater was measured relative to the mat surface and the microbial mat was assumed to be flat, a difference of a few centimeters over 200 meters in distance could account for the change in groundwater depth across a transect. However, the repeated cycle of microbial mat drying with wind action, and rain with uniform sediment deposition causes the microbial mat surface to be completely flat (Golubic, 1992). Thus, the trend of deeper groundwater in the middle of the transects is significant.

At the same time, the behavior of the mat adjacent to the marine channel and the mat adjacent to the vegetation has both similarities and differences. Both these portions of the microbial mats have shallow groundwater depth as they are close to water sources. However, near the marine channel, the tidal cycles primarily influence the groundwater depth. It is here that transect B sites show that there isn't a significant correlation of groundwater depth with the time of the day. This lack of correlation is reasonable because the tides are at equal height twice a day. In contrast, at the vegetation side of the mat, the groundwater depth is more closely tied to the time of the day. Here, evaporation plays a key role as groundwater depth increases after midnight and begins decreasing only after 6pm.

According to other studies, the groundwater values obtained at the Temae microbial mats are reasonable. For example, the previous Temae study found values of groundwater depth from 17.6cm to 27.86cm below the surface (Poetker, 2000). Although these values seem very deep in comparison to the more recent data, Poetker's method of digging a hole until seeing water probably did not allow the groundwater table sufficient time to equilibrate. She also stayed closer to the drier, southern portion of the Temae microbial mats where the groundwater depths are usually lower. In addition, the Horodyski et al. (1977) study's description of the Laguna Mormona microbial mats shows a striking resemblance to Temae, allowing for some comparison between the two systems. Neither Temae nor Laguna Momona experiences current and wave action. Shrinkage cracks are also present in both locations due to localized desiccation. At Laguna Mormona, the change in groundwater depth over the course of a day was found to be several millimeters (Horodyski et al., 1977). While this was the case close to the marine channel at Temae, where evaporation held a greater influence, the range of groundwater depths was greater than at Laguna Mormona. The week to week variation of groundwater depth at Temae was several centimeters and was similar to change experienced at Laguna Mormona over a fortnightly tidal cycle (Horodyski et al., 1977). Furthermore, Horodyski et al. (1977) noticed at Laguna Mormona that a "one centimeter drop in water level will cause an intermittently emergent active mat to become generally emergent, highly desiccated, and inactive." There were also many locations on the Temae microbial mats where a difference in just one centimeter of groundwater depth signaled a considerable change in mat texture.

Other studies have noted the similar influence of groundwater on the microscopic elements of the microbial mat. For example, desiccation induces formation of sheath material that stores water (Stolz, 2000 and references therein). Water can have even more complex effects at microbial mats. The rate of water flow and water availability can determine whether a site is colonizable, the shape of resulting structure and life span of structure (Stolz, 2000 and references therein). Furthermore, in the intertidal mats of Abu Dhabi, water shortage is seen to directly affect production rates, while decomposition is more sensitive to drainage patterns (Golubic, 1991).

### *Temperature, salinity, and groundwater trends*

Temperature and salinity are strongly correlated. This correlation is present because evaporation is related to temperature of the mat and increases salinity. During his study of temperature and salinity in the ocean, Levitus (1989) explained that thermodynamics causes a perfect correlation of temperature and salinity. In addition, at the Gavish Sabkha, temperature and salinity gradients are related, either both exhibiting stability or instability (Gerdes et al. 1985). Furthermore, the difference in temperature and salinity relationships depending on the time of the day (fig. 12) is logical. During the day, higher temperatures are correlated to high evaporation, which increases salinity. Data showed that sites with the highest temperatures usually have the highest salinities. At night, the sites of highest day temperatures may actually have the lowest or near the lowest temperature while salinity may not have changed much from the day. Therefore a negative correlation may exist

Temperature and groundwater depth did not exhibit a significant correlation in this study. Although higher temperatures increase evaporation, which would lower groundwater depth, this trend may not be linear. Therefore, it would not be recognized by the analysis of covariance statistical test. Even so, the possible relationship between temperature and groundwater depth can easily be interrupted by tidal changes and rain, making it harder to determine if a correlation existed. Ultimately, however, although salinity correlates with both temperature and water depth, temperature and water depth do not correlate with each other.

Groundwater depth and salinity show a strong correlation. Usually, a microbial mat that can withstand high salinity can survive desiccation. At the Gavish Sabkha, for example, nodules exist that prefer both high salinity and deep groundwater levels (Gerdes et al., 1985). This is probably due to the possibility that where there is deeper groundwater, the salt in what little water remains gets concentrated. Furthermore, both salinity and groundwater depth cycle seasonally together. For instance, salinity increases from late winter to late fall at the Gavish Sabkha. In very late fall and winter, the rise of the water level is accompanied by a decrease in salinity (Friedman et al., 1985). This seasonal cycling of both salinity and groundwater depth almost certainly occurs at Temae although the sampling period was too short to be conclusive.

### *Day 1 and 2 analysis*

If the previous day's value in a physical characteristic is particularly low or high, a correlation is seen with the values of the next day. Although strong with all studied physical factors, the day to day correlation was particularly great with temperature, less so with groundwater depth, and least with salinity. Temperature, largely determined by weather, does not change rapidly enough to interfere with relationships between day 1 and day 2. Groundwater depth is similarly stable because tidal heights do not change significantly from day to day. In addition, it rained little during the sampling period while the large rain storms could have introduced significant changes from day to day. Salinity, however, has a more complex relationship depending on both groundwater and temperature. The input of freshwater by some rain is quickly absorbed by the groundwater system, but dilutes the salinity at a fast pace. At the same time, this rain may hardly impact the temperature of the microbial mat system. In contrast, an increase in temperature will raise evaporation rates to concentrate salinity. Therefore, the complex dependence of salinity on both groundwater and temperature dynamics reduce the day to day correlation of salinity.

### *Future work*

Many further studies could be conducted at the Temae microbial mats. Microbial composition, for one, could be analyzed of each mat texture type, verifying differences between texture types. In addition, certain mat textures such as the grey textures look like dry mud. The microscopic analysis of this texture type could prove whether this area is or is not microbial mat. Data could also be gathered from different seasons for comparison and to assess patterns of a larger time scale. Furthermore, gathering weather and tidal height data, while also measuring temperature, salinity and groundwater depth at the microbial mat, would allow clearer conclusions about the influence of environmental factors on the physical factors of the microbial mat. An additional study could also link values of temperature, salinity and groundwater depth to rates of mat growth. Finally, models and empirical equations of the physical dynamics of the microbial mats could also be developed.

### *Fate of Temae Microbial Mats*

Unfortunately, the Temae microbial mats are destined to become a golf course within the near future. It is regrettable that these microbial mats are going to be destroyed as changing the substrate salinity and hydrology to allow for the growth of normal, low saline soil plants will prove extremely difficult and costly. Furthermore, the natural state of microbial mats holds several alternative uses that do not require destruction. Krumbein (1985), for example, summarizes the possibilities of microbial mats to be altered slightly to produce salt, mined for accumulated heavy metals and phosphates, cultivated for nitrogen for animal food pellets, and farmed as a form of salted soil agriculture, which already occurs in the southern hemisphere. In addition, microbial mats prevent erosion, by biostabilizing the sediment below (Nofke et al., 2003). In the end, microbial mats are a long established and fascinating ecosystem that exhibits a unique beauty.

## Conclusions

Zonation based on mat thickness correlates with temperature, salinity, and groundwater depth. All of these physical factors also cycled diurnally, but changed significantly during part of a lunar cycle due to probable seasonal variation. In addition, the physical conditions of one day at a certain time were shown to correlate with the physical conditions of the next day at the same time. Temperature also correlated with low and high tide, while both salinity and water depth significantly correlated with the distance from the marine channel. Groundwater depth & salinity, and salinity & temperature show additional correlations. Finally, temperature, salinity, and groundwater depth dynamically interact and play a critical role in the distribution of the microbial mat zones.

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## LITERATURE CITED

Bowen MM, Geyer WR (2001) Salt transport and the time-dependent salt balance of a partially stratified estuary. Journal of Geophysical Research. 108(C5 3158): 27-1 to 27-15.

Friedman GM, Sneh A, Owen RW (1985) The Ras Muhammad Pool: Implication for the Gavish Sabkha. In Friedman GM, Krumbein WE (eds) Hypersaline Ecosystems. Springer -Verlag, Berlin, Heidelberg, 218-237.

Gavish E, Krumbein WE, Halevy J (1985) Geomorphology, Mineralogy and Groundwater Geochemistry as Factors of the Hydrodynamic System of the Gavish Sabkha. In Friedman GM, Krumbein WE (eds) Hypersaline Ecosystems. Springer -Verlag, Berlin, Heidelberg, 186-217.

Gerdes F, Spira J, Dimentman C (1985) The Fauna of the Gavish Sabhka and the Solar Lake – a Comparative Study. In Friedman GM, Krumbein WE (eds) Hypersaline Ecosystems. Springer - Verlag, Berlin, Heidelberg, 322-345.

Gerdes G, Krumbein WE, Holtkamp E (1985) Salinity and Water Activity Related Zonation of Microbial Communities and Potential Stromatolites of the Gavish Sabhka. In Friedman GM, Krumbein WE (eds) Hypersaline Ecosystems. Springer -Verlag, Berlin, Heidelberg, 238-266.

Golubic (1991) Modern Stromatolites: A Review. In Riding R (Ed.) Calcareous Algae and Stromatolites. Springer-Verlag, Berlin, Heidelberg, 541-561.

Golubic S (1992) Microbial Mats of Abu Dhabi. In Margulis L, Olendzenski L (eds) Environmental Evolution: Effects of the Origin and Evolution of Life on Planet Earth. MIT Press, Cambridge, Massachusetts, 103-130.

Golubic S (1992) Stromatolites of Shark Bay. In Margulis L, Olendzenski L (eds) Environmental Evolution: Effects of the Origin and Evolution of Life on Planet Earth. MIT Press, Cambridge, Massachusetts, 131-147.

Horodyski RJ, Bloeser B, Haar SV (1977) Laminated Algal Mats from a Coastal Lagoon, Laguna Mormona, Baja California, Mexico. Journal of Sedimentary Petrology. 47(2): 680-696.

Jannasch, HW (1995) Microbial Interactions with Hydrothermal Fluids. Geophysical Monograph. 91: 273-296.

Javor J, Castenholz Rw (1980) Laminated Microbial Mats, Laguna Guerrero Negro, Mexico. Geomicrobiology Journal. 2(3) 237-273.

Krumbein WE (1983) Stromatolites – challenge of a term in space and time. Precambrian Res. 20: 493-531.

Krumbein, WE (1985) Applied and Economic Aspects of Sabkha Systems – Genesis of Salt, Ore and Hydrocarbon Deposits and Biotechnology. In Friedman GM, Krumbein WE (eds) Hypersaline Ecosystems. Springer -Verlag, Berlin, Heidelberg, 426-436.

Levitus S (1989) Interpentadal Variability of Temperature and Salinity at Intermediate Depths of the North Atlantic Ocean, 1970-1974 Versus 1955-1959. Journal of Geophysical Research. 49(C5): 6091-6131.

Mao Che L, Andrefouet S, Bothorel V, Guezennec M, Rougeaux H, Guezennec J, Deslandes E, Trichet J, Matheron R, Le Campion T, Payri C, Caumette P (2001) Physical, chemical and microbiological characteristics of microbial mats (KOPARA) in the South Pacific atolls of French Polynesia. Canadian Journal of Microbiology. 47: 994-1012.

McLane C, Magelky R, Siebling D (2002) Effect of withdrawals from a simulated island freshwater lens aquifer system; an analytic element modeling approach. Abstracts with programs Geological Society of America. 34(6): 26.

Nofke N, Hazen R, Nhleko N (2003) Earth's earliest microbial mats in a siliciclastic marine environment (2.9 Ga Mozaan Group, South Africa). Geology. 31(8): 673-676.

Poetker, S (2000) Intertidal and Supra-littoral Microbial Mats of the Temae Mudflat on Moorea, French Polynesia. The Biology and Geomorphology of Tropical Islands, Student Research Papers. University of California, Berkeley, 167-184.

Rothrock RJ, Garcia-Pichel F (2002) Community Structure and Diversity of Cyanobacterial and bacterial populatons in intertidal microbial mats along a desiccation gradient. Astrobiology, 2(4): 548.

Sprachta S., Camoin G., Golubic S., Le Campion Th (2001) Microbialites in a modern lagoonal environment: nature and distribution, Tikehau atoll (French Polynesia). Palaeogeography, Palaeoclimatology, Palaeoecology. 175: 103-124.

Stolz JF (2000) Structure of Microbial Mats and Biofilms. In Riding RE, Awramik SM (eds) Microbial Sediments. Springer-Verlag, Berlin, Heidelberg, New York, 1-8.

# Faunal Distribution and Abundance of a Saline Microbial Mat in Moorea, French Polynesia

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ABSTRACT. Extreme environments are found all over the world, each with their own set of extreme characteristics that make them challenging places for life to exist. Living in each of these exceptional environments is a guild of organisms uniquely adapted to survive under such harsh conditions. This study looks at one such place, a hypersaline microbial mat on the island of Moorea, French Polynesia. Located on a mudflat this severe location has salinities ranging from 6 to 132ppt, temperatures from 44°C to 20°C, and water levels from 26.5m below ground level to 4cm above ground level (Magudia). To characterize the faunal composition and distribution across the microbial mat, pitfall traps were set up along four transects beginning in vegetation and then continuing out across the mat towards the adjacent lagoon. For each transect there were two collections of arthropods during the day from 6am-6pm and two at night from 6pm-6am. A strong correlation between decreasing number of species and increasing distance from vegetation was found at night while a much weaker trend was found during the day. A significant linear decrease in density for all transects was found with increasing distance at night ($P=.00$). A similar trend was observed for all transects during the day but was not significant ($P=.09$). Distribution of individuals for all transects during the day was significantly different from at night ($P=.00$). The distribution of individuals on the mat versus in vegetation was also significantly different ($P=.00$). This was due to the cover from the sun and greater amount of food the vegetation could provide at the beginning of the transects. The vegetation present at the beginning of each transect appeared to be one the most influential in determining faunal distribution. Species distribution in the plants versus on the mat was significantly different for all transects ($P=.00$). The distribution of species during the day was also significantly different from that at night ($P=.00$). This study shows there is a significant difference between the day and night fauna of the microbial mats as well as between the fauna found in the vegetation versus out on the mat.

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## Introduction

Extreme environments are found all over the world. Each has its own unique set of environmental conditions making it a challenging place for life to exist. These extreme environments are defined by their physical environmental conditions, and the rate and range at which those conditions change. Hydrothermal vents are one example of an extreme environment where under high pressure, temperatures can get up to 400°C , pH ranges from 3 to 8, and there are extremely high concentrations of $H_2S$ (Dover 2000). The McMurdo Dry Valleys of Antarctica are one of the driest places in the world where soil temperatures under snow patches can vary from -24.9 to 23.2°C (Gooseff et al 2003). In the Namib Desert in southern Africa temperatures can get up to over 40°C and some years receive no rain.

Despite the harsh physical conditions of these habitats, they are often found to bear life. Life that is specialized to exist amidst these extreme conditions. To survive in these extreme conditions organisms have developed biochemical, physiological and behavioral adaptations to minimize the harmful effects of these environments. Using these types of strategies special guilds of organisms can tolerate these extreme conditions. For example, the communities that inhabit the hydrothermal vents not only have to deal with high temperatures but also with toxic levels of sulfide. Some inhabitants like Chemosynthic vestimentiferans, vesicomyid clams, and the tube worm *Riftia pachyptila* have developed blood borne components that bind to the sulfide and prevent it from harming bodily tissues (Zierenberg et al 2000). To adapt to the below freezing temperatures in the artic many organisms have developed "antifreeze" proteins that lower the freezing temperature of cellular fluids and protect the cell during thawing when freezing does occur. (Clarke) In the extreme heat of some deserts many organisms have developed behavioral adaptations to keep cool. When temperatures in the Namib desert get too hot the tenebrionid beetle, *Onymacris plana*, uses convective cooling by running at almost one meter per second. These organisms have each found a way to deal with the harsh conditions of extreme environments where most life could not exist.

Earth was an extreme environment when cyanobacteria, one of the first forms of life, emerged. Fossil records show their unusual success as they developed and evolved in an environment that few other organisms could survive. Today many of these ancient types of cyanobacteria can be found in microbial mats. (Golubic 1994) Today microbial mats are still primarily found under harsh conditions where there is very limited competition from other organisms. One such microbial mat can be found on the island of Moorea, French Polynesia. The high temperatures, high salinity, and large intraday shifts in conditions define this extreme environment.

This study surveys the organismal richness of a Moorea Microbial Mat, both spatially and temporally and inferences are drawn as to how each species or guild succeeds in this environment.

## Methods and Materials

The study site was located on the island of Moorea in French Polynesia on the motu Tamae (Fig 1). This is an unusual motu because it had been attached to the mainland at its southern end. Now a channel runs in from the north between Tamae and Moorea to a large body of water. As the tides change salt water from the Pacific Ocean is brought in. Along this channel to the east there is a large mud flat that is covered by microbial mats. This area is bordered on one side by a lagoon and the other by vegetation. There were two main vegetation types, hibiscus and reeds. The hibiscus vegetation consisted mainly of large hibiscus bushes, *Hibiscus tiliaceus* and a few palm trees. The reed vegetation consisted solely of thick marsh reeds.

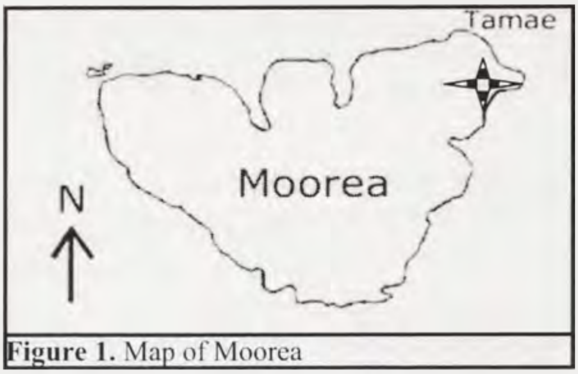

**Figure 1.** Map of Moorea

Four transects (Fig. 2) were set up to determine the abundance and distribution of fauna present between Sept. 23, 2003 and Nov. 11, 2003. Each transect began 15 meters into the vegetation. The first two transects A and D were located in an area that had thin partial mat coverage, the second two B and C were located in an area with substantially thicker mat coverage. Transect A was set up perpendicular to the first and contained twenty-six pitfall traps. It began in hibiscus and continued towards the water. Transect B contained eighteen pitfall traps beginning in the reeds and continuing towards the water. Transect C which also began in the reeds and continued towards the water, contained thirteen pitfall traps. Transect D began in hibiscus vegetation and ended in the reeds. It consisted of thirty-two pit fall traps placed five meters apart at the edges and ten meters apart towards the interior of the mat. At each transect traps were set twice from 6am to 6pm and twice from 6pm to 6am.

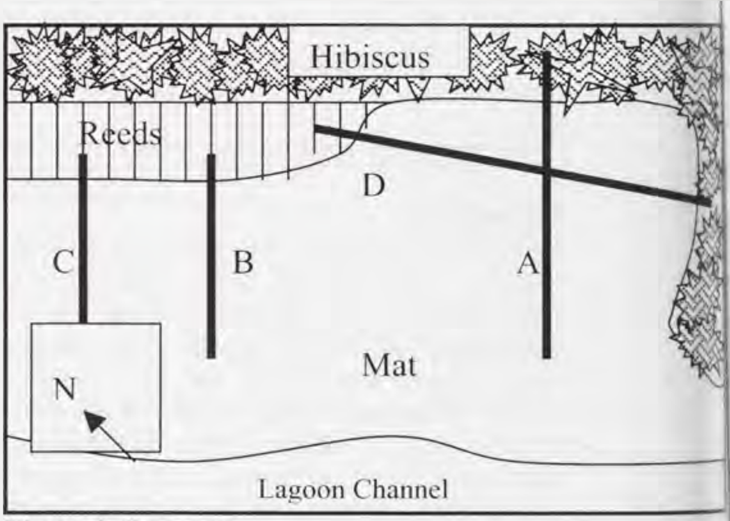

**Figure 2.** Transects

The pitfall traps were simply plastic cups filled with an inch of slightly soapy water, placed about a half inch below ground level. A piece of cardboard held up at one end with wire or a stick was leaned over each cup to prevent excessive evaporation. In areas where the water level was high and there was thick mat present, a portion of the rim of the cup was placed under the mat to prevent it from floating above ground level. In places where the water level rose above the surface, the cups were placed in small mounds of dirt a few inches above the ground level. Cups that floated up and tipped over or those that were submerged under water were redone.

At the end of the collection interval all organisms were collected from each trap with forceps and a pipette and put into vials. The organisms were then stored in 90% ethanol for preservation. The number of each type of organism in each trap was then counted.

To analyze the distribution of organisms across transects, regression, ANOVA, and Kolmogorov-Smirnov statistical tests were used.

## Results

*Density*

A total of 2,311 organisms where collected, 1,022 organisms were captured at night and 1,289 during the day (Fig. 4 and 5). Statistics were run comparing day and night distributions along whole transects and in vegetation versus the mat. Regression analysis revealed a significant linear decrease in density across transects with increasing distance from vegetation at night ($P \leq .00$, R^2=.12). During the day there was also a trend for decreasing density with increasing distance from vegetation but it was not significant ($P \leq .09$). The Kolmogorov-Smirnov test found a significant difference in faunal distribution during the day versus the night at all transects ($P \leq .00$) The distribution of fauna on the mats was found to be significantly different than the distribution of fauna in the vegetation, during the day and night at all transects ($P < .00$).

*Diversity*

Twenty-seven different species were collected (Figure 6 and 7), including 2 species of Isopods, 1 species of Orthoptera, 1 species of Amphipod, 1 species of Lepidoptera, 3 species of Hymenoptera, 4 species of Coleoptera, 9 species of Diptera, one species of Hemiptera, one species of Araneae, and three unknowen species (Table 1). No statistically significant pattern in species distribution was found using ANOVA. Using the Kolmogorov-Smirnov test a significant difference in species distribution was found between day and night at transect A ($P=.02$), while no significant difference was found for transects B ($P=.16$), C ($P=.17$), and D ($P=1.0$). The distribution of species on the mats was found to be significantly different than the distribution of species in the vegetation, during the day and night at all transects ($P < .00$).

## Discussion

Each transect began in vegetation either hibiscus-type or reed-type as described above. The vegetation provided shelter from the intense tropical sun as well as food in the form of live plant matter and detritus. The distinct line where vegetation began was most likely due to a decrease in salinity to a tolerable level (Magudia). As one crosses the line where vegetation ends the mat begins. While the surface of the mat can get dry, it was usually a very wet environment with periodic flooding depending on tides and rain. Out on the mat, where there was no cover, temperatures during the day were high and ground temperatures reached up to 44°C. The ground absorbed this heat during the day and remained warm through out the night dropping only to about 20°C (Magudia, 2003).

The fauna collected consisted almost entirely of arthropods except for two species of arachnids. Arthropods found in the vegetation could escape the heat of the sun by crawling under vegetation. This was observed when after being disturbed they would scramble under cover of the nearest object they could find. Arthropods out on the mat did not have the option of seeking cover and since they are ectotherms must use other strategies to keep cool. Arthropods can keep cool by three methods of thermoregulation. Convective heat loss can be achieved by increasing the speed of air movement past the body (Heinrich, 1996). Small insects can do this by flying because the amount of heat gained from flight muscles is less than that lost through convection (Heinrich, 1996). Wind can also produce convective heat loss especially for those larger insects who would gain too much heat from flight muscles to lose heat through flying (Heinrich, 1996). In environments where insects may be gaining heat from both the sun and the ground below they will often embark on short flights to cool off and escape the double radiation of heat (Heinrich, 1996). Evaporative cooling is also an important way of cooling off and depends on the temperature and humidity of the immediate environment. While this method is less efficient in more humid environments it is more efficient in warmer environments so it could possibly be used by the arthropods in this study (Chapman 1998). There is also behavioral regulation which includes finding shelter or where there is no shelter adjusting body posture and orientation to the sun to reduce the amount of body area exposed (Chapman 1998).

Not only must these arthropods deal with high temperatures but also with high salinity. Most arthropods' osmotic pressure changes very little over wide ranges of salinity because they regulate the ionic composition of their hemolymph (Chapman 1998). They also can limit drinking and choose foods that have the least salt content (Chapman 1998). After gaining water and salts through food they remove the excess ions by excreting urine that is hypertonic to the hemolymph (Chapman 1998). Despite these harsh conditions many arthropods were found at the site and each must have had their own way of dealing with the conditions of there immediate environment.

During the study 2,311 organisms were collected (Fig. 3 and 4). A total of 1,343 during the day. This is surprising since one would think that more would be found on the mat during the night when temperatures are much cooler. This may be because individuals using the mat during the day are inactive at night. Individuals could also be finding cover under the shade of the traps making the density during the day appear to be greater than it really is.

Over the entire area studied 27 different species were found (Fig.6 and 7). In the plants 20 different species were found while out on the mats 21 different species were found. Diversity in the vegetation versus the mat was fairly equal. In the plants during the day 16 different species were found, while on the mat 17 different species were found. Again the diversity in both places was quite similar. During the night 15 different species were found in the plants as well as on the mat. Although the number of species found in the plants was almost always the same as was found out on the mat, about six times more distance was covered on the mat than in the plants. Also there may be more of a tendency for organisms out on the mat to seek shelter under the traps therefore raising the number of things caught which also raises the chance of catching more types of things.

Out of the 27 different species collected, 17 of the species were represented by less than nine individuals. These species distributions cannot truly be discerned due to the sparse number of individuals collected of each of these species. The other ten species were found in more numerous quantities and there distributions can more accurately be made out. *Isopod* type #1 was found primarily in the plants almost certainly because the vegetated areas have a greater ability to support life, being able to provide protection from the sun and greater amounts food in the form of plant material. During the day 545 individuals were collected in the plants. Considering that overall more individuals were collected in the plants it is interesting that 744 were collected on the mat during the day. This is probably because many of the species in the plants were observed to be nocturnal. In the plants at night 798 individuals were collected. This was the highest number of individuals collected in any one type of area and time of day. This is due to the fact that there were more individuals found in the plants overall and that most of the dominant species found in the plants were observed to be nocturnal. At night on the mat only 224 individuals were collected in comparison to the 744 captured while its night day distribution was more even. *Orthoptera, Gryllidae* type #2 was mainly found at night in the plants. During the day none were found on the mat while at night a few ventured out on the mat. *Amphipoda* type #3 was found mostly at night in the plants but also during the day in much lower numbers. On the mat similar numbers of this species were found during the day and night. This is unexpected considering so many more of this species were found in the plants at night. Again this may be because those that ventured out onto the mat during the day seeked the shelter of the traps making there numbers on the mat seem higher than they really were. *Hymenoptera, Formicidae* type #5 was typically found during the day in the plants and was not found on the mats. *Coleoptera* type #8 was mostly found during the night on the mat although quite a few were also found in the vegetation. In comparison very few were found during the day, the majority of them being found on the mat. While this species is primarily found on the mat it is probably more active during the night as a way to escape the high temperatures on the mat during the day. The most numerous

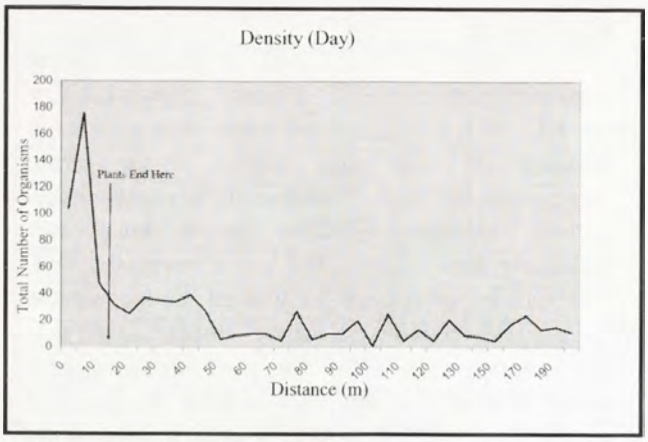

**Figure 4.** Daytime density

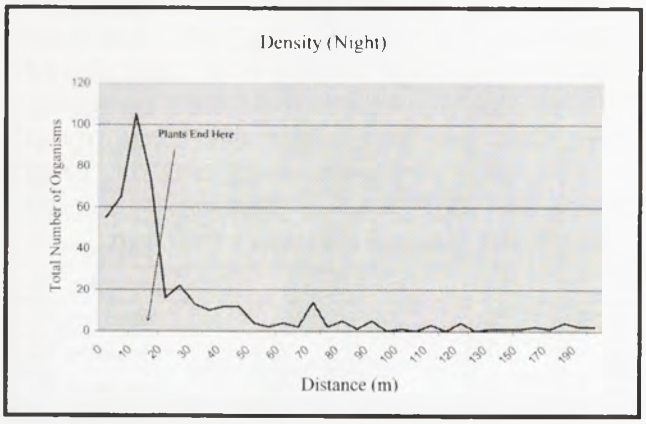

**Figure 5.** Nighttime density

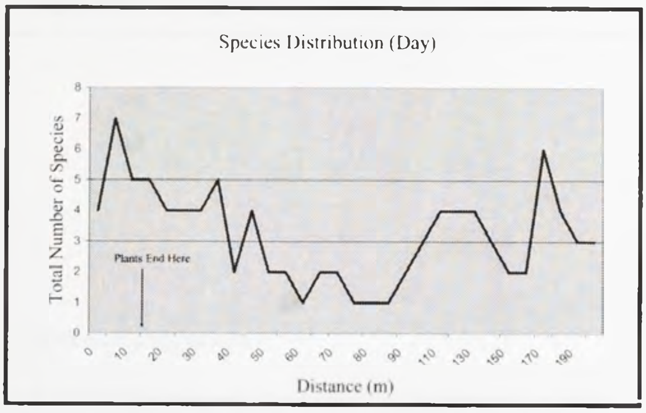

**Figure 6.** Daytime species distribution

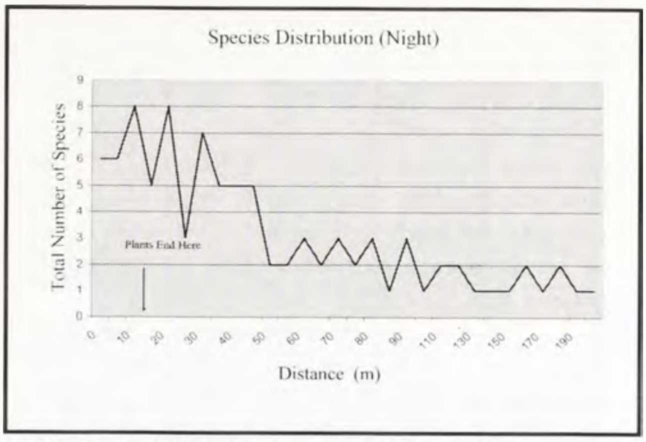

**Figure 7.** Nighttime species distribution

species found was *Diptera* type #10 which was primarily found on the mat during the day. The number of this species in the plants during the day was much higher than at night. This may indicate that the species is leaving the area at night or may be inactive at night. But, because this species can fly it may not be getting caught in the pitfall traps on the ground in the vegetation where it may not come down to the ground. *Diptera* type #11 with far fewer individuals was found mostly on the mat during the day. Not very many individuals of this species were captured so it is hard to determine true trends for this species. *Hymenoptera, Formicidae* type #13 was found primarily in the plants during the day. During the night there numbers decreased a great deal in the plants and the mat. *Diptera* type #20 was generally found on the mat during the day. The percentage of this species present in the plants out of the total number present during the day and night was about the same. Altogether the primary species in the plants were types 1, 2, 3, 5, and 13. Types 2 and 3 appeared to be nocturnal while type 1, 3, and 5 did not. Out on the mat the primary species were types 6, 8, 10, 11, and 20. During the day on the mat, types 10 and 20 were more active while at night types 6, 8, and 11 were more active.

Besides the many species of anthropoida present at this site there were also two species of crab, the larger one being *Cardisoma carnifex*, and the smaller one *Uca (Amphiuca) cloropthalmus*. These two species acted as ecosystem engineers digging holes all over the mat. By doing this they may be allowing two different species of wolf spider *Arachnida, Lycosidae sp?* to live out on the mats. During the day the spiders may be using the crab holes for shelter from the sun that they would otherwise probably not be able to stand. At night they crawl out of the holes to capture food. There was also another species of spider *Pisauridae, Dolomedes* sp. which was found in the vegetation near the edge of the mat. Out on the mat and in the vegetation there where also a variety of species of birds.

While the data collected seemed reasonable the pitfall traps did present a few problems that that may have biased the data. In the vegetation flying organisms may only subside in the plants and not be caught by the traps on the ground making there numbers appear lower than they are. Out on the mat the shade cover that prevents the water from evaporating could have attracted organisms to the traps making densities appear higher than they are. Also the rainy season begin about half way into the study and seemed to have an effect on some species abundance. This was primarily noticed with type # 2.

So is this an extreme environment? Well, it is a hypersaline environment with salinities reaching up to 132ppt and temperatures ranging from 20 to 44°C (Magudia). The mat also experiences dramatic changes in water level from 26.5m below ground level to being completely submerged with water levels 4cm above ground level. Any organism living here would have to be able to tolerate high temperatures and salinity and frequent flooding. Although "extreme" is dependent on ones point of view most life could probably not handle living under these conditions and would therefore view this as an extreme environment.

## Conclusion

A total of 2,311 organisms were captured containing 27 different species. The density and species distribution was primarily dictated by the two habitat types being vegetation and mat. Higher densities were found in the vegetation probably due to the greater available food source and cover form the sun. The number of species located on the mat versus in the vegetation was fairly similar. The mat contained mostly flying species found that were active during the day and seemed to leave at night. Future research should include measuring physical conditions along transects like temperature, salinity, pH, and water depth. Long term collections throughout a year could also determine the effect of the rainy season on species abundance. Feeding trials could also be run to determine what each species is consuming and find out more about the faunas direct interaction with the mat. Along with the feeing trials identification of all organisms would also help in being able to construct a food web.

| Type | Total Collected | Total Day | Total Night | Total Plants | Total Mat | Day Plants | Day Mat | Night Plants | Night Mat |
|---|---|---|---|---|---|---|---|---|---|
| **1.**Isopod | 177 | 103 | 74 | 152 | 25 | 85 | 18 | 67 | 7 |
| **2.**Orthoptera, Gryllidae | 441 | 89 | 352 | 395 | 46 | 89 | 0 | 306 | 46 |
| **3.**Amphipoda | 601 | 184 | 417 | 508 | 93 | 140 | 44 | 368 | 49 |
| **4.**Lepidoptera | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 |
| **5.**Hymenoptera, Formicidae | 33 | 28 | 5 | 33 | 0 | 28 | 0 | 5 | 0 |
| **6.**Coleoptera | 46 | 12 | 34 | 7 | 39 | 3 | 9 | 4 | 30 |
| **7.**Dermaptera, Forficulidae | 2 | 0 | 2 | 1 | 1 | 0 | 0 | 1 | 1 |
| **8.**Coleoptera | 72 | 13 | 59 | 20 | 52 | 1 | 12 | 19 | 40 |
| **9.**Diptera | 8 | 2 | 6 | 3 | 5 | 0 | 2 | 3 | 3 |
| **10.**Diptera | 618 | 588 | 30 | 45 | 573 | 40 | 548 | 5 | 25 |
| **11.**Diptera | 17 | 5 | 12 | 3 | 14 | 0 | 5 | 3 | 9 |
| **12.**Diptera | 6 | 2 | 4 | 6 | 0 | 2 | 0 | 4 | 0 |
| **13.**Hymenoptera, Formicidae | 147 | 134 | 13 | 141 | 6 | 132 | 2 | 9 | 4 |
| **14.**Diptera | 3 | 2 | 1 | 1 | 2 | 1 | 1 | 0 | 1 |
| **15.**Diptera | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 |
| **16.**Coleoptera (Larva) | 3 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 |
| **17.**Coloptera | 4 | 2 | 2 | 4 | 0 | 2 | 0 | 2 | 0 |
| **18.**Isopoda | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| **19.**Diptera | 3 | 3 | 0 | 3 | 0 | 3 | 0 | 0 | 0 |
| **20.**Diptera | 111 | 106 | 5 | 17 | 94 | 16 | 90 | 1 | 4 |
| **21.**Hymenoptera, Formicidae | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| **22.**unknown | 2 | 2 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| **23.**unknown | 3 | 3 | 0 | 0 | 3 | 0 | 3 | 0 | 0 |
| **24.**unknown | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |
| **25.**Hemiptera | 3 | 2 | 1 | 0 | 3 | 0 | 2 | 0 | 1 |
| **26.**Araneae | 4 | 4 | 0 | 0 | 4 | 0 | 4 | 0 | 0 |
| **27.**Diptera | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |
| **Total** | 2311 | 1289 | 1022 | 1343 | 968 | 545 | 744 | 798 | 224 |

**Appendix 1**

## Acknowledgements

I would like to thank the following for their wonderful advice and enthusiastic support: Jere Lipps, Vince Resh, George Roderick, Carole Hickman, Rosemary Gillespie, Jan Nakamura, Curtis Pehl, and Blake Suttle. Also special thanks to all those who ventured out in the mud with me to help with traping. Thanks to the Gump station and there staff. Thanks to my family for their support and the 2003 class of Moorea.

## LITERATURE CITED

Chapman, R.F. (1998) *The Insects Structure and Function*, 4th edition

Clarke,A. in *Evolution on Planet Earth: The Impact of the Physical Environment* (eds Rothschild, L. & Lister, A.)(Academic, London, in the press).

Golubic S. (1994) The continuing importance of cyanobacteria. In:bengtson S. (eds) Early Life on earth. Nobel Symposium No.84. Columbia U.P., New York: 334-340

Gooseff, Michael N., Barrett, J.E., Doran, P.T., Fountian, A.G., Lyons, W.B., Parsons, A.N., Porazinska, D.L., Virginia, R.A., and Wall, D.H., (2003) Snow-Patch Influence on Soil Biogeochemical Processes and Invertebrate Distribution in the McMurdo Dry Valleys, Antarctica. *Artic, Antarctic, and Alpine Research*, 35:91-99

Heinrich, B. (1996) *The Thermal Warriors*, Harvard University Press, and London, England

Magudia , Kirti personal communication

NASA web site, *Focus Microbial Mats & Stomatolites*, (http://nai.arc.nasa.gov/students/this_month/index.cfm)

Van Dover, C.L. *The Ecology of Deep-Sea Hydrothermal Vents* (Princeton Univ. Press, Princeton, 2000)

Zierenberg, R.A., Adams, M.W.W., Arp, A.J., (2000) Life in extreme environments: Hydrothermal vents. *PNAS*, 97: 12961-12962

# Systematic karst pool erosion within the conglomerate platforms of Moorea, French Polynesia

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ABSTRACT. Karst morphology appears as a prominent erosional feature on carbonate platforms fronting the Motu of Moorea, French Polynesia. Conglomerate platforms on Motu Temae Motu Tiahura, and Motu Ahi show varying levels of karstic influence. The horizontal surface topography of these platforms and the presence of hydrologic and lithologic layering present an environment in which karst pools may develop. Interaction between the platform with both fresh water from rain and seawater from the adjacent lagoon leads to the formation of pool and basin structures which erode vertically as well as horizontally through the platform and in some cases out to the lagoon. Two distinct evolutionary systems are recognized within these pools with stages of development defined for each system. Throughout the development of these pools, defining characteristics including surface textures, influx systems, drainage systems and physical morphology change and evolve. Differences in both small and large-scale structural elements over the area of the platform dictate where and how pools develop. The formation and evolution of these karst pools does in some cases effect the morphology of the platform on a larger scale. In addition to acting as an erosional mechanism for the platform, karst pools can also act as depositional environments for new sediment and material.

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## 1. Introduction

Karst erosion is an influential process in tropical regions with typical rates of erosion calculated at 45kg/km$^2$/year (Drew, 1985). With such high karst erosion rates noted in the tropics, one expects exposed limestone in these areas to exhibit well known karst morphologies. The conglomerate platforms which occur along the barrier reef faces of the Motu of Moorea, French Polynesia provide an environment prone to rapid lithification and solution of the calcium carbonate material they are made of. Karst type morphology is visible on these conglomerate platforms including karst pools similar to karstic basins documented in the Bahamas (Bourrouilh-Je Jan, 1998). The conglomerate platforms present on the five motu of Moorea, French Polynesia have been suggested to be deposited as a result of large storms and cyclones. (Murphy, 1992) As a storm or detrital deposit these structures contain clasts ranging in size from fine sand to large coral boulders which creates a unique environment for erosional and depositional processes.

This study examines the surface karst features of the conglomerate platforms on the Motu of Moorea to whether there is a systematic evolution to the erosion of these platforms. Further investigation is then made into the nature of the features present and the dominant environmental processes that influence the karst erosion. Bourrouilh-Je Jan (1998) describes the karstification of shallow water carbonate platforms in the Bahamas and the Tuamotu, finding that lithification and solution occur simultaneously in these environments with both freshwater and sea water adding to the development of these karst systems. The platforms involved in this study are partially emergent and partially submerged. Cementation of subaerial and submarine carbonates differ according to Matthews (1969). This study also examines whether structural differences between subaerial and submarine cemented environments influence erosional evolution. Alternatively a null hypothesis is that karst features on the conglomerate platforms evolve in the same manner and by the same physical and chemical processes at all locations along the platforms regardless of structure on a large or small scale.

## 2. Methods

### *2.1 Study Sites*

All field work for this study was conducted along the conglomerate platforms on the barrier reef sides of Motu Temae, Motu Tiahura and Motu Ahi all of which are located on Moorea, French Polynesia (17°30' S, 149°50'W). Field experiments were performed primarily at Point Aroa (17°28.402'S, 149° 46.419'W) on the northwestern end of Motu

Temae with observations for comparison made at Motu Tiahura and Motu Ahi. All experiments and observations were carried out during October and November 2003.

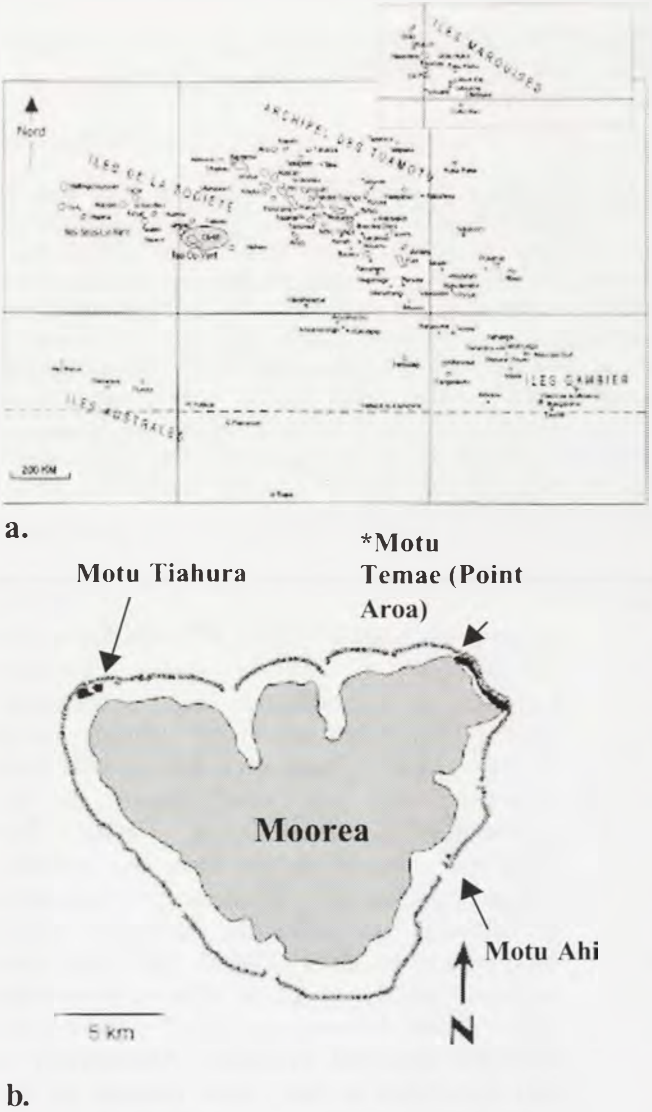

**Figure 1 . a.** Map of French Polynesia, b. Map of Moorea depicting field sites. * depicts primary area for field experiments.

The study area at Aroa Point represents only a small section of the large conglomerate platform present along the front of motu Temae. This field site includes the area 100m west of the light at point Aroa all the way to the eastern most end of the platform.

MotuTiahura(17°29.179'S.149°46.419' W) is located on the northeastern corner of Moorea. The conglomerate platform runs along the length of the motu on the barrier reef side and ranges in width from about 3 to 25m.

Motu Ahi is located on the western coast of Moorea just offshore from the village of Afareaitu. The conglomerate platform runs along the western side of the motu and wraps around following the trend of the barrier reef. The platform width at Motu Ahi ranges from less than 1m to 40 m.

*2.2 Field Work*

The conglomerate platform at Temae was observed at times corresponding to different tidal situations including morning low tide (6am), midday high tide (12pm), and evening low tide (6pm). This observation was performed to grasp the type of water movement and influx that affects different parts of the conglomerate platform. In an attempt to simulate storm like conditions and the influence of large storm events on the platform, observations were made during a period of large swell (October 9, 2003) and during two periods of rain.

In surveying the larger part of the western end of the platform the Western most 200 meters of the platform were chosen for use in field experiments due to their intense karstification. All pools were recorded in terms of distance from the lagoon platform interface, relative size ,the composition and texture of the wall and bottom cement, the composition and texture of the surrounding cement, whether the platform location containing the pool was being undercut by a current, connections to other pools or the lagoon, observable intake and drainage systems, and the presence or absence of loose material.

Upon analyzing all pool data collected the pools were separated into subcategorical systems based on common characteristics.
Each pool system was then further separated into developmental stages beginning with the un-pooled surface cement and ending pool that could signify the end of that system. Stages were defined by their various cement textures, the drainage and influx systems visible and any unique morphologies that appeared characteristic of that particular stage.

In order to determine the effect of tides on different systems and stages, stages were tested for drainage and influx at both high and low tide. To test drainage, flouresein dye was diluted in seawater and then added to water in the pool. The path of the dye functioned to track the path of water entering and exiting the pool.

In order to better understand the distribution of different stage pools along the platform, a count of pool stages was made over the whole study site at Point Aroa. Starting at the furthest island structure west of the Point Aroa light, the length of the platform was walked and pools of each stage in each system were tallied.

*Sampling*

Hand samples were taken from key platform layers and cement types using a rock hammer and chisel. These samples were then observed with a hand lens and in some cases examined in thin section with a petrographic microscope.

## 3. Results

### *3.1 Introduction*

The fieldwork performed at the Point Aroa field site resulted in the characterization of two distinct karst pool systems. These systems are referred to as the near lagoon system and the inland system named primarily for the dominant location of each. By observing each pool system, characteristic stages could then be defined to describe the development of each pool system. The following systems were described from observation made at Point Aroa. Karstic features at Motu Ahi and Motu Tiahura were also observed to compare features with those present at Point Aroa.

### *3.2 Near Lagoon System*

The near-lagoon system is defined as occurring near the edges of the conglomerate platform in contact with the lagoon. This area is affected continually by rising and falling tides, wave action, and longshore current. Interaction between the platform edge and the lagoon also create a layering system between the vadose and phreatic zones (figure 2) which is characteristic of this pool system. The near lagoon system contains 7 distinct developmental stages.

### *3.2.1 Geology*

The area of the field site dominated by the near lagoon system is largely horizontal with few large boulders cemented on top. Towards the western end, the platform breaks into island type structures. The island structures as well as the area connected to the main platform is layered with what appears as an erosional gap just below the high tide line (figure 2). This gap separates the vadose and phreatic layers. The upper vadose layer contains poorly sorted clasts of coral heads and other calcareous material. Closest to the edge of the platform it is difficult to distinguish between clasts due to the extreme pitting. In the phreatic layer, algae and bioerosion prevent clasts from being distinguishable.

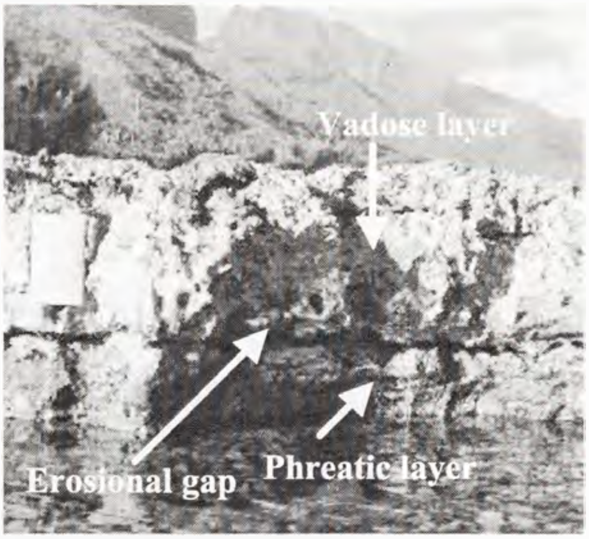

**Figure 2.** Boundary between vadose and phreatic layers. Field notebook (20cm height) shown for scale. Porosities in the vadose layer are 25-60% while those in the phreatic layer are 10-30%. (Nunn, 1994)

**Figure 3.** northwestern edge of platform from Point Aroa. Flagstone surface texture on top of platform. Island structures in the distance are characteristic of near-lagoon system.

### *3.2.2 Petrology*

In thin section the samples taken from the near lagoon setting show a distinction between material in the vadose layer and material in the phreatic layer. Sample TA01 represents the uppermost cemented layer in the near lagoon system. In thin section individual calcite clasts are surrounded by finer grained cement and large pores. There is no evidence of secondary crystallization. Sample TA05 represents the area of the platform just below the vadose-phreatic boundary. This sample is taken from just underneath the erosional gap that occurs at this boundary. In thin section one can see evidence of secondary crystallization with finer grained crystals of calcite rimming the conglomerate fragments.

### *3.2.3 Near- lagoon Stages*

*Stage 1*

Stage 1 in the near lagoon system is defined by the texture and relief of the conglomerate platform surface. Pool development has not yet started at this point but the surface cement is characteristic. The surface of the platform is rough and pitted with high relief on a small scale and algae covering a large percentage of the surface.Individual pits appear on the mm-cm scale

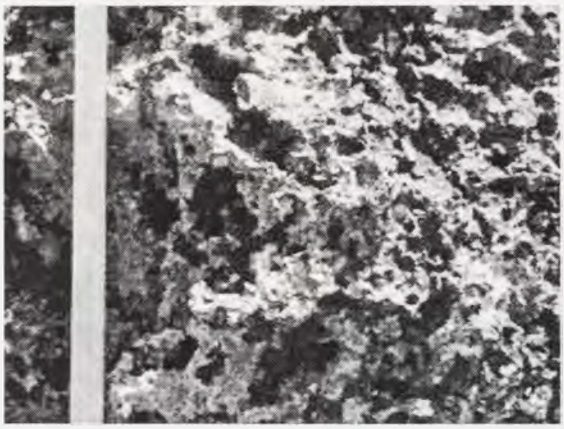

**Figure 4 .** Stage 1 of near-lagoon system. Algal colonies can be seen encrusting some of the surface.

*Stage 2*

At stage 2 (figure 5a) of the near lagoon system, pool development becomes visible. Pool shape at stage 2 is still dictated by the surrounding clast morphology. Pools of stage 2 are low points in naturally occurring topography. Pools wall are the same in texture as the stage 1 starting cement. Surfaces are still highly pitted and visibly porous. At this stage influx source waters are rain or wave action. Drainage of the pool during this stage can be observed to occur vertically through the pitted porous cement of the pool walls and bottom. When such pools are situated above undercut ledges drainage is seen to occur straight through the upper layer and into the lagoon.

*Stage 3*

Stage 3 (figure 5b) pools in the near-lagoon system show a contrast between bottom cement texture and texture of the cement of surrounding material. Pools are shallow but bottom cement is much smoother with less pitting and less visible porosity. The influx system for this stage is splash from wave action as well as water from rain. Drainage of stage 3 pools is vertical through the bottom cement although extremely shallow stage 3 pools may be flushed out by successive waves or may experience evaporation.

*Stage 4*

Pools at stage 4 (figure 5c) show physical erosion through the top vadose layer of the platform. The bottom of the pool has at this point begun to break through to the erosional gap that occurs between the vadose and phreatic layers of the near lagoon platform environment. Breakthrough to this erosional gap beteen layers offers a new pathway for both influx and drainage. Influx is derived from wave splash, rainwater, and now during high tide water may enter along the boundary between the vadose and phreatic layers. Drainage also takes advantage of this new pathway. Water may also drain via porous flow through the pool walls.

*Stage 5*

At stage 5 (figure 5d), pools have similar physical morphology as that of stage 4. Pool wall texture is similar to that of stage 4 but the pool bottom fully reveals the boundary to the phreatic layer. Influx is derived from rain and wave action but flow along the erosional gap at the phreatic boundary has increased and the pool may be filled or drained along the boundary layer during tidal fluctuations. At Stage 5 the drainage pathway along the boundary layer may erode enough to create a window like structure on the lagoon side of the pool at this layer.

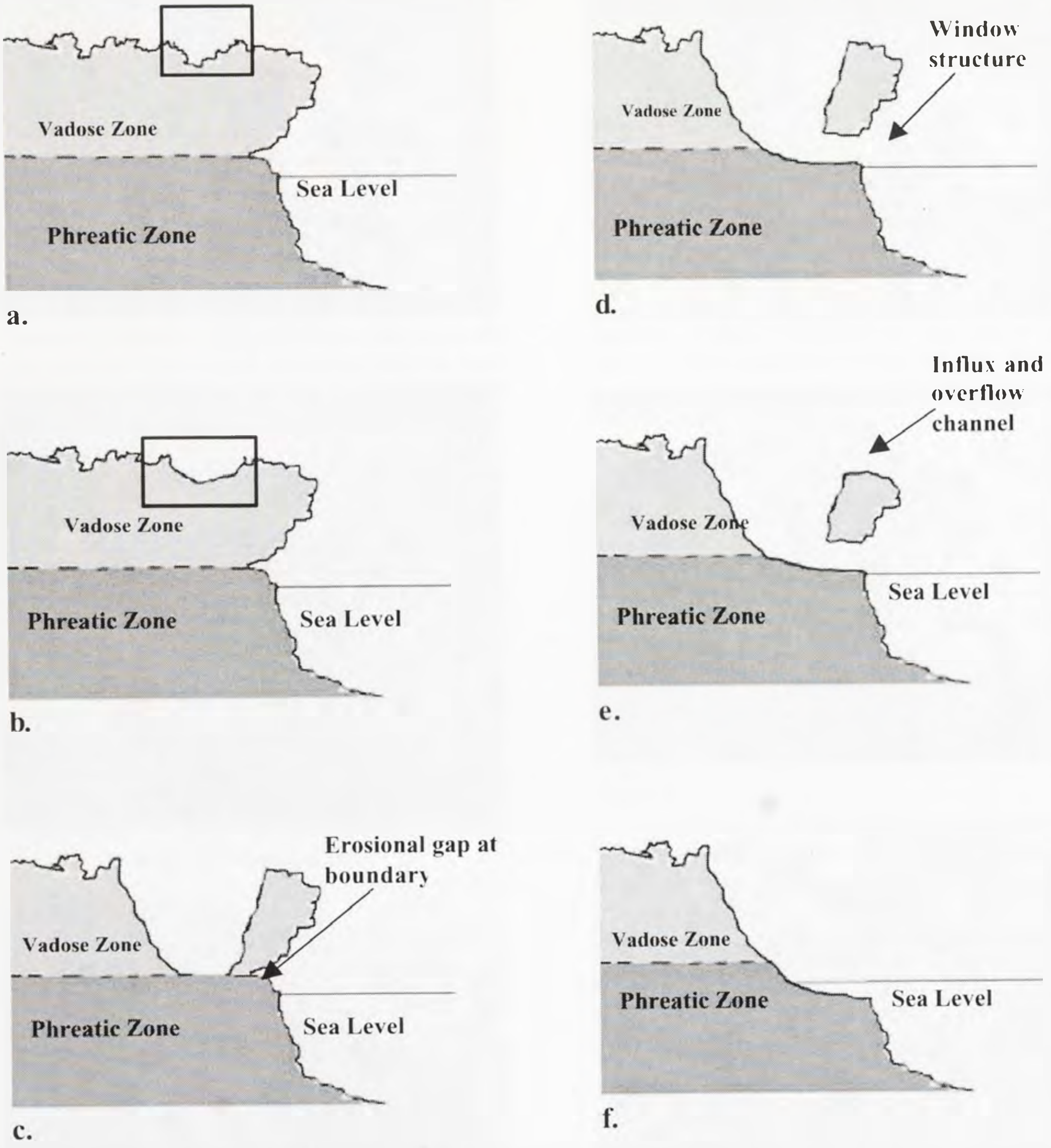

**Figure 5.** Erosional evolution of near lagoon system including stages 2-7 shown in cross-section. a. stage 2 pool, b.stage 3 pool, c. stage 4 pool. Erosional gap at boundary between vadose and phreatic zones is shown. d. stage 5 with window structure at boundary layer. e. stage6 showing window structure and dominant inflow and overflow channel. F. stage 8 pool.

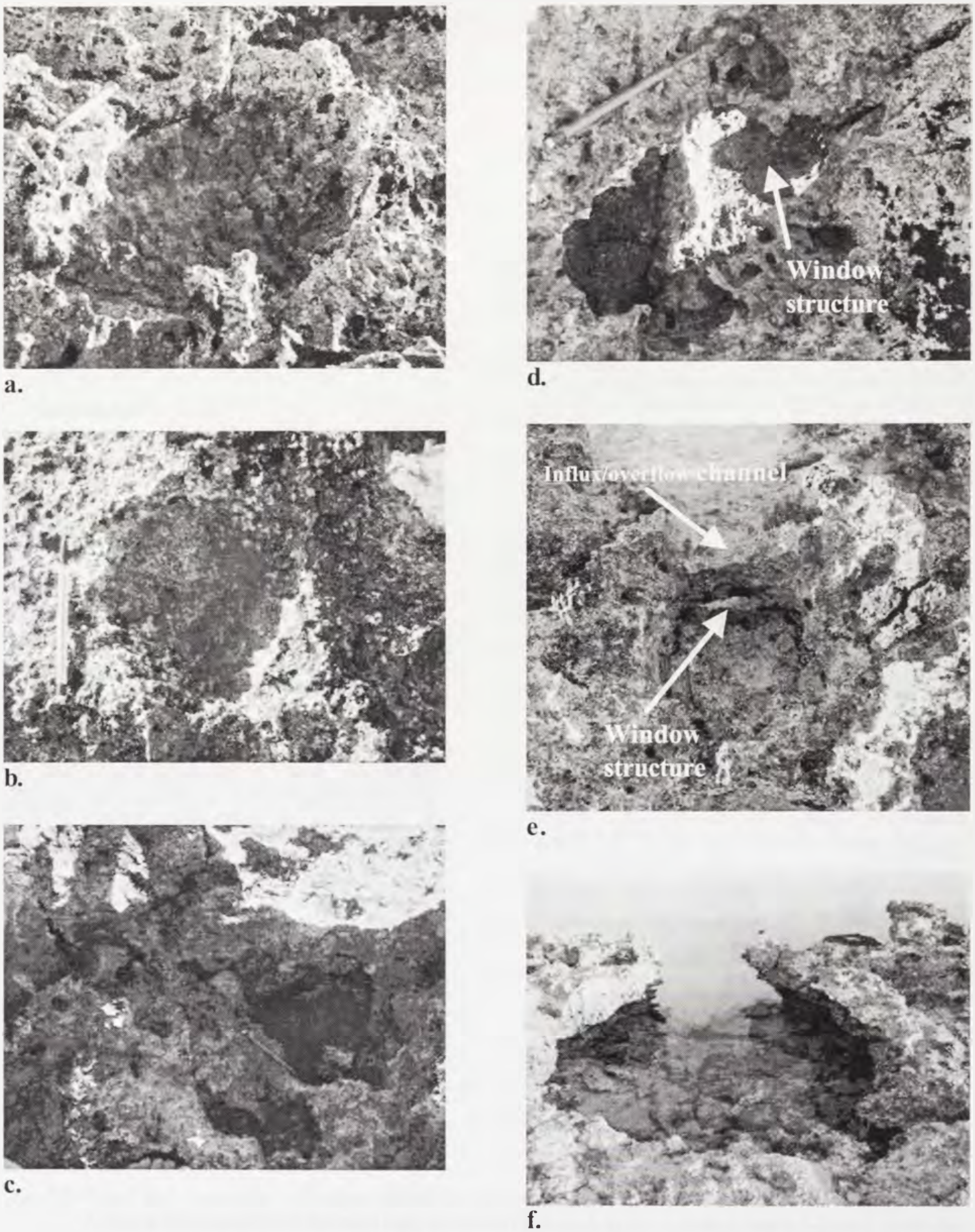

**Figure 6.** Photographic documentation of stages2-7 of the near lagoon system at Point Aroa. a. Stage 2 b. stage 3 c.stage 4 d.stage 5 e.stage 6 f. stage7

*Stage 6*

Pools at stage 6 (figure 5e) often have developed window structures at the vadose phreatic boundary layer. In addition a dominant influx channel may be developed showing the preferred direction for influx and drainage during periods when the pool overflows. Influx during stage 6 comes from rain, wave action or water flowing along the erosional gap or window structure during high tide. During low tide dominant drainage is along the vadose-phreatic boundary while at high tide when the erosional gap may be submerged, drainage may be both along the boundary as well as through the pool walls. During storms or large swells, drainage and influx tends to occur along the newly formed dominant influx channel located near the pool surface.

*Stage 7*

Stage 7 (figure 5f) is the final stage of the near-lagoon pool. At this stage the pool wall closest to the lagoon has been completely eroded away. The pool is now open to the lagoon. The bottom of the pool may or may not have eroded down below the low tide level, meaning it may be left dry at low tide. Influx and drainage during this stage are highly dependent on tidal fluctuations as there is no longer a barrier between the pool and the lagoon.

*3.2.4 Pool Abundances*

Within the Point Aroa field site at motu Temae a total of 253 pools belonging to the near lagoon system were counted. The distribution between the various stages is shown in table 1. Stage 1 is not included in this table as it represents the starting surface cement of the lagoon system.

| Stage# | Number of pool | Percent of total pools |
|---|---|---|
| 2 | 102 | 40.3 |
| 3 | 101 | 39.9 |
| 4 | 33 | 13.0 |
| 5 | 6 | 2.4 |
| 6 | 5 | 2.0 |
| 7 | 6 | 2.4 |

**Table 1.** Abundances of near lagoon stages 2-7 in the Point Aroa field site.

*3.3Inland System*

The inland pool system dominates areas of the platform that are removed from the platform lagoon interface. This area is not affected by tidal influences on a daily scale. Ocean water influx occurs only from high tides combined with storm conditions such as large waves and swells which are sufficient to deliver lagoon water onto the platform. This system is broken down into 5 characteristic stages.

*3.3.1 Inland-system Geology*

The inland system, system B occurs in areas of the platform where the conglomerate appears highly cemented at the upper most layers. The uppermost 20cm of the platform surface is often made up of a flagstone or shingle structures. This uppermost layer appears well cemented both with the naked eye and in hand sample.Individual clasts are visible but they occur with very little relief. Below the flagstone cap layer the conglomerate material becomes more easily recognizable as individual clasts. These clasts are poorly sorted and while towards the lagoon the large clasts are well-cemented, on the motu side of the platform this lower layer is poorly consolidated and barely cemented.

*3.3.2 Inland Stages*

*Stage 1*

Stage 1 of the inland surface refers to the initial surface texture and composition of the platform within the areas dominated by this system. The surface ranges from extremely flat and smooth with little pitting, to areas that are composed of a layer of large flagstone like structures that may demonstrate some pitting.

*Stage 2*

The first appearance of pooling in the inland system occurs as topographic lows in the surface cement with channels from the flagstone joints leading to a central depression. Influx during this stage is due to rain and waves large enough to reach far back on the platform. Drainage of this stage occurs vertically through the pool bottom cement or along the joint channels that may lead to topographically lower pools.

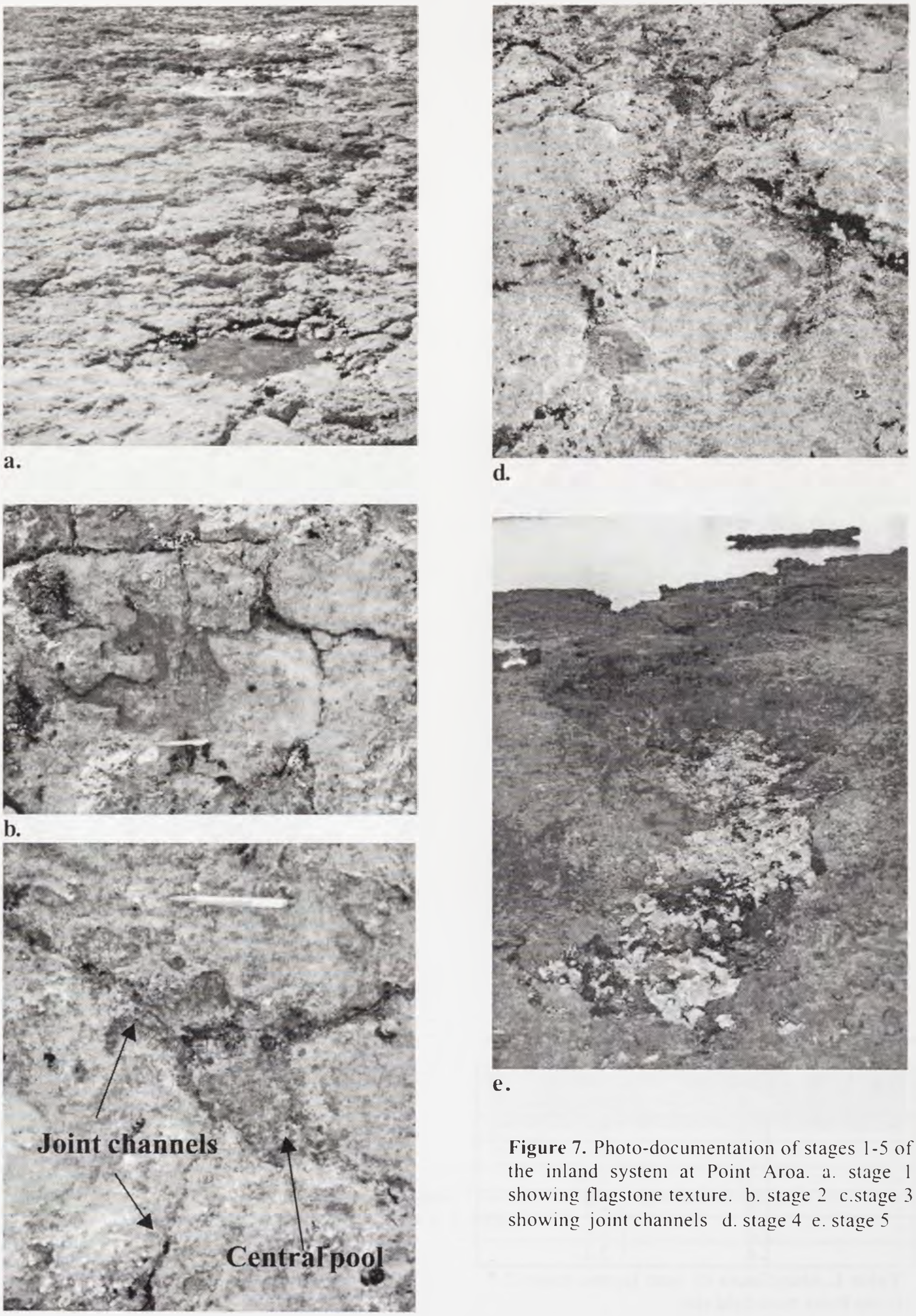

**Figure 7.** Photo-documentation of stages 1-5 of the inland system at Point Aroa. a. stage 1 showing flagstone texture. b. stage 2 c.stage 3 showing joint channels d. stage 4 e. stage 5

*Stage 3*

At stage 3 the central pool begins to deepen and associated joint channels leading into the central pool begin to widen. Influx during this stage is due to large waves during high tides, large swells or storms and rainwater. Drainage during this stage is along joint channels when the pool is overfilled either by heavy rains or large waves but when the level reaches below the overflow point, the dominant drainage is vertical through the bottom cement. Evaporation is noted in some pools of this stage.

*Stage 4*

At stage 4 in the inland system, pools have eroded vertically through the flagstone cap layer and the pool bottom begins to reveal a new lithologic layer. This new bottom layer is made up of distinguishable clasts in finer cement. Influx for this stage can come from rainwater or large waves and swells. In the case of water entering from the lagoon, the developed joint channels between nearby flagstone pieces provide directed pathways. Drainage occurs vertically through the new bottom texture or in some cases under the flagstone layer.

*Stage 5*

Pools in stage 5 of development exhibit pool bottoms that have fully eroded through the flagstone cap layer and begun to erode down into the underlying poorly consolidated layer. Both pool walls, and bottom in this stage are dominantly made of poorly sorted unconsolidated clasts. Individual clasts of detrital coral are visible and easily distinguishable. Cementing is often poor and porosity may be low enough to be visible to the naked eye. Influx of water comes from rainwater and large waves or storm swells. Drainage during this stage occurs through the pool walls and bottom. Pools in stage 5 often collect small pieces of unconsolidated material.

### *3.3.3 Abundances*

In the Point Aroa field site at Motu Temae a total of 115 pools were found in the inland system. The number of pools found of each stage of the inland system is shown in table 2. Stage 1 abundance does not appear as it represents the starting surface cement and does not yet show pool erosion.

| Stage # | Number of pools | % of total pools found |
|---|---|---|
| 2 | 54 | 47.0 |
| 3 | 37 | 32.1 |
| 4 | 19 | 16.5 |
| 5 | 5 | 4.3 |

**Table 2.** Abundances of inland stages 2-5 in the Point Aroa field site.

### *3.4 Motu Tiahura*

The conglomerate platform at Motu Tiahura demonstrates a similar visible layering to that of the field site at Point Aroa. The surface of the platform at Motu Tiahura showed more occurrence of the flagstone texture and was dotted with many large coral boulder cemented on top of the horizontal platform. The lateral ends of the platform were broken into island structures larger than those at Point Aroa. Many pools were filled in with sand and other detrital material. Late stage near-lagoon system pools are common creating a platform edge that is dotted with island structures and small peninsulas.

### *3.5 Motu Ahi*

The conglomerate platform at Motu Ahi appears erosionally different than that at Point Aroa. Undercutting along the lagoon edge is extreme. There is a small back lagoon that occurs between the platform and the main motu with only small areas where connections are subaerial. Karst pooling at Motu Ahi is not common aside from small early stage pools on the surface. Other erosional features appear dominant on this platform.

## 4. Discussion

### *4.1Evolution of near-lagoon system*

Stage 1 of the near lagoon system exhibits the most extreme pitting of all the cements seen in this study. This stage is occurring on the top most layer of the near lagoon platform environment. The algal layer on top of this cement may be adding to the karstification of the surface on a microscopic scale through a phenomenon referred to as phytokarst (Patterson and Sweeting, 1983). The formation of phytokarst can happen on a very short time frame, in as little as four years(James and Choquette, 1984). This is an area where new clasts originating from the lagoon will be deposited and may undergo simultaneous lithification and solution (Bourrouilh-Je Jan, 1998). With the possible rapid formation of phytokarst and cementation of newly deposited clasts, the texture of stage1 is likely to continuously erode and lithify in a rough manner with no time for any smoothing of cement. As this stage is entirely in the vadose layer, any water infiltrating the surface from above will flow down due to gravity and porosity and therefore it will act to constantly dissolve calcium carbonate from the top most layer and carry it farther down in the platform to be reprecipitated or carried into the lagoon waters (Nunn, 1994).

Stage 2 pools in the near lagoon system are the product of lower topography. If enough water is deposited on top of the platform there will be a flow toward the low points. The bottoms of these stage 2 pools still reflects the morphology of the clasts that form it but as the pool is inundated by both fresh water and sea water the dissolution and reprecipitation of the pool bottom will act to gradually form a smoother, less porous bottom cement that is characteristic of stage 3 pools. This planed down bottom cement may be due to the shallow nature of these early stage pools. Early stage pools are subject to influx, flushing and evaporation, all of which may cause rapid dissolution and precipitation. As stage 3 pools erode vertically due to the vadose dissolution process described by Nunn (1994) it is likely that most topographically low pools will receive some drainage from neighboring topographically higher pools and cause them to combine into larger later stage pools. This may explain why the abundance of earlier pool stages such as stage 2 and 3 is higher than that of the later stages 4,5,6, and 7. (Table 1)

As pools evolve between stage 3 and stage 4 the volume increases so they are capable of holding greater amounts of water. This increased volume allows them to erode vertically and horizontally as the water moves from the pool into the porous surrounding cement. Once the pool bottom of stage 3 pools reaches the vadose-phreatic boundary the subsequent stage 4 pool will take advantage of the differences in porosity between these layers (Nunn, 1994) and drain along the erosional gap. This erosional gap provides a new pathway for both influx and drainage. A hypothesis is that this pathway becomes the favored drainage route for pools of this stage which then accounts for the increased erosion along this boundary and the window structures often associated with stage 5 pools. This newly formed window structure in stage 5 pools means that both influx and drainage are likely to occur at this point during tidal changes. As the platform edge continues to erode vertically, a channel is eroded above the window structure leading to the morphology of a stage 6 pool. As wave action physically erodes the pool wall above the window structure, rainwater will likely continue to erode the overlying channel until the two erosional features meet and the pool is open to the lagoon in its final stage 7 form. If the stage 7 pools occur on a peninsula like structure or an area of platform surrounded on two sides by water then there is the possibility that erosion of the back pool wall will result in the formation of island structures like those seen in figure 8.

### *4.2 Evolution of the inland system*

The inland system of karst begins with flagstone surface cement defined as stage 1. This surface on a large scale is very flat allowing rain and lagoon water that infiltrate the system to deposit in extensive shallow pools. Water directed into these pools by the joint channels of the flagstones helps to define the stage 2 pool of this system. The early stages of the inland system appear to have surface cements of relatively low porosity. This is observed both in the slow drainage of these pools as well as in hand sample. The presence of this well cemented cap layer may be due to possible higher evaporation rates in these shallow regions with large surface area. If these areas are inundated with freshwater which will immediately act to dissolve the surface layer, and then are subject to evaporation that will oversaturate the water causing precipitation, then a smoother less porous surface cement would be expected. This may also explain why there is very little relief of individual clasts visible in the early stages of this system. Beneath this cap layer is a less consolidated poorly cemented layer. This porous and poorly consolidated conglomerate layer allows stage 4 and 5 pools to erode vertically as surface water flows with gravity and subsequently erodes this bottom layer. The highly porous nature of this layer may be due to influx of fresh ground water coming from the motu. This can be thought of as the phreatic freshwater lens described by James and Choquette (1984). The presence of fresh groundwater flowing out from the motu may also help to explain the erosion of the platform on the motu side. The late stage inland system pools at Point Aroa very commonly contain rubble-sized sediment suggesting simultaneous deposition and erosion making it difficult to create a well consolidated lithology.

*Motu Tiahura*

At the conglomerate platform of Motu Tiahura most of the surface cement appeared similar to that of the inland system at the Point Aroa field site. This may be due to the high influx of small sand sized sediment into the developing pools. Studies in the Bahamas showed subaerial carbonate sediments to cement rapidly under tropic conditions. (Davis, 1996) Large coral boulders cemented to the top of the platform are more common at Motu Tiahura than at Point Aroa suggesting that influx of material from large storms is common here.

*Motu Ahi*

The conglomerate platform at Motu Ahi shows far less karst pooling than at the other platforms in this study. Undercutting on the lagoon edge of the platform is extreme suggesting that dominant erosion along the platform edge is from the bottom up perhaps in part due to the longshore current that runs along the barrier reef side of Motu Ahi. This undercutting may be responsible for collapse of platform edges before late stage pools are able to develop.

**Figure 8.** Island structures at northwestern tip of Motu Temae. Stage 7 pool present in middle island

## Conclusions

Structural and lithologic variations within a conglomerate platform give rise to distinct systems of development in the formation of karst pools. Stages within systems may have similar traits but overall evolution of a stage within a particular system differs depending upon the physical structure of the platform at that location as well as the dominant intake and drainage systems that can be associated with the stage. The karst pools occurring at Point Aroa on Motu Temae show a systematic evolution that starts with surface cement and develops into a large scale erosional feature. Karst pools in this area can be categorized into stages belonging to two distinct evolutionary systems defined as a near-lagoon system with 7 distinct stages and an inland system with 5 stages. While karst erosion on Motu Tiahura and Motu Ahi share some similar features with that of Motu Temae, the dominant erosional mechanism at Motu Ahi appears to be undercutting and collapse of the platform edge. Karst pooling is a prominent feature at Motu Tiahura but the development of the pools looks to be a combination of the two systems found at Point Aroa. The majority of the surface cement at Motu Tiahura is similar to that in the inland system of Point Aroa yet the near-lagoon layering system is still a prominent influence in pool development on Motu Tiahura.

The layering of the platform into the vadose and phreatic zones with an erosional gap in between acts as a major influential structure to the development of both systems at Point Aroa and Motu Tiahura.

Future research may be interested to investigate the chemistry of the karst erosion of the conglomerate platform and how changes in rainfall and ocean surface salinity effect the development of pools at different times of the year. It is also possible that the other Motu of Moorea may offer environments that present further systems of development of these karst pools.

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**References**

Bourrouilh-Je Jan, F.G., (1998) The role of high-energy events (hurricanes and/or tsunamis) in the sedimentation, diagenesis and karst initiation of tropical shallow water carbonate platforms and atolls. Sedimentary Geology 118:3-36

Davis, J.J. (1996). Rapidity of freshwater calcite cementation- implications for carbonate diagenesis and sequence stratigraphy. Sedimentary Geology 107 :1-10

Drew, D.(1985). Karst Processes and Landforms. Macmillan Education Ltd, London, 63pp.

James, N.P., Choquette, P.W., (1984). The Meteoritic Diagenetic Environment. Geoscience Canada 11: no 4

Murphy, F., (1992). The Geomorphology and Evolution of the Motu of Moorea, French Polynesia. University of California, Berkeley, 101pp.

Nunn, P.D. (1994). Oceanic Islands. Blackwell Publishers, Oxford 413pp

Paterson, K., Sweeting, M.M. 1986 New Directions In Karst. Geo Books, 613pp

Steers, J.A., and Stoddart, D.R. (1977). The Origin of Fringing Reefs, Barrier Reefs and Atolls. Biology and Geology of Coral Reefs 4: 21-105

Viles, H.A., (2001) Scale issues in weathering studies. Geomorphology 41:63-72

# The Relationship Between Wave Energy and Features on the Barrier Reef of Moorea

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ABSTRACT. Wave energy correlates to certain features found on barrier reefs. Fourteen sites around Moorea were selected based on varying wave intensities. 40 meter transects measured the reef crest and forereef parallel to the barrier reef. The forereef transect depth was 4 meters. The features measured on the reef crest are: 1. Width of reef crest, 2. Percent algae cover, 3. Percent turbinaria cover, and 4. Topographic complexity. Four additional features measured on the forereef are: 1. Dominant coral growth type, 2. Height of dominant coral, 3. Percent cover of live coral, and 4. Percent presence of spur and groove. Wave energy at each site was based on buoy data from the last 3 years that recorded height, period and direction. Using this data, wave energy per area was calculated using the equation $E_w=1/8(pgH^2)$* The relative contribution to each site from a single wave event was then calculated using the wave energy component perpendicular to the shore orientation. Wave energy (the treatment) was compared to each measured feature. Based on an analysis of variance, there were significant treatment effects on crest width ($p=0.0050$), topographic complexity ($p=0.0006$), coral height ($p=0.0415$), and percent presence of spur and groove ($p=0.0009$). No significant treatment effects were found on algae cover ($p=0.3855$), or percent cover of live coral ($p=0.3214$). Turbinaria percentages were applied to a non-parametric Kruskal Wallis test, showing no significant treatment effects ($p=0.4336$).

*$E_w$ = Wave Energy in $[j/m^2]$ where:
p=density of sea water, a constant of 1025 $kg/m^3$
g=acceleration of gravity, a constant 9.8 m/s
H=wave height

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## Introduction

Marine environments are heavily shaped and controlled by physical processes (Stoddart 1969). Some of the most influential marine processes are currents, wave action, and upwelling. Wave action is one of the most powerful of these forces, and was chosen for study because it is one of the most influential processes on reef environments. Moorea is an ideal location for an analysis of varying wave energies due to the fact that the south side of the island receives considerably more wave energy than the north. Barrier reefs can be divided into various zones based on biological and physical differences (Krupp 2001) In this study the zones chosen for research were the reef crest and the forereef because they are the two zones most impacted by high turbidity. Observation of these zones at several sites showed clear visual differences between varying wave intensity sites. From these observed differences I decided to base my research on finding a relationship between these visual differences and wave intensity.

Although the geologic history of barrier reefs is well documented, little is known about the current physical processes that shape and control physical and biological features on a smaller time scale. Previous studies on major features of reef topography are few and largely unsuccessful due to difficulties in field measurements and calculation of wave energy. (Stoddart 1969) This study began with an initial survey of various sites around the island. Based on this initial week-long study, several observations were made. These observations primarily include that as wave energy increases: 1. The width of reef crest increases, 2. Algal growth is enhanced, 3. Percentages of turbinaria increase, 4. The frequency and size spur and groove systems increased, 5. Coral densities increase, 6. Height of corals decreases, 7. Topographic complexity increases, 8. The reef crest distance from shore increases, 9. The depth of the reef crest increases, and 10. The species richness, or diversity, of corals on the forereef changes. Considering these ten observations, the equipment available, and the feasibility of measurements with a time constraint., the following eight features were chosen to serve as the basis of research: 1.Crest width, 2. Percent cover of algae, 3. Turbinaria percentages, 4. Topographic complexity, 5. Dominant coral growth types, 6. Percent presence of spur and groove, 7. Percent cover of live coral and 8. Height of live coral.

Materials and Methods

Fourteen sites were selected around the island. These sites were chosen based on obtaining representation of all possible wave intensity areas. Furthermore, the sites selected were in areas free from much additional physical influence in order to control for wave energy. Thus, sites were also chosen away from passes to decrease the physical influences of such factors as currents, fresh water and nutrient input found at and near passes. Sites were predetermined prior to data collection and reached using a kayak or a boat. Two 40 meter transects will be done at each site; one on the reef crest and a second one just outside the reef crest on the forereef, at a depth of 4 meters. Figure 1-1

Wave Energy:

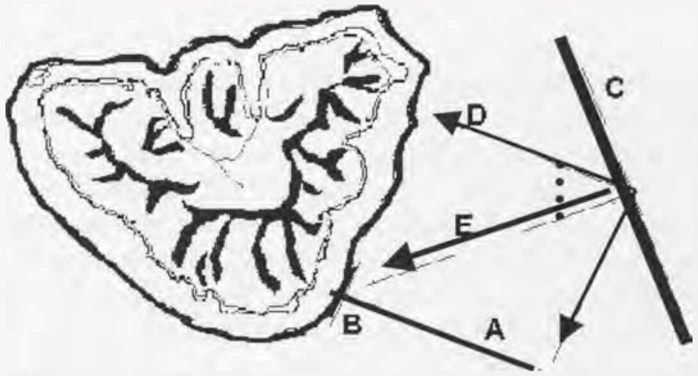
Exact wave energies were calculated for each site and placed into a categorical scale 1 to 5, from low to high. The calculation was based on information received from Meteo France, the weather information center of French Polynesia. Three years worth of wave information was obtained including dominant height, period, and direction for each day. The first step of obtaining an energy value for each site was to plug wave height into a wave energy equation to receive total wave energy $[j/m^2]$ per area of a sinusoidal wave for every day in the three year period. This equation is $Ew=(1/8)pgH^2$

$E_w$ = Wave Energy in $[j/m^2]$ where:

$p$=density of sea water, a constant of 1025 $kg/m^3$

$g$=acceleration of gravity, a constant 9.8 m/s

$H$=wave height



The daily energy values are a measurement of energy for a given wave front from a given direction. Every site has a different shore orientation, meaning that a particular site may face directly toward a dominant swell direction on a given day, therefore receiving a full amount of energy from the high exposure to the swell event. While one site may receive all the energy from this type of swell event, another site on the opposite side of the island with very little to no exposure to the given swell event will receive little to no energy. To calculate how much of the available energy from a particular wave front (C) reaches a given site (B), the shore orientation (in degrees) (A) was subtracted from the direction of the dominant swell event (in degrees) (E) to obtain alpha. Alpha is used to derive the component of energy received by the site (D). (D) represents the component of energy because alpha and the angle completing the Z shape (where (B) is the bottom left point of the Z) are alternate interior angles. This creates two angles equal to each other, just as (A) and (D) form equal angles. The equation is completed by evaluating the problem as a right triangle, and therefore, solving for the component of energy through geometric means. In the triangle above, (E) is the Hypotenus and (A) is the adjacent angle; therefore the cosign function is multiplied to alpha and to the energy available in (E). The portion of energy in a given wave front that reaches each site on each day was added together to find the total amount of wave energy reaching each site over the three-year span. The energy totals for each site were then compared and placed into a categorical scale of one to five from lowest to highest total energy value.

Reef Crest:

Materials:

-40 meter constructed transect tape that doesn't float because it has large nuts fastened on it at every meter
-meter stick
-1 meter chain
-1/4 meter quadrat
-dive slat to record data

Topographic Complexity: 1m length of chain is laid parallel to the barrier reef three times per transect at 0-1 M, 20-21 M, and 40-41 M. This 1 meter chain is rests against the surface in all of the crevices, cracks and bumps on the reef crest so that it is not fully extended. Thus, the chain measurement from the beginning to the end results in a distance less than 1 meter. This distance is the measurement of topographic complexity.

Width of reef crest: I am choosing to define a reef crest using substrate, slope, and morphological structures. On the lagoon side, the reef crest begins where the substrate changes to solid rock (calcium carbonate platform). If this point is difficult to distinguish then it will be defined by slope. When the slope is less than 2%, the reef crest will begin. On the ocean side, the reef crest will end at the first signs of spur and groove and/or at a change in slope to greater than 2%. This measurement is taken at 20 M (or the middle of the transect).

Algae Cover: A quadrat will be used at nine places every 5 M to determine the percent algae cover on solid rock.

Turbinaria Percent: A quadrat will be used to determine the percentage of turbinaria present every five meters at the same nine places along the transect as the algae cover procedure. This turbinaria percentage is a measurement of the percent of turbinaria present in relation to all algae present.

Forereef:

Materials:
-Transect line- 40 meter rope with nuts fastened to it every meter
-Meter stick
-dive slate

Dominant Coral Growth Type: The dominate coral growth type will be recorded based on visual observation from looking down on the transect line every square meter. The dominant coral is the largest and productive looking coral within a square meter. There are seven growth types or functional forms to choose from: 1. Free living, 2. Encrusting, 3. Columnar, 4. Massive, 5. Branching, 6. Rosettes, and 7. Table

Percent Cover of Live Coral: This will be recorded from above every five meters, or nine times per transect. This is a measure of the percent of live coral present within a meter squared.

Height of Coral: The height of the coral will be measured with a meter stick every five meters which is nine times for each transect. This is measured with a meter stick from the uphill side of the dominant coral.

Percent Presence of Spur and Groove: Along each transect, the width and location of each single spur and groove feature will be recorded. Based on this data, a percent of spur and groove present within the 40 meters will be calculated.

Results

Based on an analysis of variance, there were significant treatment effects on crest width (p=0.0050), topographic complexity (p=0.0006), coral height (p=0.0415), and percent presence of spur and groove (p=0.0009). No significant treatment effects were found on algae cover (p=0.3855), or percent cover of live coral (p=0.3214). Turbinaria percentages were applied to a non-parametric Kruskal Wallis test, showing no significant treatment effects (p=0.4336).

Treatment with an analysis of variances was performed for each feature unless variance tests were violated. The Krustal Wallis test was used for the turbinaria percentages, which is a non-parametric test with a different assumption of variance. The one-way ANOVA test was used to examine the influence of wave energy on response variables, accompanied by the post Hawk Tukey test in the case that a significant influence was detected. Unlike the ANOVA, The Tukey indicates where the difference actually lies. ANOVA revealed a significant influence of wave energy on crest width, topographic complexity, coral height, and spur and groove percent ($F_{DF\ treatment}4,{}_{DF\ error}9$, P=0.05). ANOVA revealed no significant influence of wave energy on percent algae cover, turbinaria percentages, and live coral cover ($F_{DF\ treatment}4,{}_{DF\ error}9$, P=0.05). For turbinaria percentages, the Kruskal-Wallis test (a non-parametric test) was also used but failed to reveal significant treatment effects. For dominant coral growth type, there was little to no difference between sites, nor was there a difference between growth types present due to rosett-type dominance.

See Appendix Tables 1-1 through 1-8 and 2-1 through 2-7

## Discussion

It is important to note that many physical factors apart from wave energy affect each site. There is no control, nor measurement, for these factors. Current flow, water temperature, water clarity, salinity, upwelling, dominant wind, and surface currents are all physical factors that could potentially have variable effects on each site. Effort was made to control for wave energy as much as possible by selecting sites away from passes.

Problems or inaccuracies associated with wave energy or buoy data were also found. Firstly, it is important to restate that my energy calculations are based on the daily average wave height and the dominant swell direction. Therefore, this is not a calculation of the total energy received at each site because it does not include energy measurements for every single wave impacting each site each day. These calculations are also missing the non-dominant swell information. This means that the final total energy values for each site are not actual total energy calculations because they are based on a single average wave height from one direction for each day. However, the 3-year data collected is the only information obtainable for energy estimations and it is not possible to get actual energy calculations for a single site over a long period of time. The information itself could be flawed. This information came from an offshore buoy and the location of this buoy could greatly affect the quality of this data. If the buoy was very close to an island, there would be a large amount of island shadowing. This results in less or smaller wave heights from a specific direction, depending on what side of the island the buoy was located. It is also important to know that this information is most likely intended for Tahiti and not Moorea. This could also lead to discrepancies in data because Tahiti shadows a lot of the swell energy from the east. This means that the intensity values assigned for the east side of Moorea could actually be less than their designated amount in this study.

A strong correlation found between crest width and wave energy was clearly seen in the initial observational study and proved true through research. The only difficulties with data collection of this feature was at sites 12 and 13. Here, reef measurement was difficult because the reef crest was so small that there was no clear and defined line to where the crest started on the lagoon side. I speculate that the reasoning for a wider crest width in areas with more wave energy is due to the assumption that wave energy increases coral growth. This assumption was based on the correlation found between wave energy and coral height. Waves bring more nutrients and oxygen, two factors often limiting coral growth

(Bertics 03). I hypothesize that coral growth is enhanced by wave energy, which increases the overall size increase of the reef crest. However, I predicted that the narrowing of the reef crest through erosional processes (spur and groove) would be more rapid process than its overall size increase due to coral growth. Spur and groove, which proved to have a correlation with wave energy, is an erosional process that carries out the eroded material from shallow water down to the ocean floor. Much of this erosion must occur on the reef crest and relate to the overall decrease in size of the reef crest. It can be inferred from my study that the balance between the increase and decrease of crest width is more greatly impacted by the coral growth or size than erosion. In other words, wave energy assists in the growth and building of a barrier reef at a greater rate than its erosional effects.

There was a correlation found for topographic complexity. With the lack of research on this particular topic, there is little to be said about why correlation was found between topographic complexity and wave energy. Despite the finding of a significant correlation, it was a weak correlation. There would have arguably been a stronger correlation had a longer chain been used because the topographic complexity is more pronounced over a larger scale. In addition, if a longer chain were used, a greater amount of reef would have been surveyed; therefore, increasing the sample area and improving the reflection of the natural state.

Turbinaria percentages are affected by wave energy (Denny, 1988) because enough wave energy will break them off the substrate and not enough wave energy inhibits growth due to a lack of nutrient flow and oxygen. Other factors likely affect turbinaria growth as well as wave energy because no correlation was found. What ever factors affects their growth, reproduction, or colonization (physical or biological factor) must vary at each of my sites. There was a trend and some kind of relationship with wave energy that could maybe be shown with lab experiment. I was just unable to prove this relationship in the field. Various other characteristics of turbinaria such as growth speed of, breaking rates, reproduction of, and substrate attachment may be related to wave energy.

Percent Cover of Algae may be a biological feature fully independent and unrelated to wave energy. The growth of and many other characteristics of algae found on reef crests are likely related to wave energy however, my study showed that the percent cover of algae is not correlated to wave energy.

The treatment on coral height showed a correlation. Some of the primary environmental factors influencing reef growth and distribution are, temperature, oxygen, salinity, water turbulence, sedimentation and nutrient availability. (Stoddart 1969) Waves enrich an area with oxygen and nutrients (Sammarco 1991) therefore creating a superior environment for coral growth. The forereef an ideal place for coral growth that can withstand high wave action (Coral Reefs 2002) Some coral growth types cannot withstand high turbidity or do not require high oxygen levels (Bertics 2003) The average of all the sites surveyed for growth type found 90% of the dominant coral to be a rosette. The forereef is the zone that receives the greatest amount of wave energy, (Krupp 2001) thus, one could infer that rosette corals are the most resistant coral growth type to high turbidity areas. Rosette corals may also thrive in these areas because they have a larger surface areas than other growth types which means they most likely require higher levels of oxygen and nutrients to adequately supply all of the polyps. The dominant coral growth type did not produce any results that could be statistically analyzed because rosette corals had a 90% or greater prevalence at each site eliminating the possibility of comparison between growth types or comparing differences between sites because they all had almost identical results.

Live Coral Cover percentages found no significant correlation with wave energy. This was an unexpected result because during data collection this feature showed the clearest relationship based on visual observation. This feature did not demonstrate the expected correlation probably due to a need for increased sample size. The ideal conditions created by high wave energy that supported increased coral heights should be equally supportive in increasing in coral density.

## Conclusion

Significant Correlation was found between wave energy, the treatment and four of the recorded features. This study showed that as wave energy increased so did the width of the reef crest, the height of coral on the forereef, and the percent presence of spur and groove while the topographic complexity decreased. While there may still be a relationship between wave energy and algae cover, percent of turbinaria, coral density this study was unable to establish a significant correlation. The dominant coral growth type found at 4 meters deep on the forereef was an overwhelmingly high percentage of rosette corals however did not vary in percentages from site to site.

## Acknowledgements

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## Literature Cited

Bertics, Victoria. Personal Interview. Moorea, French Polynesia, 17 October 2003.

Centre d¡¯Initiation a I¡¯Environment de Nouvelle-Caledonie. Coral Reefs and Mangroves what you need to know. Novelle-Caledonie. Edit¡¯ Publications

Denny, Mark W. The Biology and the Mechanics of the Wave-Swept Environment. Princeton, New Jersey. Princeton University Press, 1988. pp. 31-45, 86-103, 238-261.

Krupp, David A. (2001) Reef Zoneation and Succession. Retrieved December 11, 2003 from http://krupp.wcc.hawaii.edu/BIOL200/powerpnt/reefzone/

Preskitt, L. Marine Algae of Hawai¡¯I-Turbinaria ornate. Retrived December 11, 2003 from http://www.hawaii.edu/reefalgae/invasive_algae/phaeo/turbinaria_ornata.htm.

Osborne, K and Weaver K. (1989) The Benthic Community Structure of Vaipahu Reef, Moorea and Davis Reef, Great Barrier Reef Australia.

Salvat, F. and B. (1992) Nukutipioi Atoll, Tuamotu Archipelago; Geomorphology, Land and Marine Flora and Fauna and Interrelationships. Atoll Research Bulletin No 357 pp. 6-9.

Sammarco, Paul et all. (1991) Coral Reef Geomorphology as a function of seasonal prevailing currents and larval dispersal. Paleoclimatology: paleoecology. 88 pp. 1-12.

Stoddart D.R. (1979) Descriptive Reef Terminology. Department of Geography, Cambridge, United Kingdom. pp. 5-13.

Stoddart D.R. (1969) Ecology and Morphology of Recent Coral Reefs. . Department of Geography, Cambridge, United Kingdom. pp.433-484

## Appendix

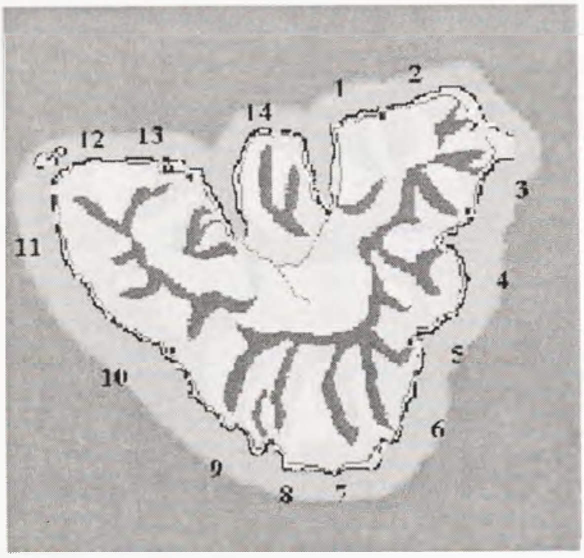
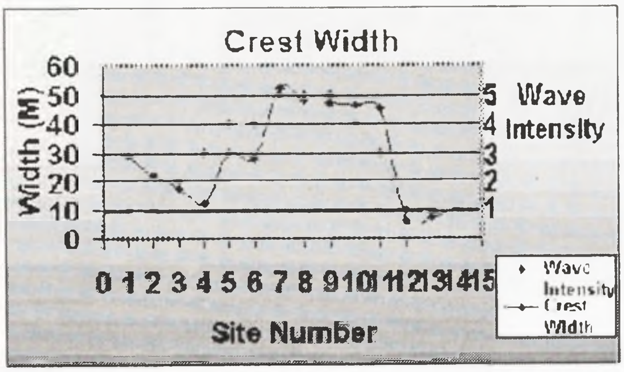


Figure 1-1 Site Map



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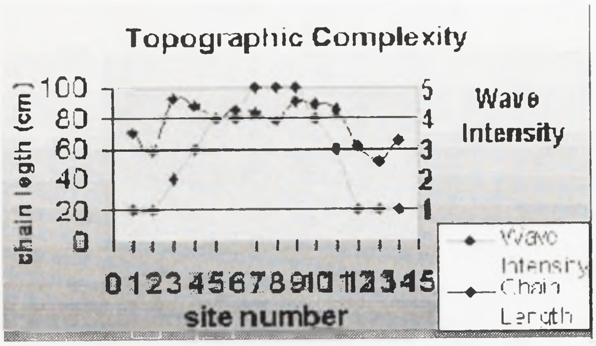

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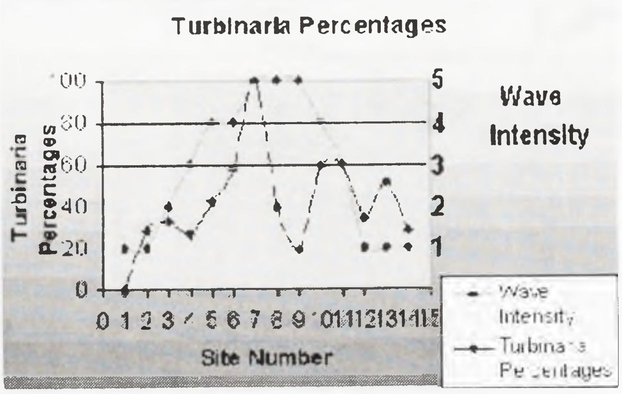

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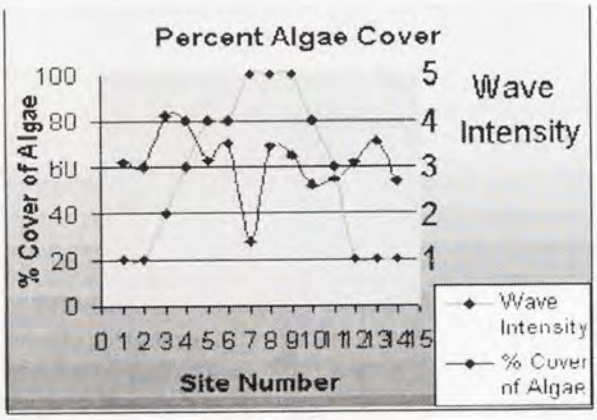

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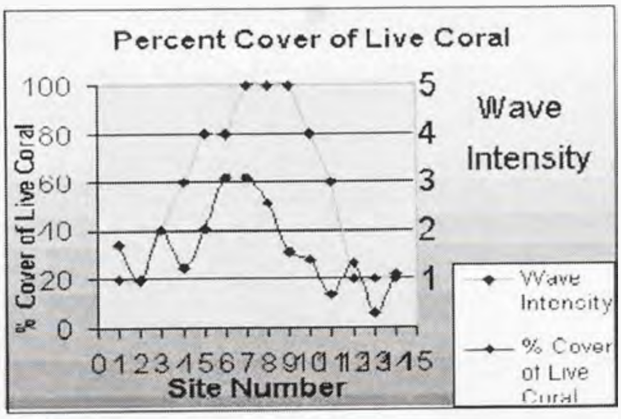

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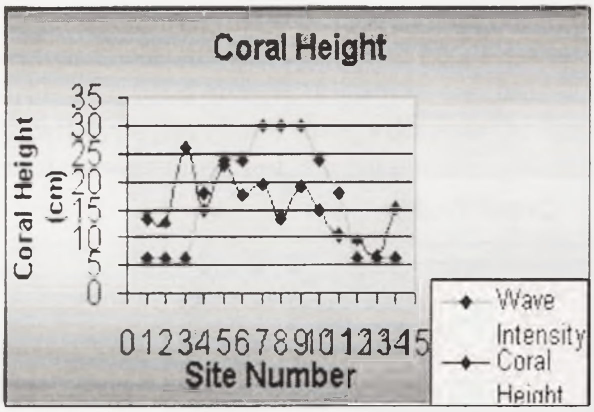

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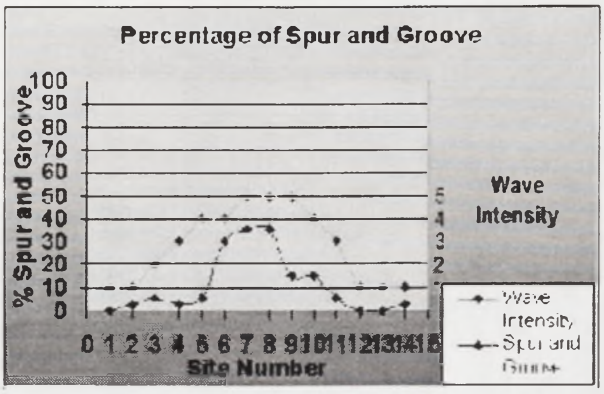


Table 1-7

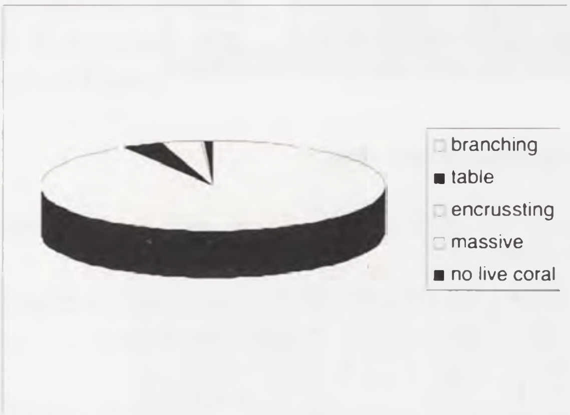
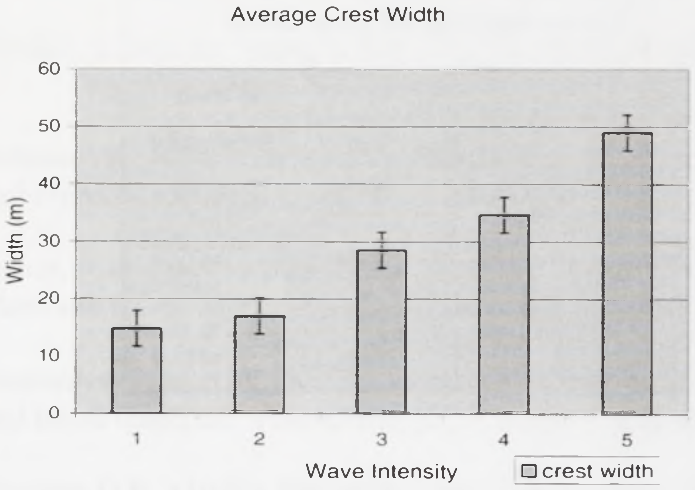


Table 1-8

In each of the below tables each bar represents an average of all the sites within that particular wave intensity category



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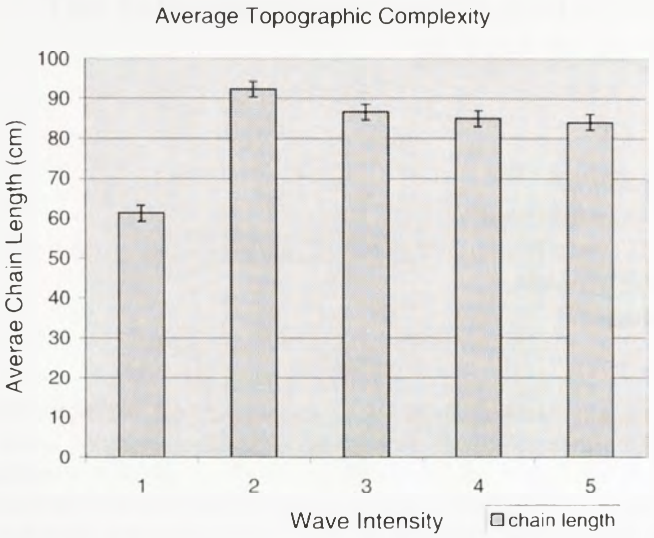

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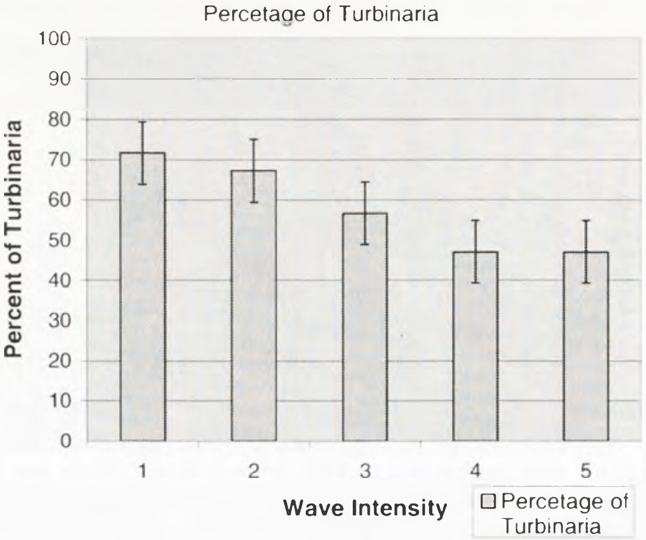

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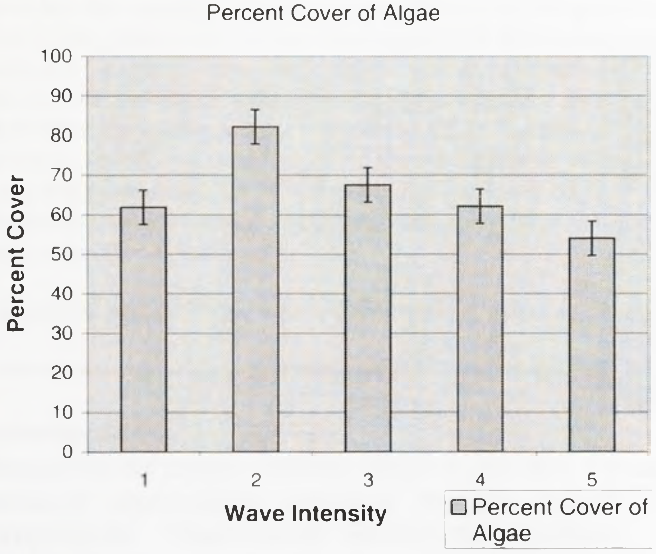

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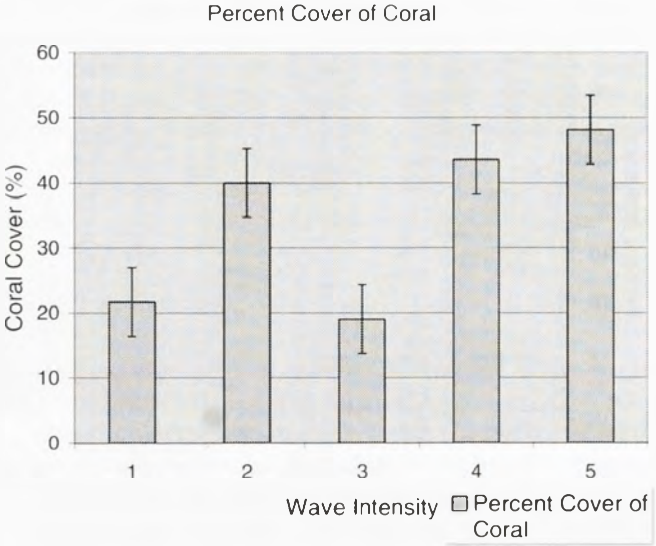

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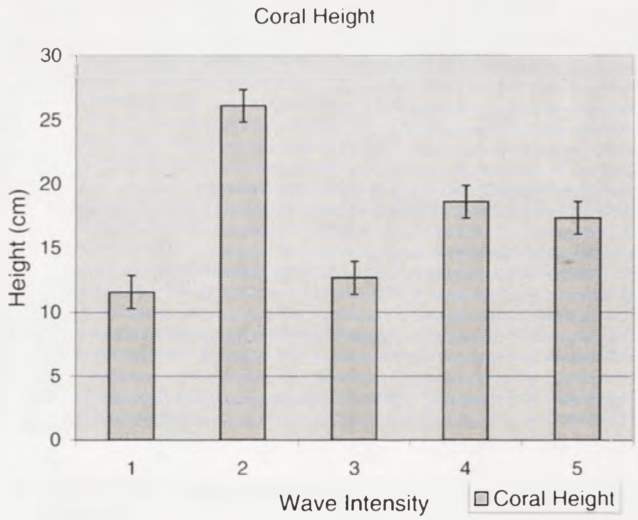

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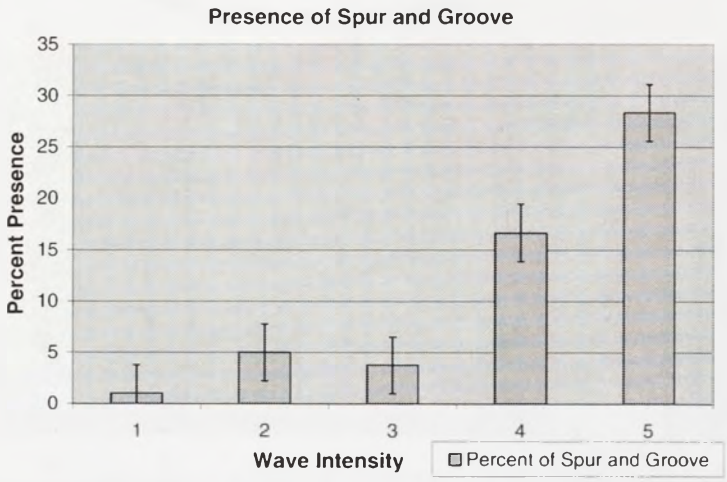

Table 2-7

# The influence of sediment and irradiance on the survival of the seagrass *Halophila decipiens* Ostenfeld

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Moorea, French Polynesia
December 15 2003

ABSTRACT. The distribution of the seagrass *Halophila decipiens* Ostenfeld was mapped in the Pao Pao Bay on Moorea, French Polynesia. Comparison to a *H. decipiens* distribution map from 1996 revealed that seagrass beds in the estuary, particularly in the southeastern portion of the bay, have shown substantial growth, while beds in the lagoon have shifted westward, but have not increased in size. Transplant experiments were subsequently carried out to investigate how sediment, irradiance, and plant type affects *H. decipiens* survival and growth rates. Seagrass beds were differentiated on the basis of location and sediment grain size. The first 2 week transplant of *H. decipiens* from both lagoon and estuary beds showed transplanting is more successful with estuary plants, regardless of the sediment used for transplanting. The second 2 week trial revealed that transplant success is not affected by the percentage (7.01%, 17.4%, 56.72%) of fine grain ($<125\mu m$) sediment. One of the primary factors that limits growth in the lagoon bed appears to irradiance caused by light reflecting off of carbonate sediment. Light tolerance transplant experiments conducted over a 50 hour period in uncovered outdoor flow-through tanks showed that chlorophyll from lagoon plants degrades more rapidly when transplanted in carbonate sediment (21.17% survival) than when transplanted in the terrigenous (72.03% survival). In addition, lagoon plants have a significantly higher survival rate in black (53.38% survival) sediment than in carbonate sediment. In addition, estuary plants transplanted in the same manner in both terrigenous and carbonate sediments experienced limited chlorophyll degradation. Estuary plants are more adapted to fluctuating environmental conditions, and are typically found at shallower depths and would therefore have higher survival rates than lagoon plants

Keywords: *Halophila decipiens*, transplanting, mapping, irradiance, sediment preference

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## Introduction

Seagrasses are unique vascular plants in that they are monocot angiosperms confined to the marine environment. These marine macrophytes contribute to the detritus in coastal areas (Cushing 1976, Klumpp and Howard 1989), which supports benthic diversity and contributes to the buffering and filtering of nutrient and chemical inputs and removal of ammonia out of sediment (Short and Short 1984, Connell 2001). In addition, grasses buffer and recycle nutrients that can reduce eutrophication and can bind organic pollutants. Seagrass beds contribute to highly productive ecosystems that are economically important by providing a complex physical canopy structure for juvenile fish, and support high secondary productivity by providing substratum for epiphyte and epifaunal organisms (Short 2000 et al.). Seagrasses can be impacted by increasing human development along coastal areas, in particular through increase of nutrient rich runoff which can lead to algal blooms that shade seagrass, limiting growth, and out compete seagrass for resources.

Seagrass distribution is determined by various factors such as turbidity, depth, sediment type and chemistry, and nutrient loads (English 1997). In the South Sulawesi both biogeochemical properties of the sediment type and the degree of influence from terrigenous run-off have proven to be important factors affecting the availability of nutrients to seagrass growth and determining the response in morphology, biomass and chemical composition of the seagrass material (Erftemeijer 1994). Seagrass beds are found in varying sediment types and depths in coastal areas. Some seagrasses have the ability to adjust both structure and function of light harvesting apparatus in response to changes in irradiance (Kurtz 2003). In addition, high light plants can synthesize smaller photosynthetic units to prevent photodamage (Peralta 2002) and can have a higher photosynthetic conductance.

### 1.2 *Halophila decipiens* distribution and characteristics

In general seagrasses can be found in extensive beds off of every continent except for Antarctica (World Atlas of Seagrasses 2003), however *Halophila decipiens* Ostenfeld occurs pan-tropically (fig. 1.2). On the island of Moorea this seagrass is characterized by monotypic beds which can stretch from the shallow areas of turbid bays to the deeper, clearer waters of the lagoon. This seagrass can also favor areas with increased pollution and organic material (den Hartog 1989). The morphology is highly adaptive to its environment, as shown by morphological analyzes of *H. decipiens* in varying habitats (Vowles 2000, Emmet 1996, Rowderick-Jones 1998). In addition, *Halophila* species are well adapted to high levels of disturbance because they have rapid biomass turnover rates (Walker 1999). Between the Potamogetonaceae and Hydrocharitaceae family there are approximately 48 species of marine angiosperms; *H. decipiens* is one of 11 species in the *Halophila* genus, which is a member of the Hydrocharitaceae family. *Halophila decipiens* is characterized by toothed leaf margins that can be seen under a dissecting microscope, pubescence on leaf surface, and monoecious with male and females flowers on the same floral shoot. Photographs taken of this plant were identified as *H. decipiens* (Kuo 2003).

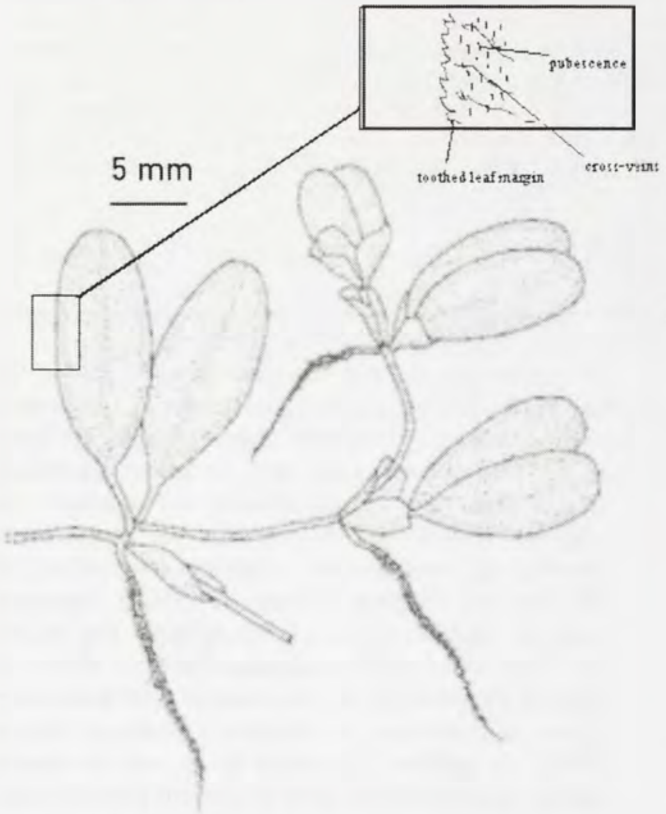

**fig. 1.1** Drawing of *Halophila decipiens* Ostenfeld showing toothed leaf margins and pubescence (World Atlas of Seagrasses 2003).

### *Objectives*

The objectives of this study are

1. to map *Halophila decipiens* beds in Pao Pao bay and compare the distribution to that of beds mapped in 1996.
2. to compare light tolerance between estuary and lagoon populations of seagrass
3. to determine whether sediment reflectivity affects light tolerance, in terms of plant health
4. to investigate whether a correlation exists between terrigenous and carbonate sediment and plant growth

**Figure 1.2** World-wide distribution of *Halophila decipiens* (World Atlas of Seagrasses 2003).

## Materials, Methods and Site Description

### *Study Site*

This study was conducted on the island of Moorea, in the Society Island chain of French Polynesia at 17°30'S latitude and 149°50'W longitude. This volcanic island was formed between 1.5 and 2 million years ago and has since been eroding, forming sharp mountain ridges and two large bays. This study was conducted in the vicinity of Pao Pao Bay in estuary and lagoon environments. This bay receives much of the runoff water from the Pao Pao valley, via the valley river and various storm drains which empty directly into the bay. The lagoon area is composed of mostly carbonate sediment which is biogenically produced and derived from erosion of the reef. The lagoon is not exposed to as much runoff or fluctuations in salinity and as those seagrass beds directly in the bay and adjacent to land. The bay is composed of mainly terrigenous sediment which is derived from erosion of the basalt from land, and since reef structures are not as prevalent as in the lagoon, the sediment is also darker is color.

### Mapping

Seagrass beds were first located from previous maps (Emmett 1996, Rowderick-Jones

1998, Hu 2000) by kayaking and snorkeling. Upon location of the beds, depth measurements and measurements from shore were made while snorkeling. Once bed margins had been traced, the beds were retraced while in a kayak using hand-held GPS equipment with a spatial resolution of 10-17m. Initially this project intended to encompass mapping of both the Opunohu and Pao Pao Bays, however the high turbidity of the Opunohu bay made it difficult to survey without the use of SCUBA. GPS coordinates were recorded and transferred to a map of Moorea where outlines of the beds were subsequently drawn and compared to the 1996 survey. The most recent formal mapping done of the seagrass beds was a study conducted in 2000 (Vowles 2000), however when considering seagrass bed growth, the map made by Emmett was used for comparison since my methods for mapping beds were more similar to Emmett's than to Vowles.

### Basis for Transplanting

Upon comparison with the map (Emmett 1996), estuary beds had grown, while the lagoon bed had roughly remained the same size. Further experiments were conducted to test for sediment type and light tolerance as possible limiting factors for growth. All plants used in these experiments have been removed using a small gardening trowel, and only the top 10cm of sediment was collected for transplanting and grain size analysis, because root growth does not extend beyond this depth (Coles 1995). In addition all plants were shielded from the sun during transport to the lab, and all transplants were initiated less than 12 hours after plant collection.

### Transplant Study #1 – Sediment Preference in Relation to Population Type

A comparison of seagrass distribution between 1996 and the present, showed more extensive growth in the estuary beds (see Results for details). This experiment investigates whether or not *H. decipiens* sediment influences the growth rate and transplanting success.

Twenty plants were collected from both the interior of estuary and lagoon beds. Ten lagoon and 10 estuary plants were transplanted into 3-4cm of the two sediment types. All transplants were removed from their original sediment, as part of the procedural control, and placed in a covered outdoor tank for 2 weeks. An initial leaf count was made prior to planting, and a final leaf count was made at the end of 2 weeks, after transplants had been removed from their sediment. Each transplant had between 28-77 leaves. From initial and final leaf counts a percent survival was calculated to determine plant growth rates.

### Transplant Study #2 – Light Tolerance in Relation to Plant and Sediment Type

Upon initial observations which showed leaves of lagoon plants deteriorating in a high light environment more rapidly than estuary plants, a preliminary transplant study was done with 3 estuary transplants in estuary sediment and 3 lagoon transplants in lagoon sediment placed in uncovered outdoor tanks at approximately 1m depth for 50 hours. When this initial study showed some difference in light tolerance, it was necessary to conduct more extensive trials. To eliminate the possibility of estuary sediment influencing the success of lagoon transplants, and to specifically test for the effect of sediment color on light tolerance, a fine layer of black Tahitian sand was used to mimic the dark color of estuary sediment.

One-hundred eighty plants were collected from the lagoon and 120 plants were collected from the estuary beds over the course of this study. Transplants were not standardized for this particular study. Sixty plants from the estuary were transplanted into lagoon sediment and 60 were transplanted into estuary sediment. Thirty transplants from each sediment type were placed in covered outdoor tanks, and 30 were placed in an uncovered outdoor tank at 1m depth, and the trials were run for 50 hours. The same was done for the 180 lagoon plants, only there is additional sediment type: lagoon sediment with a fine layer of black Tahitian sand. To determine light tolerance, leaves were examined at the end of the trial and compared with leaves that at been kept in the covered aquarium. The ratio of number of green leaves to total leaves was used as a measure of light tolerance. Those leaves which had lost most or all of their green pigmentation were considered not green. All plants were transplanted within 12 hours of collection to lessen the amount of plant degradation taking place before the transplant.

### Transplant Study #3 – Sediment Preference

Plants were collected from the Gump bed for transplanting into 3 different sediment types, based on percentage of fine grain sand (<125μm). Sediments used in transplants were taken from the lagoon, estuary, and Gump seagrass beds and have increasing percentages of fine grain sand, respectively. Each transplant was standardized and consisted of one strand of seagrass with 8 leaves and all roots intact. Plants were transplanted into containers in covered outdoor tanks; at the end of two weeks plants were dried for 4 hours at 60°C and immediately weighed to determine an average dry biomass. Growth was measured with a final leaf count per transplant. For the purposes of transplant #4, all plants were collected from the Gump bed because of its close proximately to the station and depth at which plants are found, which makes for a more efficient collection process.

To determine an average dry biomass to compare with the biomass from experimental data, 63 plants from the Gump bed were collected and an average dry biomass was found. If transplants show a significant difference in biomass from the calculated average of 63 plants, then biomasses will be used as another measure of growth in addition to leaf counts.

**Additional Analyzes**

In addition to the mapping and transplanting, water quality measurements, temperature and salinity, were taken for a comparison between lab and field settings, as well as for confirmation of salinity fluctuations in seagrass beds within the bay.

Sediment taken from 10 different sites in each of the estuary, lagoon, and Gump seagrass beds were analyzed for grain size before sediment was used in transplant #4. The following (table1.1) shows the conditions of each type of transplant experiment conducted.

**Transplanting Conditions**

| Transplant Type | Sediment Preference | Light Tolerance |
|---|---|---|
| duration | 2 weeks | 50 hours |
| temperature | 26.6°C | 26.6°C |
| water depth | 11cm | 1m |
| covered | yes | no |
| sediment depth | 3-4cm | 3-4cm |
| type of tank | flowthrough | flowthrough |

**Table 1.1** Conditions of sediment preference and light tolerance transplant experiments.

### 3. Results

### 3.1 Mapping

Map of Pao Pao Bay, shows the boundaries of seagrass beds from the 1996 study and from current mapping results. The boundaries for the lagoon bed have shifted in a westward direction, however the area of coverage is roughly equal to what it was in 1996. The estuary bed has grown considerably since 1996, in particular along the eastern edge of the bay and on the western edge adjacent to the two churches.

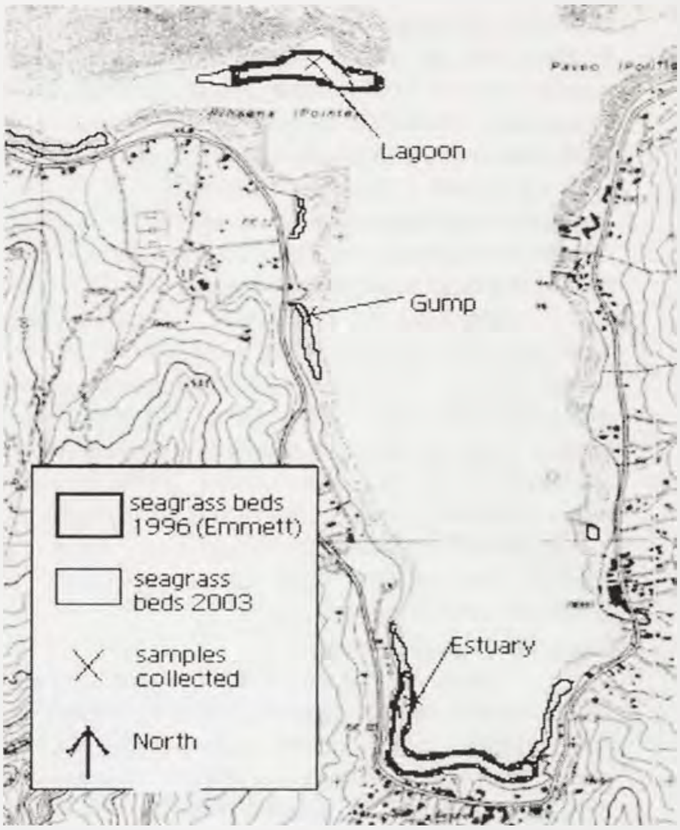

**Fig 3.1** Map of Pao Pao Bay showing the distribution of *H. decipiens* beds in 1996 (Emmett) and 2003.

In terms of environmental and physical factors, estuary seagrass beds are found at shallower depths, on terrigenous sediment and have more disturbances from fluctuating salinity, turbidity, and within close proximity to storm drains. The lagoon beds are found at greater depths, on carbonate sediment, and have more consistent environmental conditions.

**Environmental Factors**

| Seagrass Bed | Estuary | Lagoon |
|---|---|---|
| Depth | 0.5m -5m | 6m - 20m |
| Salinity | fluctuating (32-39ppth) | constant (37-38ppt |
| Turbidity | fluctuating | constant |
| Sediment Color | dark/terrigenous | light/carbonate |
| Temperature | constant (28°C) | constant (27°C) |
| Storm Drains | adjacent to beds | none |

**Table 3.1** Comparison of environmental and physical factors between lagoon and estuary seagrass beds.

### 3.2 Plant Type and Sediment Preference

The investigation of plant and sediment type in relation to survival shows that estuary plants have a higher rate of survival, and that plants seems to transplant slightly better into lagoon sediment.

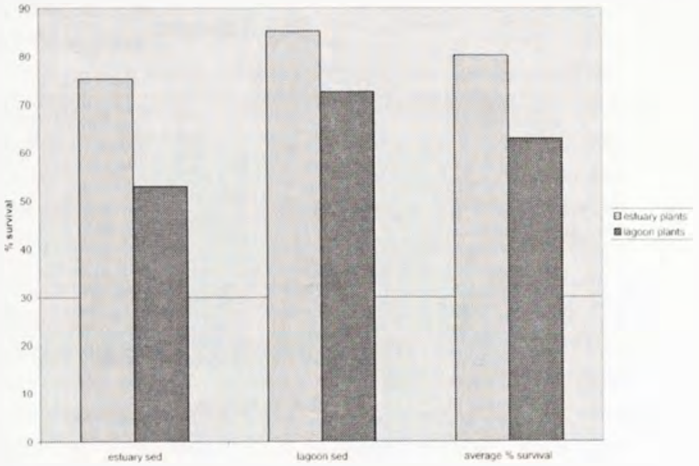

**Fig. 3.2** Percentage survival of estuary and lagoon plants transplanted into estuary and lagoon sediments. Estuary plants have an overall higher transplanting success.

### 3.3 Light Tolerance Transplants

Preliminary transplants studies were conducted to see if light tolerance varies amongst estuary and lagoon plants. Estuary plants had 63.89% green while lagoon plants only had 11.11%. In addition, lagoon plants transplanted into estuary sediment appeared to have a slower rate of degradation; lagoon plants in estuary sediment had 78.68% green while lagoon plants in lagoon sediment had 33.56% green after the 50 hour study. These results are based on 3 replicates of each transplant, further investigations include 30 replicates for each type of transplant.

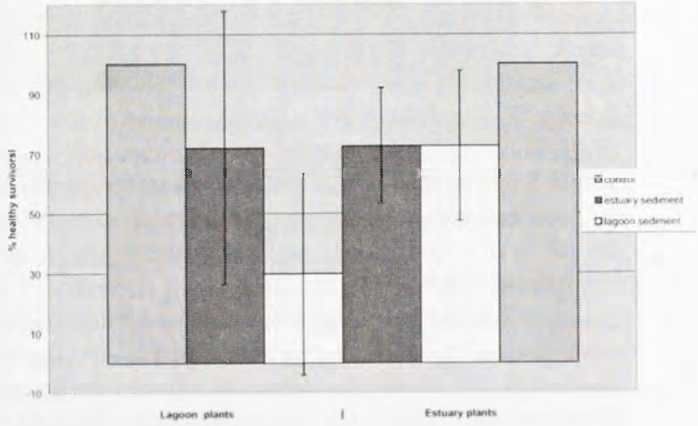

**Fig. 3.3** Percent of transplants from lagoon and estuary retaining green leaves (healthy) after 50 hours on sediments of two different irradiance properties. Lagoon plants are affected by the reflectivity of the carbonate sediments as shown by the lower survival rate on lagoon sediment.

The t-test run for estuary plants in lagoon and estuary sediment gives a t-calculated value of -0.037 that is lower than the t-critical value of 1.689, shows that estuary plants survival is not compromised by being transplanted in the light colored lagoon sediment.

The t-test run for lagoon plants in lagoon and estuary sediment gives a t-calculated value of -4.018 which is lower than the critical value of 2.262, therefore even though there is a noticeable different between the health of lagoon plants when transplanted in the carbonate sediment, the t-test shows that these results are not significant.

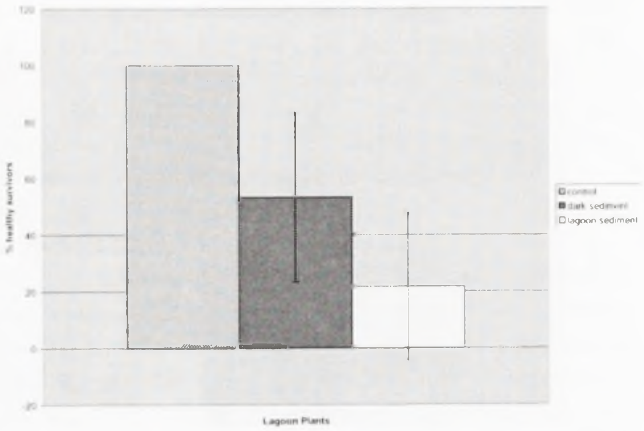

**Fig. 3.4** Percent survival of Lagoon plants measured as the percentage of green (healthy) leaves after 50 hours on sediments of two different irradiance properties. The less reflective dark sediment allows for a higher survival rate than the highly reflective lagoon sediment.

Lagoon plants transplanted in lagoon sediment with a fine layer of black Tahitian sand have a higher light tolerance than when transplanted in light colored carbonate lagoon sediment. Since transplanting in a dark colored sediment (fig 3.4), and estuary sediment (fig 3.3) produced similar results, sediment color is the main determinate of light tolerance with lagoon plants.

At-test run on lagoon plants in lagoon sediment and lagoon plants in dark sediment gives a t-calculated of 2.865 and a t-critical one-tailed of 1.717, therefore it is significant that lagoon plants survive better when transplanted into uncovered flow-through tanks in dark sediment than in the light colored lagoon sediment (Fig 3.4).

### 3.4 Sediment Preference Transplants

### Grain size analysis

| | Estuary | | Lagoon | | Gump | |
|---|---|---|---|---|---|---|
| grain sizes | average % | std dev | average % | std dev | average % | std dev |
| 2mm | 6.33 | 3.14 | 3.92 | 2.86 | 1.61 | 2.81 |
| 500µm | 35.61 | 14.01 | 34.95 | 12.41 | 7.22 | 9.31 |
| 250 µm | 13.84 | 3.96 | 29.39 | 5.8 | 7.97 | 5.61 |
| 125µm | 25.76 | 13.68 | 24.96 | 6.1 | 25.35 | 9.37 |
| **<125µm** | **17.04** | 10.57 | **7.1** | 3.05 | **56.72** | 14.49 |

**Table 3.2** – A total of 10 sediment samples were collected from each bed where seagrass was collected. The Gump bed has the highest average percentage of fine sand (<125µm) with 56.72, followed by the estuary bed 17.04, and then lagoon bed 7.1.

*H. decipiens* can growth in a wide range of grain sizes and sediment types. The grain size analysis shows a difference in the average percentages of grains <125µm ranging from 7.1% - 56.72%.

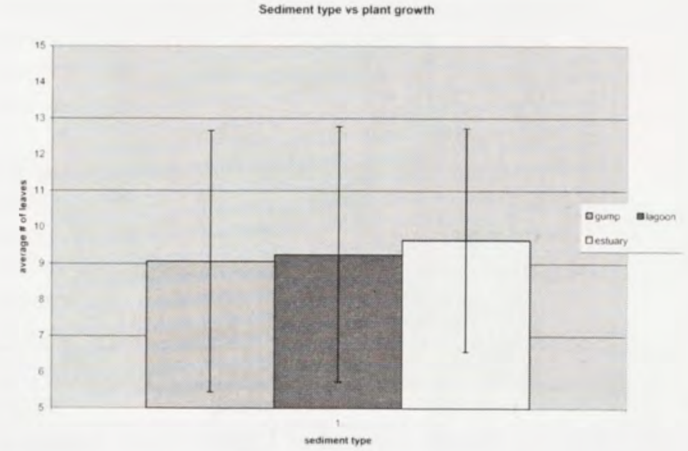

**Fig. 3.5** Average number of leaves in transplants of Gump plants into 3 different sediment types. Each transplant began with 8 leaves and at the end of the 2 week study plants in all sediment types have similar growth rates.

Plants from the Gump bed transplanted into 3 different sediment types, based on location and grain size (table 3.2) show similar average growth rates, which indicates that *H. decipiens* will not preferentially survive on a particular sediment type. Plants in estuary sediment have a slightly higher average number of leaves at the end of the study than those in Gump and lagoon sediment.

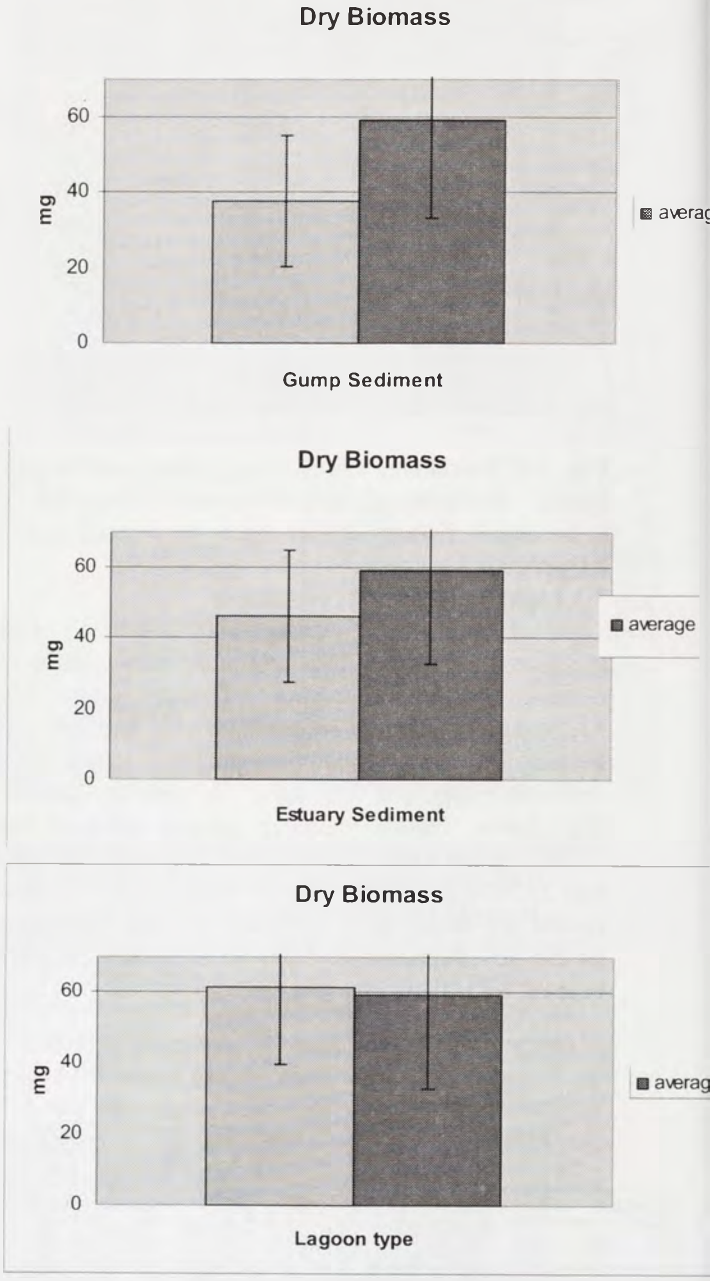

**Fig 3.5** Comparisons of dry biomass for plants in lagoon, estuary, and Gump sediments at the end of the 2 week study and a calculated average dry biomass derived from 63 plants.

The only transplants with a biomass higher than the calculated average are plants in lagoon sediment . However, none of the average dry biomass calculations for the transplants (fig 3.6) in different sediment types are significantly different from the calculated average dry biomass. Lagoon and average, t-calc is 0.349 and t-crit one-tailed is 1.692, Gump and average t-calc is -3.110 and t-crit one-tailed is 1.664, and for estuary and average t-calc is -2.051 and t-crit one-tailed is 1.663.

## 4. Discussion

### 4.1 Mapping

A comparison of the methods for earlier used for mapping done by Vowles(2000) and Emmett(1996), mapping with this project indicates that sampling was conducted in a manner similar to Emmett's due to the lack of SCUBA equipment, time and resources. Although Vowles method of mapping is thorough, and is an extensive mapping of both Pao Pao and Opunohu bays, this study did fail to recognize the presence of at least one bed just outside Pao Pao Bay, that was clearly present in 2000 because it was sampled for study (Hu 2000). In addition, the Vowles study notes that seagrass strands less than 50m long were not always mapped due to inadequate resolution to map in this detail. An advantage of the methods used in this current study is that any size bed or strand of seagrass can be mapped, provide it is within a depth that can be reached through free diving. Mapping discrepancies between these two techniques shows neither procedure is flawless, and that each type of mapping technique has intrinsic limitations.

Although there appears to be no marked growth since the 2000 study, there has been growth since the 1996 study, and this growth appears to be legitimate because Emmett's mapping methods would have shown a presence of seagrass in the shallow and continuous beds along the edge of Pao Pao bay, in particular in front of the churches in the south western portion of the bay, and on the eastern edge of the bay

Possible reasons for a change in distribution of *H. decipiens* distribution in the estuary include, but are not limited to, variations in runoff, rainfall, and nutrient loading into the bay from year to year. Since this mapping study was done at the same time of year as the study in 1996, time of year is not the main factor influencing distribution, however it is possible that sedimentation following heavy rainfalls, particularly in the estuary beds, could have caused portions of seagrass to be covered and not to be noted during mapping in 1996.

### 4.2 Sediment preference in relation to plant type

Transplanting success differs between estuary and lagoon plants. Estuary plants have a higher transplanting success than do lagoon plants. Although the difference is slight, it could be attributed to estuary plants inhabiting a continually fluctuating environment where flexibility and adaptability is necessary for survival. Estuary plant populations are often in close proximity to storm drains, undergo changes in salinity, nutrient inflow, and sedimentation. They can survive while covered by dense canopies of epiphytic algae and at depths of less than one meter. In contrast, plants in the lagoon bed are found only at depths of 6m or greater, do not have a dense covering of algae, and experience fluctuations of salinity and turbidity.

Different methods of transplanting provided different kinds of useful information. This sediment preference study did not regulate plant size based on numbers of leaves or presence of roots, and therefore the transplants were more successful. The grain size transplants were most successful and included standardized "plants" each one consisting of a strand of *H. decipiens* with 8 leaves and all roots intact. This second method of transplanting revealed less variable growth amongst a particular type of plant, and an average overall positive change in the number of leaves from the start of the experiment. The disadvantage to this more successful procedure is that many of the plants collected cannot be used, and therefore it is necessary to have larger collections which are more damaging to seagrass beds.

### 4.3 Light Tolerance in relation to plant and sediment type

Sediment type in terms of irradiance properties influences growth significantly. Irradiance on carbonate sediments is an important factor limiting growth of the lagoonal seagrass beyond its current distribution. Controlled lab results (fig 3.3, 3.4) suggest that reflection of sunlight through the clear lagoon water could cause chlorophyll breakdown and leaf degradation if lagoon beds stretched to shallower depths. In the estuary, seagrass is found starting in less than 1m of water because the leaves are not as sensitive to irradiance (fig. 3.3) and are better adapted to living in a high stress, and fluctuating environment. In addition, irradiance levels are not as high due to the darker sediment color.

Other factors may be correlated with irradiance to affect survival. Various additional environmental factors contribute to lagoon plants restricted growth. Herbivory by reef fish (Rowderick-Jones 1998) limits seagrass growth from encroaching upon the back reef area, growth could also be limited by low nutrient availability (Stapel 1997). The steep slope that separates the back reef and the areas where the lagoon bed is found, is subject to hydraulic stress from strong currents caused by water flowing in and out of the nearby channel and from wave action on the reef crest. These stresses combined with irradiance could also prevent growth into shallower depths.

### 4.4 Sediment preference including biomass and leaf count change

Sediment type in terms of grain size and location does not appear to be affecting colonizing ability and survival rates. From these transplants *H. decipiens* does not appear to favor a sediment type based on grain size, which is further evidence that it is a highly plastic species, and able to colonize a wide range of sediment types. In addition, the seagrasses *Thalassia hemprichii* and *Hadule uninervis* were uninfluenced by sediment conditions in transplant experiments (Hojilla 2001). Because each transplant has such a wide range of dry weights and when the plants are dried their biomass is so small, it is difficult to compare transplants to an average biomass. Since the calculated average that was used for comparison was taken from plants that could only have theoretically been used in transplants, a more accurate measurement of growth would be to actually weigh plants before the transplant experiment begins using a wet biomass measurement. Provided that measurements could be made without causing damage to plants, and that plants could be blotted dry so that excess water is not falsely attributed to plant biomass, using wet biomass might be a more effective measurement of growth.

### 4.5 Further Research

*Halophila decipiens* can inhabit a wide range of environments and can withstand a array of environmental variation. *H. decipiens* is tolerant of salinity fluctuations as is apparent from colonization of estuarine environments; future research could include transplanting with increasingly hyposaline conditions, to determine a minimum salinity necessary for survival. In addition, comparisons can be made between lagoon and estuary plant populations to determine whether the estuary population is more tolerant of hyposaline environments. *Halophila ovalis*, a species which bears close resemblance to *H. decipiens* has been rumored to inhabit the areas of Moorea, further investigation could focus on locating this other species, and from there looking at niche partitioning and distribution of the 2 species. In addition, a comparative survey of benthic meiofauna and macrofauna abundance and diversity in areas of seagrass beds and areas without beds, would be useful for quantifying the diversity these seagrass habitats can support.

## 5. Conclusion

The distribution of the seagrass beds in Pao Pao Bay have changed in some areas since 1996, and in particular in the southeastern portion of the bay. With the expansion of seagrass beds limited to estuarine areas, various factors are limiting growth in the lagoon bed. Although herbivory and hydraulic stress might prevent seagrass from colonizing the shallower back reef area, another major factor limiting growth appears to be irradiance from the light colored carbonate sediments.

While sediment does not appear to be significantly influencing plant survival, the plasticity within the *H. decipiens* is apparent in how estuary and lagoon plants tolerate transplanting, and how fast they experience chlorophyll degradation at shallow depths. In addition the number of stresses that must be endured by estuary plants, including algal growth nutrient input and turbidity shows that this population of seagrass is highly adaptable, and due to its high rate of turnover, able to colonize a much wider range of conditions.

## 6. Acknowledgements

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GPS coordinates for seagrass bed boundaries given to Zia Maumenee (University of Montana) Voucher specimens are deposited in the University of California Herbarium.

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## LITERATURE CITED

Coles, R.G., Lee Long, W.J. and L.J. McKenzie. (1995) A standard for seagrass resource mapping and monitoring in Australia. In: "Australian Marine Data Collection and Management Guidelines Workshop 5-6 Dec. 1995, CSIRO Marine Laboratories, Hobart, Tasmania."Environment Resources Information Network.

Connell E.L. and D. Walker. (2001) Nutrient cycling associated with the seagrass *H. ovalis* in the Swan-Canning estuary based on seasonal variations in biomass and tissue nutrients. Hydrological Processes. 15(3): 2401-2409.

Cushing, D.H. and J.J. Walsh ed. (1976) The Ecology of the Seas. W.B. Saunders Company. Toronto, Canada. 226-227.

den Hartog, C. (1989) Distribution of the seagrass *Halophila decipiens* Ostenfeld in the Indian Ocean. Acta Botanica Neerland 38(1):81-83.

Emmett, M. (1996) The distribution and morphology of seagrass (*Halophila decipiens*) in Moorea, French Polynesia. University of California, Berkeley. Unpublished.

English, I.S., et al ed. (1997) Survey Manual for Tropical Marine Resources. 2nd ed. Townsville, Australia. 239-271.

Erftemeijer, P. L. A. (1994) Differences in Nutrient Concentrations and Resources Between Seagrass Communities on Carbonate and Terrigenous Sediments in South Sulawesi, Indonesia. Bulletin of Marine Science. 54(2): 403-419

Hojilla, Wilfredo Uy, et. al. (2001) The interactive effect of shading and sediment conditions on growth and photosynthesis at two seagrass species, *Thalassia hemprichii* and *Hadule uninervis*. Functioning of Phillippine seagrass species under deteriorating light conditions. Ph.D.dissertation. Wageningen University.

Hu, Jia. (2000) Reproductive allocation in the seagrass, *Halophila decipiens* on Moorea, French Polynesia. University of California, Berkeley. Unpublished.

Kelly, N.M. (2001) Predictive mapping for management and conservation of seagrass beds. Marine Freshwater Ecosystems. 11(6):437-451.

Klumpp, D.W. and R.K. Howard. (1989) Trophodynamics and nutritional ecology of Seagrass communities. 394-457. In: Biology of Seagrasses: A treatise on the biology of seagrasses with special reference to the Australian region. Elsevier, Amsterdam.

Kurtz, Janis et al. (2003) *Vallisneria americana* and the community of root-associated heterotrophic bacteria. Journal of Experimental Marine Biology and Ecology. 291(2):199-218.

Kuo, John. (2003) University of Western Australia. Personal correspondence. 16 Oct. 2003.

Peralta, G. et al. (2002) Effects of light availability on growth architecture and nutrient cycling content of the seagrass *Zostera noltii* Hornem. Journal of Experimental Marine Biology and Ecology. 269(1):9-26.

Roderick-Jones, Rowan A. (1998) Seagrass, *Halophila decipiens* Ostenfeld, populations in Moorea, French Polynesia, and their response to herbivory and light. University of California, Berkeley. Unpublished

Short, F.T. and C.A. Short. (1984) Purification of estuarine and coastal waters. In: Kennedy, V.S. ed. (1984) The estuary as a filter. International Estuarine Research Conference. Academic Press. Orlando, Florida.

Short, FT, et al. (2000) Developing success criteria for restored eelgrass, salt marsh and mud flat habitats. Ecological Engineering. 15: 239-252. In: Green, Edmund P and Frederick T Short eds. (2003) World Atlas of Seagrasses. University of California Press. 15-17.

Stapel, Johan. (1997) Biomass loss and nutrient redistribution in an Indonesian *Thalassia hemprichii* seagrass following seasonal low tide exposure during daylight. Marine Ecology - Progress Series. 148(1-3): 251-262.

Vowles, Edward, et. al. (2000) Ecological Seagrass Survey in Moorea. Oxford University. Unpublished.

Walker, DI, et. al. (1999) Status of Australian seagrass research and knowledge. In: Butler, A and P. Jernaknoff, eds. Seagrass in Australia: Strategic review and development of an R&D plan. CSIRO, Collingwood, Australia. 1-24.

World Atlas of Seagrasses. (2003) Marine Programme. UNEP World Conservation Monitoring Centre. Online. Available: http://www.unep-wcmc.org/marine/seagrassatlas/index.htm

# A comparative germination of four coastal strand plants on Moorea, French Polynesia: with emphasis on *Pemphis acidula.*

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**ABSTRACT.** *Pemphis acidula, Thespesia populnea, Scaevola sericae* and *Suriana maritima* are all coastal vegetation that inhabit the reef islands (motus) of Mo'orea, French Polynesia. Few species of plants can survive on a motu due to the high temperature and high salinity conditions. The purpose of the study was to examine the salt tolerance of each species during germination and to assess whether salt tolerance during germination affected the distribution of the species across the motu. Observations were taken in the field to compare with experimental results. *Pemphis acidula* grows closest to the tide line and was expected to have the highest tolerance to salinity. *Thespesia* grows farthest from the tide line on the motu in the broad leaf tree zone and was expected to have the lowest tolerance to salt. Seeds from each species were put in Petri dishes in conditions of varying salinity. The salinities ranged in five degree intervals from 0 to 60 practical salinity units (psu). Trials were repeated ten times. Further studies included a heat trial to examine temperature influences on germination. Studies were also done to compare the water absorption and seed weights. As expected, as salinity increased, germination decreased. *Pemphis acidula* germinated in the most saline conditions (20 psu). *Suriana* and *Thespesia* tolerated sanities up to 10 psu. While *Scaevola* only germinated in non-saline conditions. Salinity does affect germination and the salt tolerance during germination may affect where each plants grows on the motu.

## Introduction

Mo'orea, part of the Society Islands in French Polynesia is known for its lush and profuse vegetation. Unfortunately, the coastal strand vegetation of Mo'orea is threatened by development along the coasts. Coastal strand vegetation is a narrow strip of plants that grow in the sand and rocks of beaches and coastal ridges and often thrives on a motu. A motu is a reef island that lies off the coasts of atolls and islands. Five motus occur along the barrier reef of Mo'orea (Figure one).

The severe conditions of the motu cause the vegetation to be low in species diversity, mainly dominated by strand vegetation. There is a strict zonation of vegetation across the lagoon, from the coastal beach to the lagoon (Fosberg 1949). A freshwater lens lies beneath the porous soils of the motu. It is formed when fresh rain water seeps through the soils and displaces the salt water (Murphy 1993). The lens is dynamic; the amount of freshwater is constantly rising and falling. The size of the lens also varies for each motu. It effects where plants with deeper roots grow, however has little effect on strand plants which can withstand the salinity stress (Burford 1994).

*Pemphis acidula*, a pioneer species of these motus grows on the limestone platform in dry and saline conditions. *Pemphis* is an important part of the environment. It stabilizes the platform and protects against wind, wave and erosional stress. However, the populations of *Pemphis* on the motus are beginning to decrease due to development. The most outstanding example is on Temae, where only nine individuals still thrive.

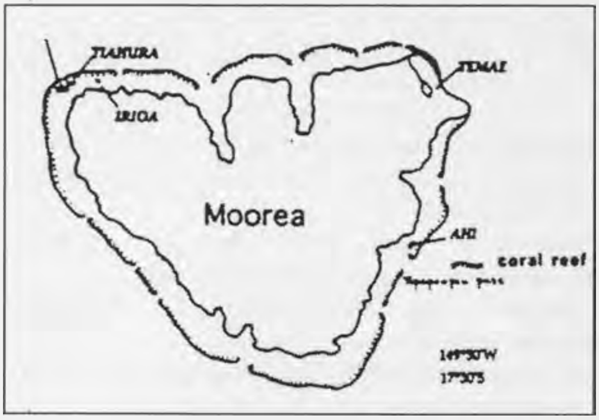

**Figure 1**. Motus of Mo'orea

Studies were performed at two motus, the Temae and Tiahura motu.

The Tiahura motu (S 17□°29', W 149° 54') is on the northwest corner of Mo'orea. Due to the availability of boat taxis from major hotels and tour groups this motu is a large attractor of tourism. However, development is at a minimum and the habitat is only modestly disturbed.

The Temae motu (17°29' S, 149°46' W) is located at the northeast tip of Mo'orea. Temae was originally a disconnected motu. Through time, the motu grew so large that it connected to Mo'orea. Temae is an area of concern due to the rise in development. A road passes along the eastern shore of the motu. There is a hotel near the south end, and an airport immediately to the southeast. Threats include disturbance from the nearby airport, pollution from domestic waste and the spread of housing along the coast. There are proposals to create an 18-hole golf course in the area, and to extend the runway of the nearby airport (UNEP 2001). These developments cause severe disturbances to the local fauna and flora. No efforts for conservation are currently taking place. Only nine *Pemphis* shrubs are found on the Temae motu.

In addition to *Pemphis acidula*, the included in this study were *Scaevola sericea*, *Suriana maritime*, and *Thespesia populnea*. All species included in the study are tolerant to salt spray, saline soils, dry conditions and wind (Fosberg 1949).

*Pemphis acidula* (Lythraceae) is a prostrate shrub that grows on the harsh limestone platforms. *Pemphis* is distributed across tropical East Africa to eastern Polynesia and inhabits most major archipelagos of Micronesia and Polynesia. *Pemphis* is an essential part of the environment and Polynesian culture. As mentioned before, Pemphis stabilizes the beach and platform environment by hindering erosion and blocking wind. The Polynesians often use the hard-wood for building and carving. Fish hooks, boat parts and other tools can be constructed out of the roots and bark. In the past years *Pemphis* has become endangered in several regions including Singapore, Thailand and India.

*Scaevola sericea* (Goodenia) grows on sandy beaches and seashores. It originated in East Africa, India, Southeast Asia, Australia and the Pacific Islands (EPPC 2003). It has globular fleshy fruit containing 1-2 seeds and has flowers that vary in color from white to violet. *Scaevola* leaves are used in native medicine. *Scaevola* grows easily and abundantly. It is highly invasive and has become a troublesome weed in some areas including South Florida, replacing the native vegetation and establishing itself as the most common plant.

*Suriana maritima* (Surianaceae) is a shrub that is exteriorly similar to and often confused with *Pemphis*. The most obvious difference is that *Suriana* has yellow flowers and *Pemphis* has white flowers. *Suriana* has as large global distribution. It is native to southern Florida, Bermuda, Bahamas, West Indies, Eastern Mexico, Brazil, East Africa, tropical Asia and the islands within the Pacific and Indian oceans (Howards 1988). Like *Pemphis*, *Suriana* is essential to the stabilization of beaches and platforms. The leaves and bark may be used to treat rheumatism and skin ulcers (Logier 1990).

*Thespesia populnea* (Malvaceae) is one of several trees that populate the strand habitat (Mueller-Dombois, Fosberg 1998). Thespesia is an evergreen tree with hibiscus-like flowers. This is one of the reasons it is commonly confused with sea hibiscus (Hibiscus tilaceus). The specific name means "looks like the common plant". *Thespesia* originated in the Old World, most likely the Asiatic tropics and now inhabits areas throughout the tropics. It grows along sea coasts of bays and islands (Small 1933).

During this study observations and collections were taken at two motus, Tiahura and Temae. The strand vegetation of these motus grows on or near a coral platform. The platform, or upraised reef, forms a limestone coast that lies on the north-facing side of the motu, parallel to the barrier reef. The motu habitat is harsh due to salt spray, high temperatures and lack of soil (Burford 1994). Few species thrive in these difficult conditions. This paper will discuss and compare several of the plant species that can withstand this environment. The purpose is to examine the ability of the seeds to germinate, grow, in saline conditions. And with this data, to conclude whether the seeds tolerance to salt during germination affects where the plants grow across the motu.

This paper will compare the tolerances to salt during germination of the four coastal strand plants. The goal of the paper is to reveal whether salt tolerance during germination determines the distribution of the plants across the motu. It is hypothesized that *Pemphis* will have the highest tolerance to salt during germination because it grows closest to the tide-line. It is then expected that tolerances will decrease moving inland. And that *Thespesia* will have the least tolerance to salt because it grows farthest from the tide line. Further comparison experiments include a heat study, measurements of seed weight, and water absorption. Also, *Scaevola* and *Pemphis* were transplanted to soil to observe their ability to grow after germination.

## Material and Methods

### *Location*

Studies were conducted in Mo'orea (17°30' S, 149 °50'W), French Polynesia. Studies were performed from September to mid-November.

The Tiahura and Temae motus were the sites of study. To describe the distribution of the plants across the motu, the species were classified into three zones. Zone one ranges across the limestone platform, the area closest to the tide-line. *Pemphis* inhabits zone one. Zone two is located further away from the shore. It is a "mixed-shrub" zone (Fosberg 1971). *Scaevola* and *Suriana* inhabit zone two. Zone three is inhabited by broad-leaf trees. Zone three lies behind the mixed-scrubs. *Thespesia* grows in zone three

### *Seed Collection*

All seeds collected were mature. Seeds of *Pemphis acidula* were collected at the Tiahura Motu and Temae Motu. In the lab, fruit capsules were broken open to release numerous seeds. Seeds of *Suriana* and *Scaevola* were collected from the plants and sands of the Temae motu. *Thespesia* seeds were collected on the UC Berkeley Gump Station and in surrounding areas on Cook's Bay. Fruits were broken open in the lab to release about ten seeds.

### *Observation Studies*

Temae and Tiahura motus were sites of observational field work. Ground water samples were taken within the areas of growth of the studied plants. Ground water was reached manually with a shovel. A refractometer was used on site to determine salinity. Five samples were taken at each motu for five days.

Salinity and temperature of the soil were measured at various sites. Sites were chosen based on abundances of Pemphis, Scaevola, Suriana or Thespesia. Samples were taken near the roots of the plants. 20 mL of soil was mixed with 20 mL of non-saline water. The salinity of the water-sediment mix was measured with a refractometer. A thermometer was used to measure the temperature at the site. Fifteen sites were studied on each motu.

### *Seed Weight*

Seeds of each species were weighed.

### *Imbibition Study*

Seeds of *Thespesia, Pemphis, Scaevola and Suriana* were used in this experiment. The purpose of the experiment is to measure the ability of water to permeate the seeds. Water absorption of scarified seeds was compared to that of non-scarified seeds. To scarify a seed, the seed coat was nicked with a razor blade. The initial weights of both the scarified and non-scarified seeds were taken. The seeds were then placed in Petri dishes atop moistened filter paper and cotton. The seeds were allowed to absorb water over a twelve hour period. Seeds were weighed every four hours. The amount of water imbibed was calculated using the equation:

$$Wi = (Wi - Wd) / Wd$$

With Wi being the weight of the imbibed seed and Wd being the weight of the dry seed (Baskin et al. 1998).

Observing the permeability of the seed coat to water will help explain the patterns of germination. A non-scarified seed that does not grow in saline conditions cannot be assumed to be intolerant to salt. The seed coat may be protecting the seed from sufficient water absorption to germinate to avoid germination in unfavorable conditions, although the seed may be actually able to tolerate high salinities.

### *Salinity Study*

Vaimato bottled water was used in the place of distilled water. Sea water was mixed with the bottled water to make saline waters below the salinity of sea water (38 psu). Sea water was boiled to create saline waters greater than 38 psu. A refractometer was used to test the salinities of the waters.

The salinity study was performed in a dry lab, a controlled environment. Seeds of *Pemphis, Scaevola, Suriana* and *Thespesia* were used in the germination study. *Thespesia* seeds were scarified. For each species of plant, ten seeds were put in thirteen different Petri dishes. The seeds were placed atop filter paper and cotton that was moistened with 10 cc of water of the various salinities. Due to the scarcity of Petri dishes, seeds in the third trial were placed in plastic plates with the moistened filter paper and cotton and put in zip-lock bags to prevent evaporation. Each Petri dish or plate was moistened with a different salinity of water. The salinity trials started at 0 psu. The water salinity was then increased at five degree intervals for each following dish, until reaching sixty psu. The trial was repeated ten times and data were analyzed with a t-test analysis.

### *Heat Study*

Seeds from *Pemphis*, *Scaevola* and *Thespesia* were used in the heat study. Heat may breaks down the seed coat and certain seeds with a tough cotyledon may have significantly more successful growth in heat. It is also important to see if high temperatures hinder seed growth. The seeds were placed in plastic plates atop filter paper and cotton moistened with bottled Vaimato water and then put in sealable bags to prevent evaporation. Ten seeds were used from each species of plants. The plates were kept in the lab, no less than twelve inches from a heat lamp. The lamp was left on twenty-four hours. These seeds were to be compared with the control seeds (zero salinity) from the salinity study. A t-test was run to analyze the data.

### *Growth Study*

Seedlings of *Pemphis* and *Scaevola* were grown in soil, outdoors of the lab. After germinating in the lab, *Pemphis* sprouts were transferred into trays filled with soil. In each tray five *Pemphis* sprouts were each individually planted in 20 mL of soil.

*Scaevola* sprouts were collected from the beach at Temae. Sprouts collected had two leaves and were no more than 1 cm. over the sand. Five *Scaevola* sprouts were put into glassware filled with soil. Glassware was used because most *Scaevola* sprouts had longer root developments than *Pemphis* seedlings.

The trays and glassware were transferred to an outdoor covered lab. One set of samples were placed under a heat lamp. The remaining samples were placed in non-heated conditions. The seedlings were watered every other day with 4 cc of bottled Violator bottled water. The experiment was repeated three times. The growth was reviewed after four weeks.

### *Viability Study*

An experiment was performed to observe the ability of *Pemphis* to grow in the lab. *Pemphis* was grown on moistened filter paper and cotton. Ten seeds were placed in each Petri dish. The salinity increased at intervals of ten, beginning at 0 and ending at 50 psu. Two trials were performed. After three weeks the seeds that germinated were removed. The seeds that did not germinate were left in the Petri dishes for another experiment.

The second part of the experiment tested the ability of *Pemphis* to maintain viability after soaking in saline conditions. The seeds that did not germinate in the initial trials were left in the Petri dishes and washed with non-saline water. The purpose of the experiment was to observe whether the seeds would germinate in the secondary experiment after resting in various saline conditions for a three week period.

## Results

### *Field Observations*

The Tiahura and Temae motus had distinct differences in *Pemphis* size. On the Tiahura motu, *Pemphis* grew tall and dominated the large expanse of coral platform. The opposite was observed on Temae where nine shorter, shrubbier plants of *Pemphis* were localized on a small strip of the platform.

*Scaevola* dominated the mixed scrub areas (zone two). In contrast, Suriana was sparse. *Thespesia* was scarce in Temae and not observed on Tiahura.

The ground water measurements averaged to almost the same salinity as sea water (38 psu). In Temae the average was 36.6 psu and in Tiahura the average salinity was 38.2 psu (Table 1).

Using a t-test, the gross temperature and salinity measurements were found to have a low correlation ($p=0.0313$). The measurements were not statistically significant. However, the maximum and minimum measurements of temperature and salinity were consistent with lab observations.

|  | Temperature ( °Fahrenheit) | Salinity (psu) |
|---|---|---|
| Minimum | 80 | 0 |
| Maximum | 105 | 12 |
| Mean | 89.448 | 2.833 |
| Standard Dev. | 7.772 | 2.394 |

**Table 1.** Temperature and Salinities observed in the field.

---

### *Seed Weights*

*Pemphis* seeds were the lightest (x=0.064 g) (Table 4). *Scaevola*, the heaviest, weighed three-hundred and eighty times more than *Pemphis*

Possibly the small seed size is a mechanism for high dispersal. The seeds are easy to carry by wind. They may attach to birds and larger insects.

*Salinity Study*

As the salinity increased, germination decreased. *Pemphis* seeds germinated the most successfully. Pemphis seeds germinated at the highest salinity (20 psu) and with the most success in lower salinities (Figure 2). *Pemphis* was the most tolerable of saline conditions. 3% of *Pemphis* seeds germinated in saline conditions of 20 psu and 20 % germinated in saline conditions of 15 psu. No other species germinated in these salinities. At 10 psu, 42 % of *Pemphis* seeds germinated. Both Suriana and Scaevola had low germination in comparison to *Pemphis* (p=0.00) (table 3). *Suriana* had 2% germination in saline conditions of 10 psu. *Scaevola* germinated in non-saline conditions.

Scarified seeds of Thespesia *had* the second highest number of seed germination after *Pemphis*. Scarified *Thespesia* germinated up to 10 % in 10 psu. *Thespesia* populations of seeds germinated similar to Pemphis (p=0.069) in 10 psu.

There were similar germination numbers between Thespesia and the zone two shrubs Scaevola (p=0.182) and Suriana (p=0.391) at ten psu. *Thespesia* had population germination numbers comparable to other species at each level of salinity in which it germinated.

*Suriana* and *Scaevola* had similar population growth patterns. In 10 psu conditions the growth patterns are the same (p=0.182).

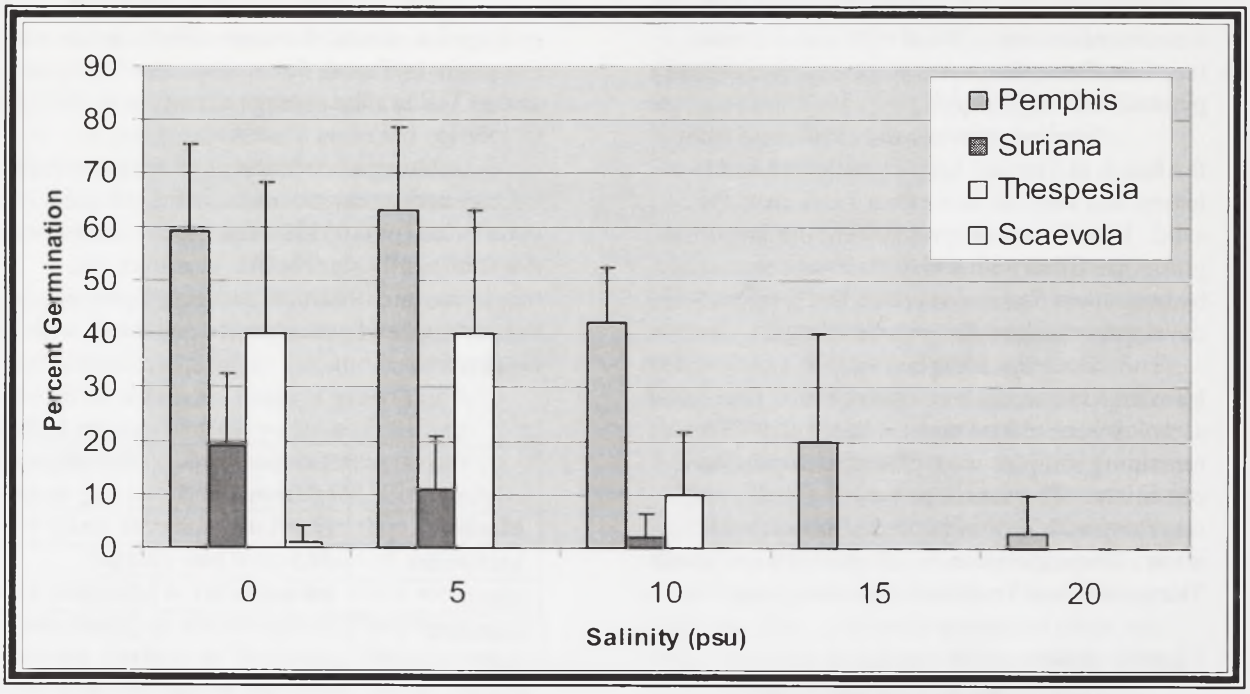

**Figure 2.** Percent Germination of *Pemphis*, *Suriana*, *Thespesia* and *Scaevola* in increasing salinity.

| | Mean Salinity (psu) | | Standard Deviations | |
|---|---|---|---|---|
| | Temae | Tiahura | Temae | Tiahura |
| Site 1 | 38 | 36 | 5.700877 | 4.1833 |
| Site 2 | 34 | 36 | 4.0045 | 4.0336 |
| Site 3 | 34 | 39 | 4.1833 | 7.416198 |
| Site 4 | 39 | 40 | 7.905694 | 2.738613 |
| Site 5 | 38 | 40 | 5.70087 | 7.905694 |

**Table 2.** Ground water salinities observed in the field.

| Similarities in germination patterns between species | p-value at salinity of 0 psu | p-value at salinity of 5 psu | p-value at salinity of 10 psu |
|---|---|---|---|
| *Pemphis-Suriana* | 0.001 | 0 | 0 |
| *Pemphis-Thespesia* | 0.423 | 0.069 | 0.069 |
| *Pemphis-Scaevola* | 0 | 0 | 0 |
| *Suriana-Thespesia* | 0.448 | 0.065 | 0.391 |
| *Suriana-Scaevola* | 0.001 | 0.001 | 0.168 |
| *Thespesia-Scaevola* | 0.065 | 0.065 | 0.182 |

**Table 3.** T-test Results of Salinity Experiment

| | *Pemphis* | *Scaevola* | *Suriana* | *Thespesia* |
|---|---|---|---|---|
| *Minimum weight (g)* | *0.04* | *19.320* | *0.960* | *15.260* |
| *Maximum weight (g)* | *0.08* | *30.700* | *1.040* | *22.180* |
| *Mean weight (g)* | *0.064* | *24.262* | *1.012* | *18.888* |

**Table 4.** Seed Weights

*Imbibition*

*Thespesia* seeds were the only seeds to react to scarification (Figure 3). The other species showed no significant change in water absorption when the seed coat was cut. The scarified seeds exceeded that of the non-scarified seeds by 220%.

| | |
|---|---|
| Mean final weight scarified | 2.35 |
| Mean final weight non-scarified | 1.062 |

*Viability*

The initial purpose of the experiment was to test whether *Pemphis* would germinate in the lab. *Pemphis* seeds germinated in 0 and 10 psu (Table 5). Seeds that germinated in the initial experiment were removed.

In the second part of the experiment, no seeds germinated in 0 psu and one germinated in 10 psu. All viable seeds already germinated in the non-saline/saline conditions of the initial experiment. There is a notable peak in germination at 20 and 30 psu. There is a slight decrease in germination as the salinities increase to 40 and 50 psu (Table 6). Less germination was seen in seeds that had been soaked in 50 psu conditions.

| Salinity (psu) | # seeds removed | percent germination |
|---|---|---|
| 0 | 9 | 45 % |
| 10 | 7 | 35 % |

**Table 5.** Initial *Pemphis* Salinity Test

| Salinity (psu) | % germination |
|---|---|
| 0 | 0 |
| 10 | 5 |
| 20 | 70 |
| 30 | 65 |
| 40 | 50 |
| 50 | 40 |

**Table 6:** Viability study: percent germination per salinity. Seeds were in saline conditions for three weeks.

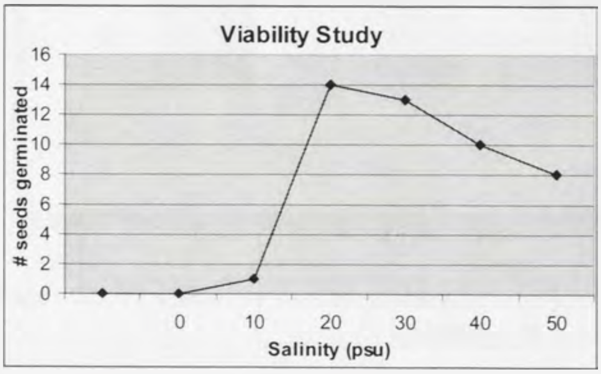

**Figure 2.** Viability of seeds after soaking in various saline conditions.

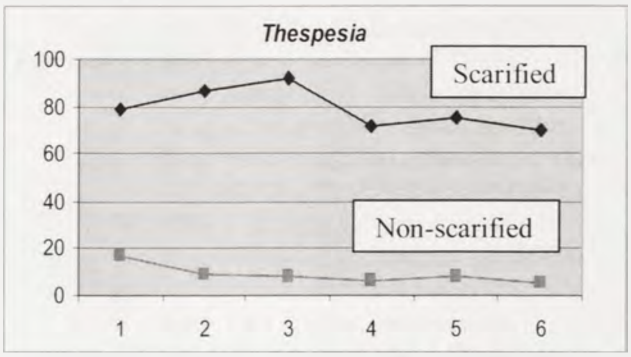

**Figure 3.** Water imbibition of scarified vs. non-scarified seeds of *Thespesia*.

| | No heat | heat |
|---|---|---|
| Minimum | 3.0 | 3.0 |
| Maximum | 8.0 | 8.0 |
| Mean | 5.4 | 4.8 |
| Standard Dev. | 1.667 | 1.612 |

**Table 7.** Results of Heat trials

*Growth Studies*

*Pemphis* did not grow outside of the lab. There was a 0% survival rate for *Pemphis* seedlings planted in soil. On the contrary, Scaevola seedlings had a 66% survival rate. Five plants grew in the heated trial. The plants in the heated trial grew a maximum height of 6 inches and had a maximum number of twelve leaves. The five plants in the non-heated trial had a maximum height of only one inch and the most leaves observed were three.

*Heat Trials*

Heat is not a significant factor for the germination of *Pemphis*. *Pemphis* germinated in the maximum temperature observed in the field (105° F). There was no significant relationship between the growth of *Pemphis* seeds in heated and non-heat trials ($p=0.447$) (table 7). The mean of the non-heated trials ($x=5.4$) was higher than the heated trials($x=4.8$), differing by only 0.6. Heat is not a crucial factor affecting the germination of *Pemphis*.

In contrast, *Thespesia* germinated significantly more successfully in heated conditions. *Thespesia* seeds (non-scarified) germinated three times more in heated trials.

## Discussion

As expected, based on field observations, as the salinity increased, the germination decreased. The seeds germinated most successfully in non-saline and slightly saline conditions. Past studies support the preference of salt tolerant plants to less saline conditions during germination (Mariko S 1992; Williams and Ungar 1972). Lesko (1969) confirmed that most salt tolerant plants do not germinate in salinities over 1.0%-1.5% (10-15 psu). Although, plants can tolerate salt spray and saline soils, the seeds will not germinate in high salinities. The seeds do not germinate in salty areas in order to avoid establishment in unfavorable environments. As a plant develops, it may develop a higher tolerance to salt. By becoming less sensitive to salt the plant can survive in saline environments.

The maximum salinity measured in the field was 12 psu. In experimental results, *Pemphis* germinated in salinities of 20 psu. *Suriana* and *Thespesia* germinated in saline waters of 10 psu. The plant species in the lab germinated at the highest percentage in conditions of lower salinity, between 0 and 5 psu which is consistent with the mean salinity of 2.833, observed in the field.

*Pemphis* was the most tolerable of saline conditions during germination. *Pemphis* germinated in the highest salinity (20 psu). *Pemphis* also maintained viability after being in saline conditions of up to 50 psu for three weeks. *Pemphis* seeds can therefore withstand sea dispersal and will germinate when put in less saline conditions.

*Pemphis* was the only species to germinate in the higher salinities. *Pemphis* had 20% germination in saline conditions of 15 psu, while no other species germinated in salinities this high. This indicates that to inhabit zone one a species must be able to germinate in high salinities. *Pemphis'* ability to germinate in high salinities is a crucial factor for life on the platform near the tide line.

No other species germinated in the high salinities (both Suriana and Scaevola had notably low germination in comparison to *Pemphis* (p=0.00). Likewise, no other species inhabit the platform environment. This further supports the proposal that germination in high salinities is necessary for a species to inhabit the zone one environment.

In contrast, *Scaevola* only germinated in non-saline conditions. Lesko (1969) concluded that *Scaevola* will only germinate in fresh water conditions although it inhabits saline environments. Salt tolerance during germination is not a factor for survival in zone two. A *Scaevola* seed may wash up on shore on a rainy day and germinate. As the seedling develops, *Scaevola* will adapt to be more tolerant to salt (Mariko 1992). *Scaevola* can adapt to any soil (Gilman, E 1999). This was seen in the high level of success of *Scaevola* growing in soil outside of lab. When transplanted into soil, 66% of *Scaevola* seedlings survived. The ability of *Scaevola* to successfully adapt is why it can inhabit the zone two, slightly saline environments.

The low level of germination of *Scaevola* (1%) is most likely because the seeds did not soak in salt water. *Scaevola* seeds are well adapted to floating in the salt water. They can travel through the ocean for up to one year and still germinate. The best conditions for germination are after soaking in salt water for 250 days (Bornhorst 1996). This is most likely an adaptation for dispersal of the seeds, and also explains why the seeds only germinate in non-saline environments. The seeds are waiting for optimal conditions. Once the seeds have germinated, seedlings adapt to the saline soils and grow abundantly.

*Suriana* tolerates mid-salinity conditions. The germination of *Suriana* in mildly saline conditions is responsible for *Suriana's* coastal distribution. *Suriana* had 2% germination in saline conditions of 10 psu. *Suriana* does not have a salt tolerance during germination high enough to inhabit zone one. *Suriana* does not have tolerances or adaptations to compete in less saline environments. Therefore it cannot inhabit zone three, inland areas due to out-competition. *Suriana* is restricted to zone two. Zone two competitors, such as *Scaevola*, may not germinate in saline conditions (Mayer 1982). Therefore, *Suriana* has an advantage over these competitors. Its ability to germinate in salty areas establishes its presence when competition is high.

Non-scarified *Thespesia* did not germinate in saline conditions. However, scarified *Thespesia* had the second highest amount of germination in saline conditions. In imbibition trials, *Thespesia* was the only species to react to scarification (Figure 3). The seed coat of *Thespesia* is more resistant to water imbibition than the other species. The weights were 220% greater and 400% more water was absorbed in scarified seeds. Scarified seeds also had a much higher germination. The higher percent of germination can be correlated with the increase in water absorption. The seeds that had been cut had 40 % germination. Non-scarified *Thespesia* had only 1% germination. The tough seed coat is a means for the seeds to resist water absorption to enable longer periods of floating in the sea (EPPC 2003). The seed coat provides protection against germination in poor conditions. For example, *Thespesia* is known to tolerate dry conditions (World Agroforestree Centre 2003). The seed coat may protect the seeds in these dry areas. Also *Thespesia* can germinate in higher salinities. The seed coat may be a mechanism to prevent germination in highly saline areas. The tough seed coat offers protection against germination in unfavorable areas.

The high salt tolerance was not consistent with the proposal that being part of the zone three environments, *Thespesia* would be least tolerant of salty conditions during germination. This higher tolerance to salinity is probably an adaptation for survival along the coasts of bays and islands. Like *Suriana*, *Thespesia* is a poor competitor, often over-dominated by its look-a-like *Hibiscus*. Its ability to germinate in higher salinities may be an adaptation to asserting seedling establishment in areas of competition. Possibly *Thespesia* does not compete well in less saline inland habitats of the motu which explains its scarce distribution.

Scarified *Thespesia* had salt tolerances similar to Suriana (p=0.365) at mid-salinities. *Thespesia* has a wide distribution along the coasts of bays and islands: environments characteristic of *Suriana's* zone two habitats on the motu. The data does not support the proposal that based on its zone three distributions within the motu Thespesia would have the least tolerance to salinity. However, considering other environments inhabited by Thespesia, the findings are reasonable.

*Thespesia* also germinated more successfully in heated conditions. *Thespesia* seeds (non-scarified) germinated three times more in heated trials. *Thespesia* is a cold-sensitive plant adapted to living in heated, dry conditions (World Agroforestree Database 2003). It is likely that heat is related to the amount of water the seed absorbs. Possibly, heat treatment loosens the cuticle (seed coat) to increase water imbibition (Keeley 1997). This is supported by the fact that the heat-treated seeds have germination numbers similar to scarified seeds. Scarified seeds had 30% germination in non-saline conditions; heat-treated seeds had 10% germination. Non-scarified seeds had only 1% germination in non-saline conditions. Due to the small number of seeds germinated, this experiment should be run again with more data sets, including sets of heat-treated, scarified seeds.

Heat is, however, not a significant factor for the germination of *Pemphis*. *Pemphis* can germinate in maximum temperatures; however salinity has a stronger influence on the distribution of *Pemphis*. The species does not prefer heat conditions over non-heat conditions. There was no significant correlation between the heated and non-heat trials (p=0.352) for *Pemphis*. The mean of the non-heated trials (x=5.6) was higher than the heated trials(x=4.8), differing by only 0.8 (Table 5). The theory that *Pemphis* seeds would germinate more successfully in heat is rejected.

Seedling establishment did have an influence on *Pemphis* growth. Seedling establishment is dependent on the environment and its diversity (Harper 1977). The limestone platform is crucial for the development of *Pemphis*. No *Pemphis* seedlings grew in potting soil or other substrates. After observing the growth of *Pemphis* following germination, it was determined that *Pemphis* does not grow in substrates or environments other than the limestone platform. This suggests specific factors of the platform are crucial for the growth of *Pemphis*. Also, competitors, such as *Scaevola*, block Pemphis from colonizing and adapting to other environments in the motu beyond the platform.

Possible reasons for Pemphis' preference to the platform may be that growth and seedling establishment are dependent on the characteristics of the rocky limestone substrate. Perhaps the platform protects the seedlings from the harsh sea spray and wind. The *Pemphis* seeds are the smallest of all four species (Table 4). Being so small, the seeds may need extra support and protection. Perhaps there is a mineral dependence. However, more studies should be performed on the impact of substrate on the growth of *Pemphis*, as well as the other species.

Factors of seedling establishment, competition and primarily the influences of salinity keep *Pemphis* distinctly localized. The rise in coastal development is disrupting the localities where *Pemphis* grows. Only nine

Pemphis plants were observed on the Temae motu. Temae is the most impacted of all Mo'orea's motus. Most of the area has been cleared for homes and garden plantations. This is unfortunate because Pemphis is important to both its community and the Polynesian people. It stabilizes the platform against wind and wave stress and provides wood for the Polynesians. Although, this is only the beginning of the problem, preventative actions could be helpful to prevent the depletion of *Pemphis* as has been seen in other areas of the world. Only one tree of *Pemphis acidula* grows in Singapore (Yong, 1993). Hopefully studies focusing on *Pemphis* and its sensitivity to its environment will begin in the future, taking into consideration manners of conservation.

**Conclusion**

Salinity does have a different effect on the germination of each of the four coastal strand plants. These varying salt tolerances during germination may have an effect on distribution of the vegetations across the motu. Studies across a wider range, examining salinity, germination, distribution as well as substrates would build a broader knowledge of these plants.

Future studies examining the growth behaviors and preferences of *Pemphis* should be performed to prevent its endangerment. However, the ongoing issue of protecting and preserving the environment while allowing for the inevitable expansion and growth of civilization must be taken into account when suggesting conservation efforts. The goal should be to find a solution that can satisfy both sides. By learning more about the plant and how it grows, more options and means of preservation will develop.

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## LITERATURE CITED

Baskin, Jerry M et. al. (1998) A comparative study of seed dormancy and germination in an annual and perennial species of Senna (Fabaceae). *Seed Science Research* 8:501-512

Burford, Martha O. (1994). The Vegetation of Reef Islands (Motus): A study of the Ecological and Anthropogenic Effects on the Motu Temae. Biology and Geomorphology of Tropical Islands: 150-165.

EPPC: Florida Exotic Pest Plant Council (2003). Scaevola Sericea. Retrieved December 3, 2003 from *http://www.fleppec.org.*

Fosberg, F. Raymond (1949). Atoll Vegetation and Salinity. Pacific Science 3:89-92.

Fosberg, F. R., M. Sachet and R. Oliver. (1979). A Geographical Checklist of the Micronesian Dicotyledonae. *Micronesia,* 15:1- 2.

Howard R.A. (1988) Flora of the Lesser Antilles Leeward and Windward Islands. Dicotyledoneae, Part 1. Vol. 4: 673.

Keeley, J E and Fotheringham, C J. (1997). Trace Gas Emissions and smoke-induced seed germination. Science276:1248-1250.

Khan, M. Ajmal and Gulzar, Salman (2003). Light, salinity, and temperature effects on the seed germination of perennial grasses. *American Journal of Botany* 90: 131-134.

Kingston, Naomi et. al. (2003) The phytogeographical affinities of the Pitcairn Islands- a model for south-eastern Polynesia?" *Journal of Biogeography* 30:1311-1328.

Lesko, G.L. and Walker, R.B. (1969) Effects of sea water on Seed germination in two Pacific atoll beach species." *Ecology* 50: 730-734.

Liogier, H.A. (1990) Plantas mediciales de Puerto Rico y del Caribe. Iberoamericana de Ediciones, Inc., San Juan, PR: 566.

Mueller-Dombois, D. and R.F Fosberg (1998). Vegetation of the Tropical Pacific Islands. Ecological Studies 132: 773 pp.

Murphy, Francais J. (1993). The Natural and Environmental Effects on the Motu of French Polynesia. Acted des Troisiemes Journees de la Recherte en Polynesie Francaise. Pa
pette: Institut Malarde.

Small, John Kunkel. (1933). Manual of the Southeastern Flora. New York, NY.

UNEP World Conservation Monitoring Centre (2001) Protected Areas Programme: Lac Temae. Retrieved December 5, 2003 from *http://www.unep-wcmc.org/sites/wetlands/lac_tema.htm* (2001).

Yong, Jean (2003). Nature Watch: The struggle for survival: Five threatened coastal plants once common to our shores. Retrieved December 3, 2003 from *http://habitatnews.nus.edu.sg/pub/naturewatch/text/a061d.htm.*

# Factors affecting growth of big-leaf mahogany, *Swietenia macrophylla*, on Moorea

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ABSTRACT. Big leaf mahogany, *Swietenia macrophylla*, has been planted sporadically on the island of Moorea, French Polynesia since the late 1960's. Recently, planting of the species has been more frequent as part of a timber program specializing in precious hardwoods. Study plots were placed in plantations from age three to thirty-six in order to characterize growth and analyze management and environmental factors affecting growth rates. The site quality of plantations on the island ranged from 13 to 47, indicating good sites compared to other plantations in the Pacific. Mean Annual Increment (MAI) for the study sites ranged from 5 to 33 $m^3$/ha, which is also consistent with *S. macrophylla* plantations in other parts of the world. Regression analysis showed that increased rainfall ($p=.057$) had a significantly positive effect on site quality, while slope, elevation, and density had no effect. Rainfall and plantation density ($p=.057$) did have a significant effect on mean annual increment. A Student t-test revealed that plantations that had been cleared of competing vines such as *Merremia peltata* showed significantly higher MAI than uncleared plantations. Slope did not have any correlation with growth rate. Permanent plots were also established in order to study growth more accurately over a longer time scale.

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## Introduction

As unsustainable forest management has depleted the worldwide timber reserve, many countries are turning to plantations as a sustainable form of wood production. The pressures of logging are felt disproportionately in tropical regions and islands, where poorly enforced environmental standards and limited area conspire to exhaust natural resources. Plantations of commercial timber species can alleviate pressure on native forests, and will only become more important as current logging practices become impossible (Cassells and Scheyvens 1999).

Forestry programs were started on the island of Moorea in French Polynesia in the 1960's as an effort to make the island's wood consumption self-supported. Private landowners and government agencies such as the Service du Developpement Rural (SDR) have experimented with plantation-style forestry on Moorea during this time, planting tree species from around the world. Due to the limited amount of land and the almost year-round growing season, a trend toward planting so-called precious hardwoods has become popular. *Swietenia macrophylla*, or big leaf mahogany, is a tree species native to Latin America that has become the most widely planted of these precious hardwoods. The wood of this mahogany species is quite valuable due to its beautiful color and grain.

This paper attempts to determine the growth rate of S. macrophylla on Moorea in order to estimate standing tree volume, construct a growth curve and estimate a rotation age for the species on Moorea. Trees characteristically grow faster earlier in their life, before slowing down and putting on less annual wood as they mature. Using the annual growth of plantations at different ages, it is possible to determine at what age the trees are growing the fastest and when their growth slows. This piece of information is crucial for managing land sustainably and economically. Plantations ranging from three years old to thirty-six years were studied to determine the size of trees throughout their life.

Also, the effect of various factors on *S. macrophylla* growth rates was analyzed. Environmental factors such as rainfall, elevation, and slope were considered. Human management factors such as plantation spacing, plantation age, and clearing of competing understory were also analyzed. Increased rainfall can assist tree growth if water is a limiting resource. Steeper slopes usually lead to thinner soil and lower growth rates. Young plantations suffer from severe competition with understory shrub and vine species. The most aggressive of these vines, *Merremia peltata*, can kill young saplings by climbing up the stem and shading the trees' foliage. Clearing of these plants is a regular practice. While the vine clearing is done mostly to prevent tree mortality, here its affect on tree growth was studied.

## Methods and Materials

### *Pilot Study*

An initial pilot study was done to determine variability in the plantations. The data showed that 20 trees at each plot should yield sufficiently significant results.

### *Research Methods*

Measurements of tree diameter and height were taken at various plantations in order to construct a growth model for *S. macrophylla* on Moorea. At each plantation, a starting point was randomly chosen. Then trees were measured along the rows of the plantations. Diameters were measured at a height of 1.3 meters using a diameter tape, and heights were measured using a clinometer.

Various factors affecting growth of plantations were analyzed. At each site, many factors possibly affecting growth of *S. macrophylla* were determined, including age, elevation, slope, vine and brush clearing, and annual rainfall. Ages were determined using records of plantation dates provided by the SDR. Elevation was determined using a handheld GPS unit. Slope was found using a clinometer. Tree spacing was measured on site. Vine clearing was determined visually. Evidence of past brush clearing was either the absence of the vine, or dead vines wrapped around healthy trees. Evidence of untreated stands was live vines wrapped around trees. Annual rainfall was found using the MeteoFrance weather service.

### *Site Description*

I established study sites at 13 plantations of *S. macrophylla* around the island. Most plantations were in the Opunohu Valley agricultural region, on government land run by the Service Developpement Rural. Several private plantations in other parts of the island were also considered. The plantations ranged in age from 3 years old to 36 years old. Refer to **Figure 1** for a map of the study sites

Site 1, FOJEP 2, was located at S 17° 31.510', W 149° 49.870' and at an elevation of 50 meters. *S. macrophylla* was planted here in 2000. There was no slope at the sample plot. The trees were planted at a 3 meter by 3 meter spacing. The area has not been cleared of brush and vines. This plantation has an annual rainfall of 3400 mm/year.

Site 2, Pied du Rotui 1 was located at S 17° 31.269', W 149° 49.926' at an elevation of 66m. This plantation was established in 2000. There was a 30% slope on the site. The trees were planted at a 3 meter by 4 meter spacing. The area had been cleared of vines. This plantation has an annual rainfall of 3400 mm/year.

Site 3, Pied du Rotui 2, was located at S 17° 31.257', W 149° 49.986' at an elevation of 67m. This plantation was established in 1999. There was a 40% slope on the site, the trees were planted at a 3 meter by 4 meter spacing. The area had not been cleared of vines. This plantation has an annual rainfall of 3400 mm/year.

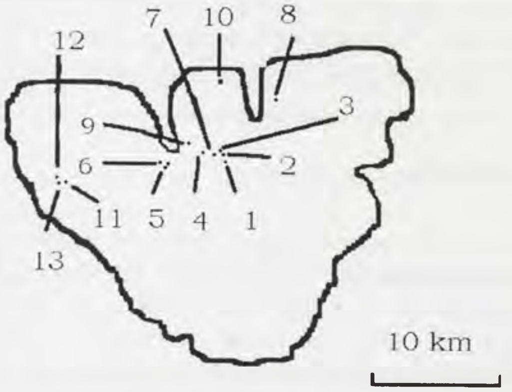

**Figure 1** Map of Moorea indicating location of each study site. Refer to text for GPS location of each site.

Site 4, Lotissement Rotui 2, was located at S 17° 31.288', W 149° 50.354' at an elevation of 56m. This plantation was established in 1991. There was a 40% slope on the site. The trees were planted at a 3 meter by 3 meter spacing. The area showed no sign of vine growth. This plantation has an annual rainfall of 3400 mm/year.

Site 5, Colline rouge 2B, was located at S 17° 31.786', W 149° 50.945' at an elevation of 69 meters. This plantation was established in 1998. There was a 40% slope on the site. The trees were planted at a 3 meter by 6 meter spacing. The area had been treated for vines. This plantation has an annual rainfall of 3400 mm/year.

Site 6, O 2.70, was located at S 17° 31.648', W 149°50.917' at an elevation of 53m. This plantation was established in 1970. There was no slope on the site. The trees were planted at a 5 meter by 5 meter spacing. The area showed no sign of vine growth. This plantation has an annual rainfall of 3400 mm/year.

Site 7, O 1.67, was located at S 17° 31.331', W 149° 50.062' and at an elevation of 33 meters. This plantation was established in 1967. There was a 30% slope on the site. The trees were planted at a 4 meter by 4 meter spacing. The area showed no sign of vine growth. This plantation has an annual rainfall of 3400 mm/year.

Site 8, Tetuanui Jean-Pierre, was located at S 17° 30.278', W 149° 48.577' at an elevation of 55m. This plantation was established in 1986. There was a 20% slope on the site. The trees were planted at a 3 meter by 3 meter spacing. The area showed no sign of vine growth. This plantation has an average rainfall of 2000 mm/year.

Site 9, Kellum Medford, was located at S 17° 30. 647', W 149° 51.036' at an elevation of 5 meters. This plantation was established in 1981. There was a 50% slope on the site. The trees were planted at a 5 meter by 5 meter spacing. The area showed no sign of vine growth. This plantation has an average rainfall of 2350 mm/year.

Site 10, Wilder, was located at S 17° 29.374', W 149° 49.934 at an elevation of 77m. This plantation was established in 1982. There was a 30% slope on the site. The trees were planted at a 5 meter by 5 meter spacing. The area showed no sign of vine growth. This plantation has an average rainfall of 1700 mm/year

Site 11, CAMICA 2, was located at S 17° 32.012', W 149° 53.569 at an elevation of 100 meters. This plantation was established in 1992. There was no slope on the site. The trees were planted at a 3 meter by 3 meter spacing. The area had been cleared of vines. This plantation has an average rainfall of 2050 mm/year.

Site 12, CAMICA 3, was located at S 17° 31.901', W 149° 53.614' at an elevation of 127 meters. This plantation was established in 1995. There was a 40% slope on the site. The trees were planted at a 3 meter by 4 meter spacing. The area had not been cleared of vines. This plantation has an average rainfall of 2050 mm/year.

Site 13, CAMICA 98, was located at S 17° 32.022', W 149°53.639' at an elevation of 108 meters. The plantation had been established in 1998. There was a 35% slope on the site. The trees were planted at a 3 meter by 4 meter spacing. The area had been treated for vines. This plantation has an average rainfall of 2050 mm/year.

*Growth Models*

Two values were used to represent the growth rate at each site: site index and mean annual increment. Site index is a value representing the dominant height of trees at a certain age. See **Figure 2** for details. This value can be entered into an accompanying growth function to characterize height growth over the life of the tree. Site index was calculated by fitting each site to existing growth curves for *S. macrophylla* from plantations on the island of Fiji (Wescom 1979). The Fijian growth function for site index curve used was

$$H_d = S10\verb|^|((1.2304-2.7373(A^{-1}-0.1))) \qquad (1)$$

where $H_d$ is Pre-dominant height, or average height of 100 trees of largest diameter per hectare, A is age and S is site index. In this model, site index values were calculated for age 10. Site index values were used in order to remove the variable of age from later analysis of environmental factors affecting tree growth.

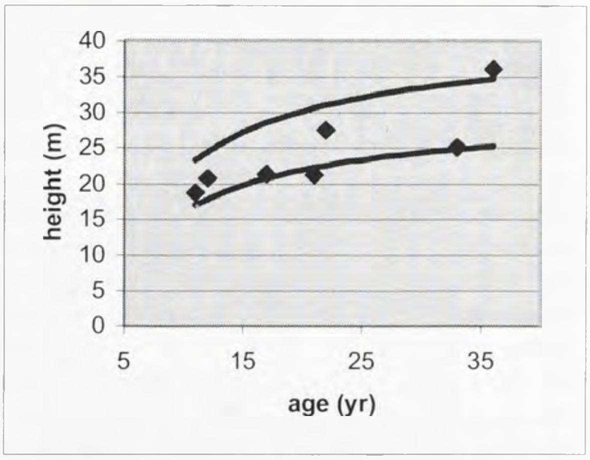

**Figure 2** Graph illustrates method used to calculate site index. Lines are existing growth curves for plantations in Fiji. Each point represents a sample plot on Moorea. Curves best fitting each point were interpolated, giving individual site index numbers.

Mean annual increment was also calculated for each site. This is a measure of average yearly volume growth, expressed in cubic meters per hectare per year. Tree volume was estimated using the formula

$$V=pi(dbh/2)^{2*(h/3)} \tag{2}$$

where V is volume, dbh is diameter at 1.3m, and h is height, following the method suggested by Yamada and Gohlz (2002). Volume data was extrapolated to a per hectare basis.

Mean diameter was plotted with age to estimate optimal rotation length. By extrapolating when the mean diameter of a stand will reach harvestable size, a rough estimate of rotation age can be determined.

*Growth Rate Analysis*

Multiple regression tests were run to determine any relationships between slope, rainfall, and elevation of each site on site index and mean annual increment. A Student's t-test was run to see any relationship in growth rates of sites with and without vine competition.

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**Figures for Results Section**

| Site | Age (yr) | SI | MAI |
|---|---|---|---|
| 1 | 3 | 37 | 5.32 |
| 2 | 3 | 47.5 | 6.82 |
| 3 | 4 | 27.5 | 4.26 |
| 4 | 12 | 19 | 21.97 |
| 5 | 5 | 31.5 | 11.36 |
| 6 | 33 | 16 | 13.43 |
| 7 | 36 | 23 | 22.37 |
| 8 | 17 | 16.5 | 33.80 |
| 9 | 22 | 19.5 | 16.36 |
| 10 | 21 | 15.5 | 14.64 |
| 11 | 11 | 17.5 | 13.34 |
| 12 | 8 | 15 | 5.53 |
| 13 | 5 | 28 | 8.69 |

**Table 1**. Site index values are expected height in meters of dominant trees in each site at age 10. MAI represents average yearly volume growth, in $m^3$/ha/year.

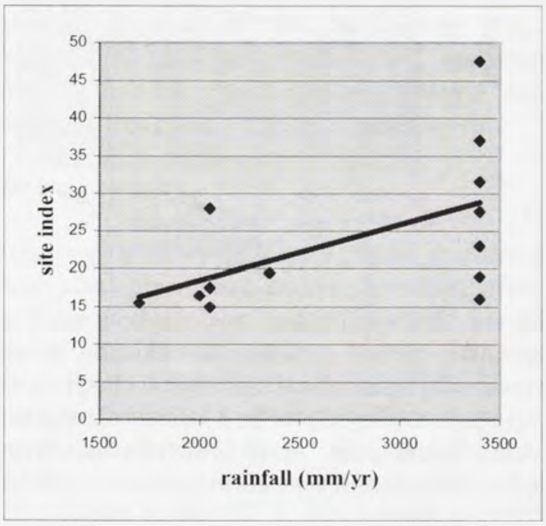

**Figure 3** Site index and rainfall of Moorea *S. macrophylla* plantations. Regression shows a positive correlation ($R^2$= .29, p=.057) between site index and rainfall.

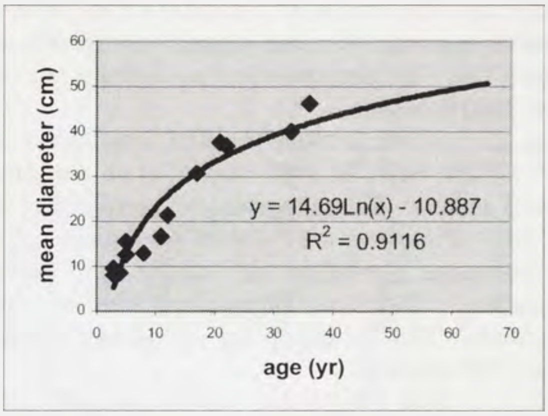

**Figure 2** Mean diameter of each plot against age. The fitted line is a preliminary growth curve for mahogany on Moorea

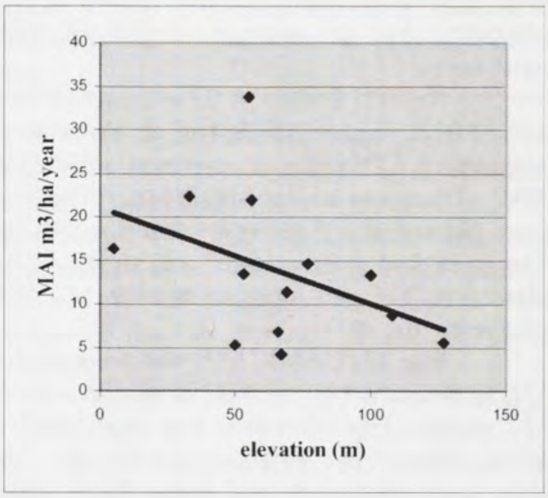

**Figure 4** Mean annual increment against elevation for *S. macrophylla* on Moorea. Regression shows a negative ($R^2$=.17, p=.057) correlation between the two variables.

## Results

The calculated site index and mean annual increment values for each site are given in **Table 1**.

Mean diameter for each stand was plotted against age in order to estimate rotation length, as shown in **Figure 2**. The mean diameter per stand reaches 50 cm at age 63.

Multiple regression tests were run comparing site index of each site against rainfall, elevation, and slope. Only one of these factors proved to be statistically significant. Rainfall had a positive correlation with site index ($R^2$= .29, p=.057), as shown in **Figure 3**.

A multiple regression was also run on mean annual increment, comparing the correlation of MAI with rainfall, elevation, and slope. Again, only one factor proved to be significant, although this time it was elevation ($R^2$=.17, p=.057). **Figure 4** shows the regression line.

A Student's t-test compared the mean annual increment of stands that had been cleared of vines and underbrush and those stands that still had vines. Because stands older than ten years had closed canopies that prevented vine growth, these sites were excluded from the analysis. The only sites considered were young stands where vines are a potential problem and recent clearing would have taken place. The test revealed that those stands without vines had a significantly higher MAI (t= 2.85, p=.046).

The environmental factor of slope was not found to have a significant effect on either of the growth rates.

## Discussion

The site index values calculated using the adopted growth curve from Fiji ranged from a low of 15 to a high 47.5. The range for these curves given by Wescom (1979) in Fiji is 10-25. While this seems to indicate that the plantations in Moorea are growing at an astounding rate, enthusiasm must be tempered. Mayhew and Newton (1998) warn that such curves are designed for older stands, and using them may over estimate growth of younger stands. This can be seen in the results, as all stands under ten years of age have site index values above 25, and all older stands have values within the bounds of previously published results. The growth functions from Fiji were used because they fit the Moorea data better than any other published models, as well as being the closest geographically. Hopefully the permanent plots established in this study will allow site index curves to be established for specifically for Moorea.

Mean annual increment for the stands on Moorea ranged from 4 to 33 $m^3$/ha/yr. While this falls within reported MAI values from around the world, this wide range indicates the high amount of variability from site to site present in the Moorea plantations. Local factors such as rainfall, elevation, plantation density and soil quality play too big of a role to generalize the growth rates for the island.

The minimum stem diameter necessary for harvest on Moorea is 50 cm. By extrapolating the mean diameter per site data, it is possible to estimate when the mean diameter of a stand will reach 50, a good substitute for a harvest age. The estimated rotation age falls at age 63, which compares favorably with other published data (Tillier 1995). It must be emphasized that these figures are preliminary. Because there are no stands of harvestable age on the island, it was necessary to forecast outside the model. Permanent plot data will provide more accurate rotation length figures, and data derived from this initial study should not be used in any serious planning of rotation length.

Rainfall was shown to have a positive correlation with site index. Height growth of *S. macrophylla* in the sample plots is more vigorous in areas of higher rainfall. The $R^2$-value (.29) of this line is low, indicating that the data is only weakly correlated. However, the p-value (.057) indicates even these weak findings have a significant trend. This finding agrees with Worbes (1999), who found that monthly increment in plantations of *S. macrophylla* in Venezuela had a high correlation with monthly precipitation. While rainfall is often a benefit to plant growth, the relationship specifically on Moorea was worth studying. For a rainforest tree species such as *S. macrophylla*, other macronutrients and fertilizers are sometimes the limiting factor for tree growth, and water is often in abundant supply. In this situation, an increase in precipitation may not lead to increased growth. The study showed that water is a significant factor for growth on Moorea.

In contrast to height growth, the volume growth expressed by mean annual increment was not found to have a significant correlation with rainfall. Worbes (1999) emphasizes that rainfall correlates highly with increment growth. However, Worbes looked at only diameter-based increment using tree ring studies, not the volume based increment used in this study. The fact that rainfall was a significant factor in one growth rate and not another suggests that further sampling was needed. Additional study sites could have provided more exact numbers and better statistical analysis. However, the sites available on Moorea proved to be a limitation is the study. Mahogany has only recently been planted in great numbers on the island, so the number of study sites is comparably less than studies in areas with natural, native stands or greater histories of mahogany plantations.

A negative correlation was seen with mean annual increment and elevation, indicating that mountain plantations were growing at a slower rate ($R^2=.17$, $p=.057$). As in the rainfall-site index regression, the low $R^2$ values indicates poor correlation, but the p-values make what variation is explained significant. While this pattern is not surprising, the scale at which the data was significant was interesting. Elevation, or latitude, is often used as a surrogate for decreased temperature, which can lead to slower growth rates. Klinka, et.al., (1996) showed a clear decrease in site index for Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) when elevation or latitude increase, but this work was done with temperate species in Canada, not tropical species. Also, Klinka, et.al. sampled a much larger number of sites that ranged over several hundred meters in elevation, while this study only had a one hundred meter range. It should be stressed that this analysis shows correlation, not causality, and elevation here may only be coinciding with another, unrecorded gradient. Alternately, the work in Moorea may show that elevation can have an impact even over small ranges.

No significant relationship was found for slope percentage when compared to site index or mean annual increment. This finding is not surprising given the general disagreement on whether slope affects tree growth. Mayhew and Newton (1998) report mahogany trees growing either faster or slower on steep slopes, depending on other factors. Steep slopes with thin, rapidly draining soils can lead to drought conditions for roots, leading to slower growth rates. Alternately, if flatter planting sites contain soil with high clay content, water-logging may occur and also negatively affect growth. It seems that slope is important only in how it affects soil quality. Because no relationship between growth and slope was observed, nothing about the correlation between soil quality and slope on Moorea can be inferred.

Creeping vines such as *Merremia peltata* and *Lantana* sp. were found to decrease mean annual increment significantly. Young plantations that had been cleared of vines showed significantly higher growth than plantations that had been left alone. Once trees reached about ten years of age, the closed canopy shaded out any competition from these competing vines. This finding is consistent with other literature on creeping vines being weeds in tropical plantations. Dan-Pratiwi (1991) lists these vines as well as *Merremia umbellata* as the most damaging in industrial forest plantations in Indonesia. The vines can lead to wood quality deformation in addition to slower growth. The practice of vine-clearing is not universal in Moorea, perhaps through lack of time or resources. The data presented in this paper strongly supports more intensive vine-clearing for land managers. In addition to its main purpose of preventing mortality in young stands, the vine-clearing also increases growth on remaining trees.

## Conclusions

Rainfall was shown to have a positive correlation with height growth of *Swietenia macrophylla* in the form of site index, indicating that trees are growing taller in areas of high rainfall. Elevation had a negative correlation with mean annual increment, indicating that mountain plantations are growing slower than in the valleys. Clearing of creeping vines like *Merremia peltata* sould be strongly encouraged. All mahogany growers should adopt the practice, as it not only prevent mortality but also increases growth. Preliminary indicators of growth rates on Moorea show healthy growth compared with plantations in other tropical regions, but these numbers should be regarded cautiously until further work can be done. Avenues for future study are clear. Permanent plots have been established in order to study growth and yield more accurately in the long term (see **Appendix A**). Further research is also recommended for other trees in the SDR's precious hardwood program, such as small-leaf mahogany, *Swietenia mahogani*, and Tamanu, *Calophyllum inophyllum*.

## Acknowledgements

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## LITERATURE CITED

Cassells R, and Scheyvens R. (1999) 'Sustainable Forestry Options in the Solomon Islands'. In J. Overton and R. Scheyvens (ed.) *Strategies for Sustainable Development: Experiences from the Pacific*. UNSW Press, Sydney, pp. 199-211.

Dan-Pratiwi M.N., (1991) An ecological study of weeds of industrial forest plantations in South Kalimantan, Borneo, Indonesia. *Buletin Penelitian Hutan*. 534. 15-26.

Klinka K, Wang Q, Carter RE, Chen HYH. (1996) Height-growth elevation relationships in sub-alpine forests of interior British Columbia. *Forestry-Chronicle*. 72:2, 193-198.

Mayhew J.E., and Newton A.C. (1998) *The Silviculture of Mahogany*. CABI Publishing. New York.

Tillier, Sylvain. (1995) Le mahogany grandes feuilles en Martinique. *Bois et Forêts des Tropiques*. 244, 55 -63

Wesom R.W. (1979) Silvicultural Research Division Annual Report of 1978. Department of Forestry, Fiji.

Worbes M. (1999) Annual growth rings, rainfall-dependent growth and long-term growth patterns of tropical trees from the Caparo Forest Reserve in Venezuela. *Journal of Ecology*. 87 (3) 391-403.

Yamada M, and Gholz H.L. (2002) Growth and yield of some indigenous trees in an Amazonian agroforestry system: a rural-history-based analysis. *Agroforestry Systems* 55:17-26.

## Appendix A

*Permanent plot data*

Permanent plots were set up in order to measure growth data more accurately over the long term. The data is recorded here for use by the SDR and any future researchers. Permanent plots were set up in plantations of different ages. 20 trees were marked and numbered with red paint at the given location. In younger stands, 30 trees were marked in anticipation of thinning. Diameters were taken with a diameter tape. Heights were taken of 20% of the trees, chosen at random.

Lotissement Rotui
planted 1991 plot size(m) 9x28
S 17° 31.288’, W 149° 50.354’

| tree | diameter at 1.3m (cm) | height (m) |
|---|---|---|
| 1 | 17.4 | 18 |
| 2 | 25.3 | 20.6 |
| 3 | 24.8 | |
| 4 | 20.8 | |
| 5 | 24.7 | |
| 6 | 19.1 | |
| 7 | 29.2 | |
| 8 | 24.1 | |
| 9 | 21.9 | 18.3 |
| 10 | 21.3 | |
| 11 | 23.2 | |
| 12 | 21.3 | |
| 13 | 16.4 | |
| 14 | 19 | |
| 15 | 17.1 | 12.9 |
| 16 | 35.8 | 20.6 |
| 17 | 16.9 | |
| 18 | 27.5 | |
| 19 | 17.6 | |
| 20 | 13.3 | |
| 21 | 27.5 | |
| 22 | 18.1 | |
| 23 | 30.2 | |
| 24 | 22.9 | |
| 25 | 19.3 | |
| 26 | 23.9 | |
| 27 | 17.6 | |
| 28 | 24.5 | 15.8 |
| 29 | 22 | |
| 30 | 22.8 | |

O 1.67
planted 1967 plot size(m) 16x43
S 17° 31.331’, W 149° 50.062’

| tree | diameter (cm) | height (m) |
|---|---|---|
| 1 | 46.8 | 31.3 |
| 2 | 32.6 | |
| 3 | 48.9 | 31.8 |
| 4 | 41.3 | |
| 5 | 46.7 | |
| 6 | 72.6 | |
| 7 | 46.4 | |
| 8 | 41.5 | |
| 9 | 42.5 | 38.6 |
| 10 | 37.6 | |
| 11 | 48.5 | |
| 12 | 50.8 | 39.7 |
| 13 | 40.8 | 33.2 |
| 14 | 48 | |
| 15 | 37.7 | |
| 16 | 38.3 | |
| 17 | 58.4 | 38.5 |
| 18 | 39.8 | |
| 19 | 44.3 | |
| 20 | 39.4 | |

Pied de Rotui 1 plot size 22x12
planted 2000
S 17° 31.269’, W 149° 49.926’

| tree | diameter | height |
|---|---|---|
| 1 | 12.1 | |
| 2 | 9.7 | |
| 3 | 11 | |
| 4 | 7.6 | |
| 5 | 10.4 | 10.7 |
| 6 | 11.6 | 10.8 |
| 7 | 10.1 | |
| 8 | 7.5 | |
| 9 | 9.9 | |
| 10 | 7.3 | |
| 11 | 9.8 | |
| 12 | 7.5 | |
| 13 | 10.6 | |
| 14 | 7.2 | |
| 15 | 12.4 | 10 |
| 16 | 6.3 | |
| 17 | 11.4 | 8.8 |
| 18 | 10.5 | |
| 19 | 11.2 | |
| 20 | 8.3 | |
| 21 | 5.7 | |
| 22 | 11.5 | |
| 23 | 11.4 | |
| 24 | 9.9 | 10.1 |
| 25 | 6.9 | |
| 26 | 9.8 | |
| 27 | 9.8 | |
| 28 | 8 | 7.2 |
| 29 | 7.8 | |
| 30 | 8 | |

Colline rouge 2-b plot size 48x10
planted 1999
S 17° 31.786’, W 149° 50.945’

| tree | diameter | height |
|---|---|---|
| 1 | 16.1 | |
| 2 | 13.6 | |
| 3 | 12.1 | |
| 4 | 11.5 | |
| 5 | 15 | |
| 6 | 10.2 | |
| 7 | 11.7 | |
| 8 | 16.1 | 15.8 |
| 9 | 15.9 | |
| 10 | 7 | |
| 11 | 6.6 | 6.6 |
| 12 | 12.3 | |
| 13 | 10.5 | |
| 14 | 21.3 | |
| 15 | 20 | 17.7 |
| 16 | 21.8 | |
| 17 | 15.6 | |
| 18 | 13.2 | |
| 19 | 8.5 | |
| 20 | 13.3 | |
| 21 | 16.1 | |
| 22 | 8.8 | |
| 23 | 17.6 | |
| 24 | 14.2 | |
| 25 | 6.3 | |
| 26 | 9.8 | 8.3 |
| 27 | 15.9 | 12.6 |
| 28 | 9.2 | |
| 29 | 11.2 | |
| 30 | 8.3 | 10.8 |

O 2.70 plot size 35x15

planted 1970

S 17º 31.648', W 149º50.917'

| tree | diameter | height |
|---|---|---|
| 1 | 43.3 | |
| 2 | 58.9 | |
| 3 | 60.4 | 25.8 |
| 4 | 24.2 | |
| 5 | 58 | |
| 6 | 48.2 | |
| 7 | 17 | 17.5 |
| 8 | 15.7 | |
| 9 | 44.4 | |
| 10 | 31.1 | 21.6 |
| 11 | 21.6 | |
| 12 | 24.8 | |
| 13 | 26.1 | |
| 14 | 33.2 | |
| 15 | 43.5 | |
| 16 | 50.5 | 23.2 |
| 17 | 21.2 | |
| 18 | 45 | |
| 19 | 21.5 | 15.1 |
| 20 | 29.4 | 23.3 |

# Arthropod Density and Diversity of Mo'orean Tree Groves

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ABSTRACT. The ironwood tree, *Casuarina equisetifolia*, and Caribbean Pine, *Pinus caribaea*, both support similar under story flora in French Polynesia. *Wedelia trilobata*, a non-native weed, and *Dicranopteris linearis*, a native fern, constitute dominant patches beneath these trees. Sixteen quadrats on the island of Mo'orea were swept with an insect net to determine the density and diversity of arthropods present beneath the two species of trees. *Wedelia* exhibited a much higher density of arthropods, but only a slightly higher diversity than the fern. Density and diversity were found to be dependent upon the dominant under story plant species and not upon the canopy of trees present.

## Introduction

The Caribbean Pine, *Pinus caribaea*, is a non-native tree introduced to French Polynesia within the last century as a possible source of lumber. There is a small contingent within the agricultural bureau focused on the harvesting and processing of the pine (Grady, B., personal correspondence). However, mahogany has come to replace pine as the desired plantation tree and much of the remaining pine serves the purpose of erosion control on numerous steep slopes around the island of Mo'orea.

Aito, the ironwood tree, *Casuarina equisetifolia*, frequents the shores of French Polynesia and was thought to be a native species (Chabouts, L. & F.) but may actually have been a very early introduction by the Polynesians (Meyer, J_Y). Aito has been planted in groves that share similar height and canopy cover characteristics with the pines. Though an angiosperm, the aito's twigs bear a superficial resemblance to pine needles and in numerous places create a ground cover very similar to that beneath the pines.

The under story of these tree groves is highly variable and often changes distinctly between species within the same grove. *Wedelia trilobata*, a non-native, weedy species that frequents nearly all of the disturbed areas on the island is one of the most common inhabitants. Where established it is often the only species present. The native fern, *Dicranopteris linearis*, is another common species of the under story. Like *Wedelia* it may constitute nearly 100 percent of the ground cover when present and relies on vegetative growth to spread.

It is possible that the trees determine the organisms beneath them, but more likely that the under story vegetation dictates arthropod diversity and presence. Few insects are known to feed upon fern – thus, the density and diversity of insects found upon the *Dicranopteris* are expected to be drastically less than those found on the *Wedelia*. Alternatively, elevation, percentage canopy cover, depth of under story vegetation, and site location may all be factors that dictate arthropod diversity more so than the plant species present.

## Methods and Materials

### *Methods*

Three sites were chosen within the northern valleys of Mo'orea where sampling occurred. Site locations and the number of quadrats performed at each site follow. Each quadrat was a 10 meter by 10 meter area delineated by field tape. For a total of six minutes each quadrat was swept with an insect net. The arthropods and plant matter collected in the net were then deposited into a labeled bag and returned to the field station for prompt freezing. After sweeping, the depth of the plant species (from top leaves or fronds to the ground surface) that dominated the under story was measured. The canopy cover was estimated, and the relative percentages of plant species constituting the quadrat were calculated.

For each tree species, a total of 8 quadrats were performed – 4 quadrats where *Wedelia* occupied more than 90 percent of the ground cover, and 4 quadrats where *Dicranopteris* did the same. Quadrats were chosen so as to allow for a variety of depths and canopy covers to be tested. After freezing, plant and arthropod specimens were separated and described. Arthropods to be used as type specimens were preserved in alcohol.

*Site Locations*

1. Site one is located 2 km into the Pao Pao Valley. 10 quadrats.
2. Site two is located 1 km into the Opunohu Valley. 3 quadrats.
3. Site 3 is located at a site .5 km from the Belvedere. 3 quadrats

**Results**

There was not a distinct difference between the density of arthropods found beneath the two species of trees. The total number and general type of arthropods found is very similar beneath aito and Caribbean Pine as Figure 1 and 2 illustrate. *Wedelia trilobata* supports a much higher overall density of arthropods than the native fern, *Dicranopteris linearis*.

Though a much lower density of insects was found upon the fern, the number of individual species present, to be used as an index of diversity, was found to be similar in the fern and the non-native weed. The number of different species found upon *Wedelia* and *Dicranopteris* is seen in Figure 3 and 4, again separated as to the trees above. The similarity between the diversity of arthropods found despite the tree present is evident.

**Discussion**

Aito and Caribbean Pine do not appear to dictate the arthropod density and diversity that exists beneath them. Instead, both density and diversity are easily correlated to the plant species that compose the under story. Whether it lives under pine or aito, *Dicranopteris* supports a far fewer number of arthropods per unit space than *Wedelia* does. Though it may be related to age of the grove or amount of time since last disturbance it can also be inferred that aito and pine do not exhibit an effective allelopathy, or chemical composition of their detritus, that affects the arthropod life that lives upon and within it.

The chemical composition of fern fronds has made them a difficult food item for many arthropod species, but this does not affect the ability of *Dicranopteris* to support an arthropod diversity nearly equal to that of the non-native weed. Truly, the total number of insects present upon the fern is greatly reduced in comparison, but the number of individual species gathered suggests the native fern is usable habitat for certain species, and does not prevent other species from using it as a temporary place to reside. Underneath the pine, the number of spiders present was nearly identical upon both *Wedelia* and *Dicranopteris*, suggesting that not all arthropods show the same density preferences.

*Wedelia trilobata* is an invasive species able to support much higher densities of arthropods than the native fern. However, the number of different individual species that reside in this weed is not distinctly higher than the number found in the fern. It is also quite possible

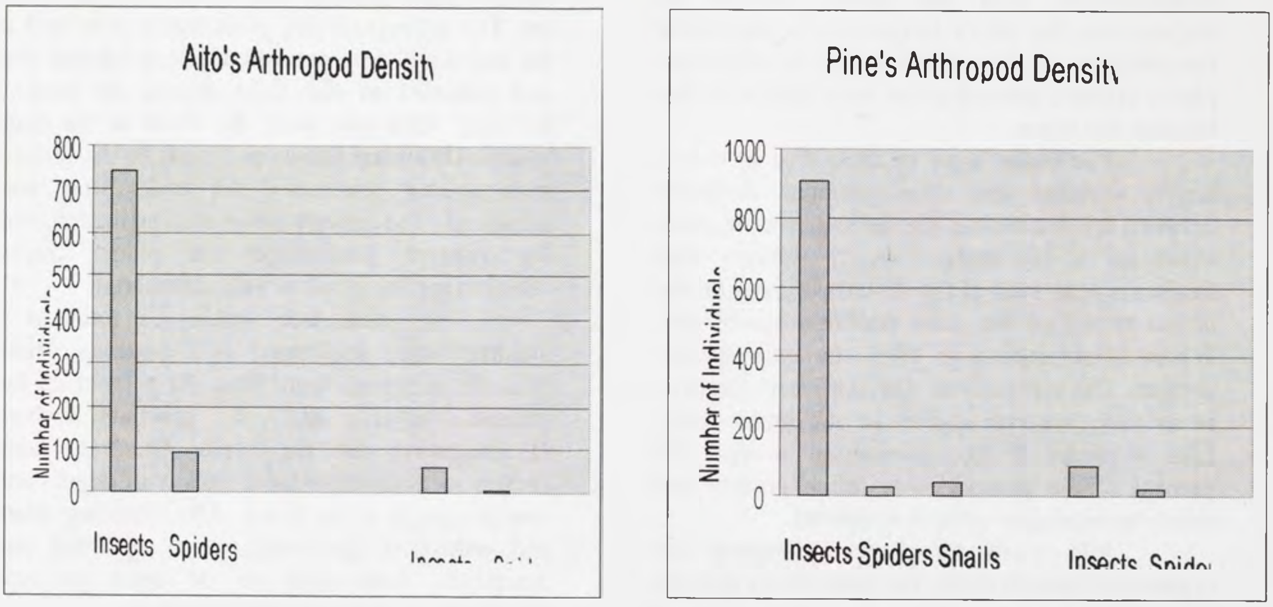

**Figure 1 and Figure 2.** The columns on the left of each chart represent the total number of arthropods found on 400 square meters of *Wedelia* and the columns on the right are the total found on *Dicranopteris*.

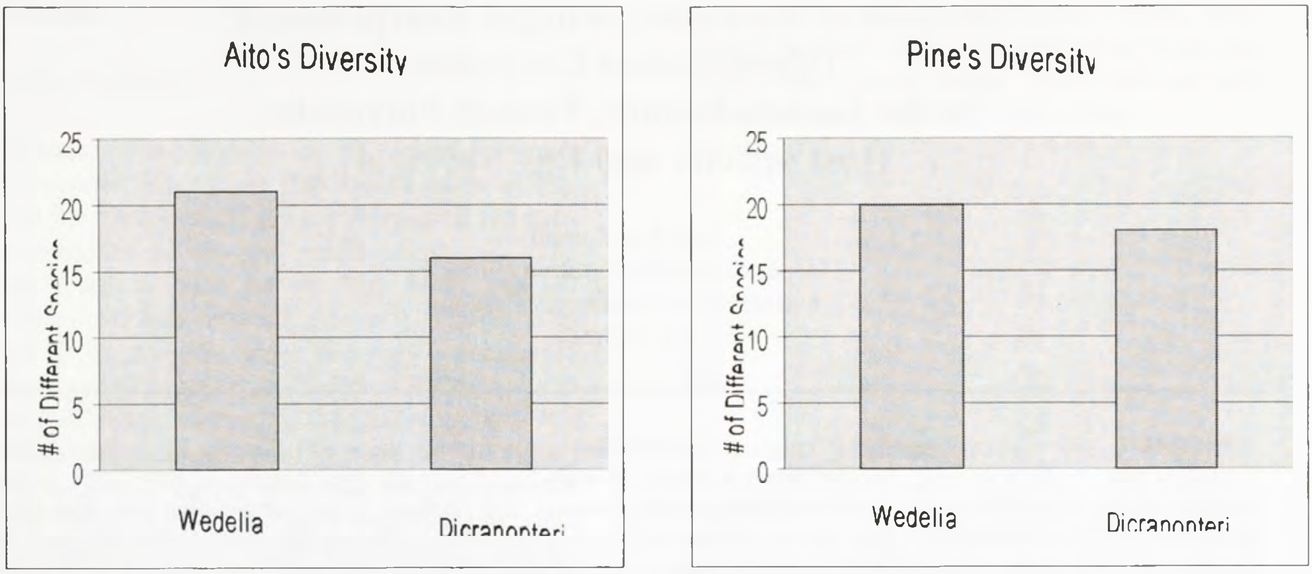

**Figure 3 and Figure 4.** The number of individual species of arthropods found upon each plant.

that the high density of insects found on *Wedelia* are primarily invasive, non-native species themselves, but closer identification and better records of native insect species would be required to fully ascertain this viability.

## Conclusion

*Casuarina equisetifolia* and *Pinus caribaea* support very similar plant and arthropod communities. The under story species that flourish beneath these two trees are what dictate the species and density of arthropods present. *Wedelia trilobata* poses a threat to tropical environs the world over in its ability to spread and easily dominate disturbed areas, such as recently planted tree groves. The high density of possibly deleterious arthropods that reside upon *Wedelia* may make this plant an even more dangerous invasive. Further studies could possibly show what percentage of the arthropods present are actually feeding upon the *Wedelia* and thus slowing its spread. *Dicranopteris linearis* is a native fern on a tropical island system threatened by countless invasive species and thus must be monitored and protected. The fact that it supports a low density of insect life is tempered by the diversity present, and like *Wedelia*, its predation by the arthropods upon it deserves further research.

## Acknowledgements

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## LITERATURE CITED

Borror, et al. (1989) An introduction to the Study of Insects. Sixth Edition. Saunders College Publishing

Chabouts, L.F. Short Flora of Tahiti. Societe des Oceanistes Paris Dossier

Meyer, J_Y (2000). Preliminary review of invasive plants in Pacific Islands SPREP Member Countries in Sherley, G (tech. ed) Invasive Sp. In the Pac. A tech rev. and draft regional strategy. South Pacific Regional Environment Programme Samo. pp. 93, 99, 100

Mueller-Dombois, Fosberg. (1998) Vegetation of the Tropical Pacific Islands. Springer.

# Invasion of the Glassy-winged Sharpshooter (*Homalodisca Coagulata*) In the Society Islands, French Polynesia: Host Species and Egg Survival

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12-14-2003

**ABSTRACT.** *Homalodisca coagulata* (Hemiptera: Cicadellidae) is a vector for the xylem clogging bacterium, *Xylella fastidiosa* that causes scorching diseases in plant crops. *Homalodisca coagulata* was introduced into Tahiti in the Society Islands, French Polynesia in 1999 and has spread to Moorea, and Huahine. It was not recorded from Raiatea or Bora Bora as of November 2003. Host species of *Homalodisca coagulata* were surveyed in a series of habitat types in Moorea: lowland ornamentals, lowland strand vegetation, mid and high elevation ridge-crest vegetation. A list of plant species was formulated from these findings. Leaves with emerged and pre-emerged egg masses were collected from each host species and survival rates were shown statistically to vary among collection site. Overall the survival rate of eggs in egg masses was high and was not influenced greatly by parasitism or predation.

## Introduction

The glassy-winged sharpshooter (GWSS), *Homalodisca coagulata*, is one of the largest leafhoppers in the family Cicadellidae (Hemiptera). It is a polyphagus xylem feeder that is a vector of *Xylella fastidiosa*, a bacterium that causes "scorching" diseases in plant crops such as, Pierce's Disease in wine grapes and Phony Peach Disease in peaches (Hoddle, personal communication). It was introduced into southern California in the late 1980's (Sorensen and Gil, 1996) from its native range of SE United States and NE Mexico (Turner and Pollard, 1959). *H. coagulata's* presence in California has serious economic concerns to the viticulture industry because of its ability to vector Pierce's Disease that was responsible for destroying wine crops in Temecula, CA in the mid 1990's (www.eppo.org). The distribution of their geographic range has been limited in more northern California habitats because they are not tolerant to cold, dry climates (Hoddle, personal communication).

In Ventura, California, a resident parasitic wasp was found in the eggs of *H. coagulata* and more recently, a potential biological control agent, a wasp from Texas and Northern Mexico, *Gonatocerus triguttatus* has been introduced into Southern California to try and reduce the numbers of *H. coagulata* (Conklin and Mizell, 2002). The tiny wasp lays its eggs inside the egg mass of *H. coagulata* and this destroys the egg (Triapitsyn and Phillips, 2000).

*H. coagulata* was introduced into Tahiti in the late 1990's possibly by egg masses on an ornamental plant shipped from California (Hoddle, personal communication). This study examines whether numbers of *H. coagulata* are limited by any native parasitic wasps or egg mass predators on Moorea, FP, and if predation differs among habitats where they can lay their eggs. It is hypothesized that GWSS is not limited in different habitats, lowland strand vegetation, planted ornamentals, and higher elevation flora, for their host species. It is possible that optimal environmental conditions and low parasite numbers allow for large GWSS populations, which may lead to an expanded habitat range. The survival rates of their egg masses are thought to be high, but variable depending on their location, with their predation numbers and parasitoid rates being low. This study will test these effects. This study also looks at the presence and absence of *H. coagulata* on other islands within the Society Archipelago and tests the hypothesis that they have spread beyond the Windward Islands and into the Leeward Islands

## Methods

### *Study Organism*

*Homalodisca coagulata* is 12-14 mm in length as an adult. They have five nymph instar stages that are wingless and gray with bulging red eyes and take ~ 45 days to reach adulthood. The adults are dorsally brown with black and off white markings on their abdomen. The females are larger than the males and have a noticeable slant on the terminal end of their abdomen with an ovipositor located on the center of their last few abdominal segments that appears as a thick black line (Hoddle, personal communication). The adults are good flyers compared to other leafhoppers in the family Cicadellidae and for this reason have a larger geographic feeding range.

The female lays her eggs by depositing them into the plant tissue (usually on the underside of the leaf) and covering them with a hydrophobic white powder consisting of brochosomes. The female can lay anywhere from 1-28 eggs/mass (Conklin and Mizell 2002). GWSS drink from the xylem of the plant stems ingesting up to 300 times their body weight per day and excrete copious amounts of fluid as they are feeding. The fluid expelled is made up of mostly water, some organic compounds and ammonia. If very high numbers of sharpshooters are feeding, the tree in which they are feeding upon will look as if it is raining beneath it and is nicknamed the "pissing fly" by the people in French Polynesia.

### *Study Sites*

#### *Locating and Collecting Host Species*

Moorea is part of the Society Islands that makes up the Windward Islands in French Polynesia. It is a high elevation volcanic Island ~1.2 million years old and is surrounded by coral reefs (Resh et al. 1990). 11 sites were designated as search sites for the host species of *H. coagulata*. 2 motus (coral islands) were chosen for their native strand vegetation, Motu Tiahura and Motu Temae (see fig. 1). Motu Temae (included off road vegetation and coastal vegetation) has been partly filled in and is connected to the main island of Moorea. It has roads and is fairly populated. The vegetation is similar to Motu Tiahura that has no roads and has a total of five people living on it. Five villages were chosen for their large varieties of planted ornamentals; Maharepa, Temae, Afareaitu, Vaiare and Haapiti (see fig. 2). Two high elevation mountains, Mt. Rotui (899m) and Mt. Mouaputa (830m) were chosen for their vegetation along their trails and ridge crests (lonely planet, 2000) and one mid elevation site in Pao Pao Valley (63m) (see fig. 3).

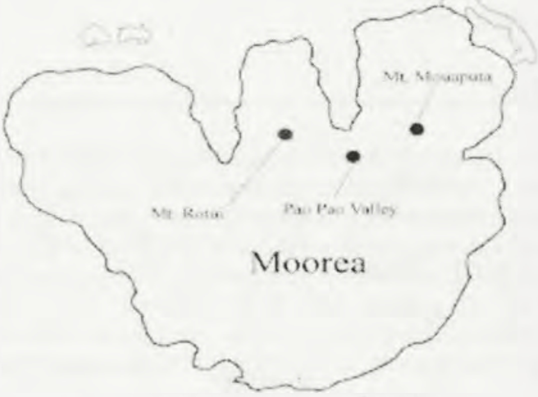
Fig.1

Native Strand Vegetation

Fig. 2

Planted Ornamentals

Fig. 3



High & Mid Elevation Sites

*Searching for H. coagulata In the Leeward Islands (see fig. 4)*

1. Huahine is 170 km from the largest island in the Societies, Tahiti (A=1045$km^2$, population 150,000). Huahine is made up of Huahine Nui and Huahine iti and its tallest peak is 669m. Its area is 75 $km^2$ and has a population of 5411 (Lonely Planet, 2000).
2. Raiatea is 220 km NW of Tahiti and is the largest of the Leeward Islands, the tallest peak is1017m and its area is170 $km^2$ (this includes Tahaa, which is 5 km away). The population is 10,057 and has the second largest city, Uturoa, to Tahiti's Papeete (Lonely Planet, 2000). It has the deepest bay and abundant rainforests and the only navigable river in French Polynesia (www.tahiti.com, 12-13-03).
3. Bora Bora is 260 km from Tahiti and its total area is 38 $km^2$ with a population of 5,767. The highest peak is 727m (Lonely Planet, 2000).

Fig. 4

The Society Islands

*Collection Techniques*

At each site every reachable leaf of every species of plant was inspected for egg masses. For village sites the roads were walked from one village to the next. For high elevation mountains the trails were walked up to the peaks. For motus the coastline was walked along with the interior roads and trails. If egg masses were found on a plant, the leaf was picked and stored in a plastic re-seal bag to store for further analysis. For unidentified plant species, pictures were taken of all distinctive parts i.e. flower, fruits, leaf, and trunk..

*Data Analysis*

The egg masses were taken back to the lab and the numbers of eggs within the egg masses were determined by counting the heads (black dots) of the larva visible through the egg casing of eggs that had not yet emerged. The eggs were counted once successfully hatched out and this number was recorded as survived. If the eggs had already emerged then the number was determined by counting the impressions of the individual eggs within the mass. If the egg masses were preyed upon, then the number of eggs were determined by how many times a .5mm piece of pencil led, which was used to represent the width of one egg, would fit into the mass vertically. The egg mass was determined to be preyed upon if all or part of the outer covering was ripped away. Parasites were determined by the presence of a small hole in an egg sac. All holes represented one parasite and one egg death.

All data was placed in table form and a total number of egg survivals and egg deaths were calculated. Counts of eggs preyed upon or parasitized were examined at for each site. The survival rates across sites were tested using a Chi-square ($\chi^2$) test of independence to see if different sites differed in egg survival. The sites were grouped by similarity in vegetation and survival rates were examined in the same format as for individual sites.

*Searching for H. coagulata in the Society Islands*

Huahine and Raiatea were visited for a total of four days and Bora Bora a total of two. The islands lowland perimeter was surveyed for any sign of *H. coagulata*. Known plants that they fed upon due to prior observations on the islands of Tahiti and Moorea were swept with an insect net. Plants were physically observed and leaves were turned over to check for egg masses on known host species.

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## Results

### *Host Species*

Host species were found in every site. *H. coagulata* seem to be occupying every niche available on Moorea and have a very wide range of host species that is not limited to high elevation, coastal regions and urban villages. Over 40 families were identified. Fabaceae was the most frequent of the entire host species observed. Nearly 100 species were observed as host species. All sizes of leaves were found to be adequate for egg laying. Some leaves, like *Hibiscus tiliaceous* ( ~15-25cm in length and 25-30cm in width) had multiple egg masses per leaf, whereas others, like *Pemphis acidula* (~1cm in length and 2-4mm in width) had only one egg per leaf.

These observations reject the null hypothesis that they are limited to certain habitats and support the hypothesis that they are not limited as to where they will lay their eggs. Fabaceae was the most frequent family of host species (see Appendix 1. List of Observed Host Species for GWSS on Moorea, French Polynesia)

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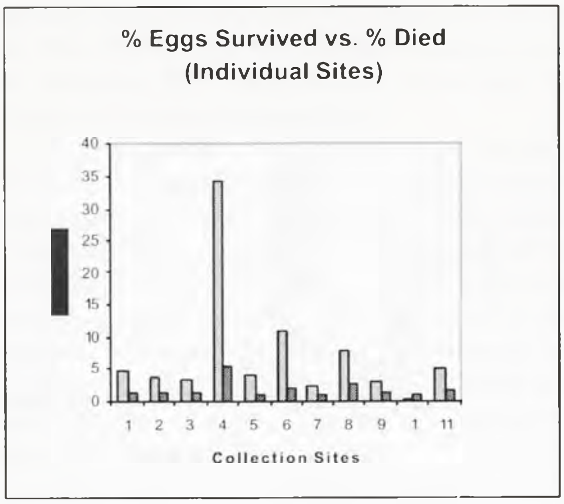
Fig.5

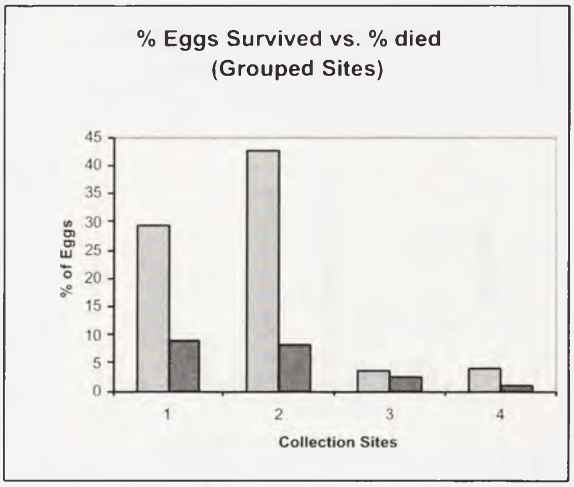


Specific Collection Sites

| | |
|---|---|
| 1=Temae Beach | 7=Temae Village |
| 2=Tiahura | 8=Haapiti |
| 3=Mt. Rotui | 9=Afereaitu Village |
| 4=Temae Mats | 10=Mt. Mouaputa |
| 5=Opunahu Valley | 11=Vaiare Village |
| 6=Maharepa Village | |

Egg survival differed across sites ($p <$ .05, df=10.0, $?^2$=232.158 ). This rejects the null hypothesis that different sites have the same survival rates and supports the hypothesis that the survival rates vary across different sites. The Temae mats (site 4) had a much larger collection size and this shows up as having a larger survival rate than the other sites. Mt. Mouaputa (site 10) was the only site that showed more deaths than survivorship.

Fig. 6



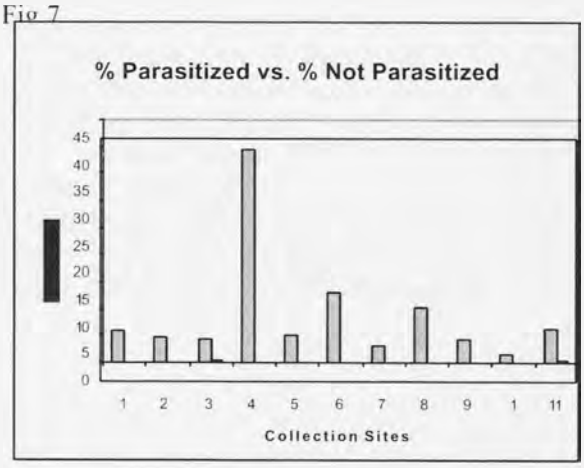
Specific Collection Sites

| | |
|---|---|
| 1=Lowland Villages (planted ornamentals) | 3=High Elevation Mountains (<800m) |
| 2=Motus (strand vegetation) | 4=Mid Elevation (0>100m) |

The collection sites were grouped together by similar species of flora; native strand vegetation (1, 2, 4), planted ornamentals (5, 6, 7, 8, 9, 11), high elevation (3, 10) and one mid elevation valley (5). Egg survival differed for sites with similar vegetation ($p<.05$, df=3.0, $?^2=61.78$).

This rejects the null that similar plant species have the same egg mass survival rates. A higher survival rate is seen in native strand vegetation and lowland villages compared to high elevation mountains.

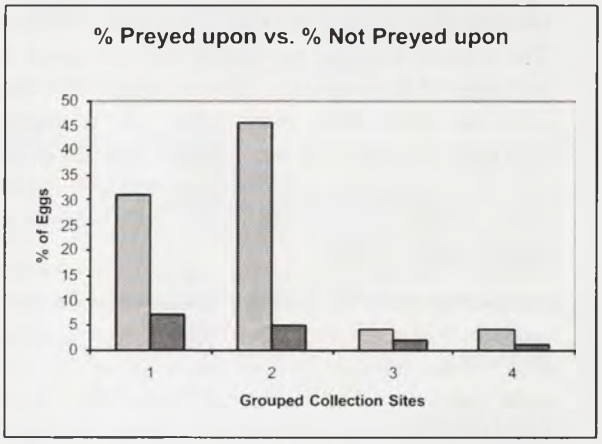
Fig 7



Specific collection sites same as Fig. 5

The parasites that were found were not grouped at only one location; they were spread throughout the sites with no pattern of vegetation or location similarity. The Chi-Squared test shows significance ($p< .05$, df=10.0, $?^2=96.867$) but more than 1/5 of the data is sparse. This does not necessarily reject the null, or support the hypothesis that parasite numbers differ at different locations. The rates of parasitism are low and are probably not influencing or reducing the survival rates of the egg masses.

Fig. 8



Specific collection sites same as Fig. 6

The sites are grouped by similar types of flora and predation rates were found to differ across these similar types of vegetation ($p <. 05$, df=3.0, $?^2=93.24$). This rejects the null that sites with similar flora have the same predation rates and supports the hypothesis that there is unequal predation of egg masses at different sites that have similar flora. Predation rates are independent of location and flora and this could make it difficult to figure out what is eating the egg masses.

*Distribution of H. coagulata in the Society Islands*

| Island | Present | Absent |
|---|---|---|
| Tahiti | X | |
| Moorea | X | |
| Huahine | X | |
| Raiatea | | X |
| Bora Bora | | X |

*Homalodisca coagulata* was found on Tahiti, Moorea and Huahine during the months of September-November of 2003. Adults, juveniles and egg masses were found on a large Tiare shrub in a house garden in Fare Village. The spreading to Huahine indicates that the *H. coagulata* has not been successfully contained to Tahiti and Moorea since its recent introduction into Tahiti in 1999. This supports the hypothesis that *H. coagulata* is colonizing other islands in the Societies.

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## Discussion

*Host species*

The host species that *H. coagulata* has occupied in Moorea is very extensive. They are found in every type of habitat investigated from lowland coastal native plants to high elevation ridge-crest plants. The invasion of many niches may be due to the very large number of sharpshooters competing for plant space. An article published by the University of Florida Institute of Food and Agricultural Sciences in 2003 by Conklin and Mizell states that the female sharpshooter lays 3-28 eggs on well-chosen leaves and that they have preferred plants for oviposition. The preference is affiliated with the nutrient needs of the juveniles once they hatch out and begin feeding.

Their large numbers and island-colonizing success may be decreasing their host species preferences and pushing them into less tolerant environments for oviposition. Being pushed out of their preferred host species range could explain why they laid eggs on leaves that were so small that only one egg fit per leaf.

If their adult population numbers continue to increase then their egg mass and juvenile survival rates may begin to decline. This decline could come about because they have to lay their eggs on plants that are not nutritionally supportive for juvenile growth. A study in 1990 by Brodbeck et al examined the preferences that adult *H. coagulata* had on four different host species based on their seasonal amino acid make-up. The xylem fluid was extracted during times of excessive and low-moderate times and the amino acid content was analyzed.

A similar examination could be done for host species in Moorea that have emergent egg masses on leaves, but are absent of juveniles. This could look more at the survival rates of the nymph instars and their tolerance to a nutrient poor host species. It is likely that even if the numbers of juveniles are being reduced by intolerant host species the impact is small and not sufficient enough to control the number of juveniles that do make it to adulthood.

*Survival Rates*

*H. coagulata's* survival rates vary at each site depending on location. Even though their success is high they are not having equal egg hatching success throughout all niches. This could be that they are laying their eggs in areas that are less desirable because their population numbers are so high and the competition for feeding and ovipositing is fierce. A less desirable place could be defined by an increased number of egg predators, or egg parasites. It could also be that the eggs do not do well in hot and moist climates like that of the tropical riparian habitats.

By not having all the same survival rates it is possible that there are areas that could have more predation and that the predators that are feeding off of the egg masses of the sharpshooter may increase and may spread to other areas and decrease the number of sharpshooters throughout the islands. To test this, it would be necessary to observe any predation on the egg masses and identify specific species of predators.

Presently the survival rates are high in Moorea, FP compared to Florida, USA where researchers Triapitsyn, Serguei et al have found an increase in the number of species of mymarid wasp egg parasites. No known species of egg parasite has been identified on Moorea as of November 2003. The data collected suggests that parasite numbers are still very low and that they are not impacting the survival rate of the sharpshooters significantly. The low numbers could be because the sharpshooters have only been in French Polynesia for four years and that has not been enough time to increase the numbers of the egg parasites. In general, the wasp parasites do not have large populations and would have to be farmed (www.calacademy.org) and released in larger numbers to make a significant decline in survival rates of the sharpshooter's egg masses.

### *Colonization of other Islands in FP*

Huahine is the closest of the Leeward Islands to the already invaded Windward Islands, Tahiti and Moorea. It is likely that Huahine was first to be invaded due to this close proximity and that the remaining Society Islands will be invaded by sharpshooters in time. It could be that they are already on other islands, but in small enough numbers that they have not yet been found.

The Cargo ships, ferries, planes and private boats visit all of the islands in French Polynesia. There are not many ways of preventing the spread of the sharpshooter throughout French Polynesia. The islands are close enough that an adult could stay alive for any of the travel durations and egg masses could certainly travel safely throughout the archipelagos.

### *Conclusion*

It is likely that some form of biological control will need to be implemented to decrease the large populations of the sharpshooters and discourage their spreading. Their normal climatic limitations are not a factor in the warm, wet climatic regions of the South Pacific. The parasite numbers are too low to make any nominal differences at this time and there are enough plant species for them to feed and oviposite on without any habitat limitations.

### Appendix 1. List of Observed Host Species for GWSS on Moorea, French Polynesia

*Thunbergia erecta*-**Acanthaceae**
*Pleomele sp*. **Agavaceae**
*Alternanthera sessils*-**Amaranthaceae**
*Crinum xanthophyllum*-**Amaryllidaceae**
*Mangifera indica*-**Anacardiaceae**
*Spondias mombin*-**Anacardiaceae**
*Pseuderanthemum carrothersii*-**Apocynaceae** (Chinese lantern)
*Allamanda cathartica*-**Apocynaceae**
*Alyxia stellata*-**Apocynaceae**
*Cordyline fruticosa*-**Aqauaceae**
*Shefflera actinofolia*-**Araliaceae**
*Polyscias guilfoylei*-**Araliaceae**
*Syagrus romanzoffiana*-**Arecaceae** (queen palm)
*Sphagneticola trilobata*-**Asteraceae** (wedelia)
*Bidens sp.*-**Asteraceae**
*Gliricidia sepium*-**Boraginaceae**
(cleomile-**Brassicaceae)**
*Cordia subcordata*-**Boraginaceae**
*Tournefortia argentea*-**Boraginaceae**
*Terminalia catappa*-**Combretaceae**
Calophyllum- **Clusiaceae**
**Unknown -Combretaceae**
*Ipomoea micrantha*-**Convolvulaceae**
*Ipomoea fistulosa*-**Convulvulaceae**
*Dioscorea bulbifera*-**Dioscoraceae**
Codiacum variegatum – **Euphorbiaceae**
*Acalypha hispida*-**Euphorbiaceae**
*Calliandra surinamensis*-**Fabaceae**
Cassia alata-**Fabaceae**
*Acacia sp.*-**Fabaceae**
Caesalpinia pulcherrima-**Fabaceae**
*Calliandra surinamensis*-**Fabaceae**
Cassia alata-**Fabaceae**
*Crotalaria pallida*-**Fabaceae**
*Delonix regia*-**Fabaceae**
*Pterocarpus indicus*-**Fabaceae**
*Hernandia nymphaefolia*-**Fabaceae**
*Leucaena leucocephala*-**Fabaceae**
Mexican lilac- **Fabaceae**
*Senna surattensis*-**Fabaceae**
*Sophora tomentosa* -**Fabaceae**
*Samanea saman*-**Fabaceae** (monkey pod)
**Unknown Fabaceae**
*Xylosoma suborbicular*-**Flacourtiaceae**
*Scaevola ( sericea* **?)-Goodenaceae**
*Heliconia sp.*-**Heliconiaceae**
*Cordyline fruticosa*-**Liliaceae**
*Fagraea berteroana*-**Loganiaceae**
*Pemphis acidula*-**Lythraceae**
*Psidium guajava*-**Myrtaceae**
*Angiopteris evecta*-**Maraltiaceae**
*Ficus sp*.- **Moraceae**
*Thespesia populnea*-**Malvaceae** (milo)
*Hibiscus rosasinensis*-**Malvaceae**
*Hibiscus tiliaceous*-**Malvaceae**
*Malvaviscus pendulilorus*-**Malvaceae** (turks cap)
*Swietania macrophyla*-**Meliaceae** (Mahagony)
*Metrosideros sp.* –**Myrtaceae**
*Myrsine sp.*-**Myrsinaceae**
*Bougainvillea sp.*-**Nyctaginaceae**
*Ochna thomasiana*-**Ochnaceae** (Mickey Mouse Plant)
*Pandana sp.* **(climbing)-Pandanaceae**
*Passiflora foetida*-**Passifloraceae**
Colubrina asiatica-**Rhamnaceae**
*Crossostylis* **(turks cap)-Rhizophoraceae**
*Gardenia anguistifolia*-**Rubiaceae**
*Morinda citrifolia*-**Rubiaceae**
**Unknown Rubiaceae**
*Gardenia tiatensis*-**Rubiaceae**
*Strelitzia (reginae?)*-**Strelitziaceae**
*Clerodendrum thomsonae*-**Verbanaceae**
*Lantana camara*-**Verbanaceae**
*Guillainia purpurata*-**Zingerberaceae**
*Areca cathewa*
*Asystasia salicifolia*-**Acanthaceae**
*Pometia pinnata*
*Igna feuillei*
*Canthananthus roseus*
*Cathanathus roseus*-(malphigia)
*Mussaenda philippica*
*Phymatosorus grossus*
*Duranta erecta*
*Ixora sp.*
*Glichodian*
*Guettarda speciosa*
*Jatropha multifida*
*Lagerstromia indica*
*Lagerstromia speciosa*
*Shefflera actinpylla*-(octopus tree)
Unkown palm 1
Unknown leaf 1
Unknown tree 1
Unknown tree 2 (weimania?)
Unknown vine 1
Unknown vine 2
Unknown flower 1
Unknown flower 2
Unknown flower 3

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*Data Analysis*

Orlo C. Steele was a tremendous help with his abilities for identifying island plants as was Jan Nakamura.

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## LITERATURE CITED

Barrow, J (1971) Useful Plants of Tahiti. Tien Wah Press, Singapore, pp 25

Brodbeck, Anderson, et al (1992) Feeding by the leafhopper (H. C.), in relation to xylem fluid chemistry and tension. Journal of Insect Physiology 38:8 611-622

Brodbeck, Mizell, et al (1990) Amino Acids as determinants of host preference for the xylem feeding leafhopper, *H. coagulate*. Oecololgia 83:3-338-345

European and Mediterranean Plant Protection Organization. (2003) Glassywinged Sharpshooter. Retrieved on 12-8-2003 www.eppo.org

Hermann, B (1974) Plants and Flowers of Tahiti. Les Editions du Pacifique, Singapore, pp 7-147

Hoddle S, Mark (2001) Distribution and plant association records for *Homalodisca coagulate* (Hemiptera: Cicadellidae) in Florida. Florida Entomologist 86: 1 89-91

Hoddle S. Mark (2003) Personal communication on 9-10 and 10-10

Kepler, Angela (1990) Trees of Hawaii. University of Hawaii Press, Honolulu, pp 11

Purcell, Alexander (2003) Personal communication on 12-10

Resh, VH et al (1990) Distribution and ecology of benthic macroinvertebrates in the Opunohu River catchment, Moorea, French Polynesia. pp195-214

Sorenson, J.T., and R. J. Gill. (1996) A range extension of *Homalodisca coagulate* (Say) (Hemiptera: Clypeorrhyncha: Cicadellidae) to southern California: Pan Pacific Entomol. 72 160-161

Triapitsyn, Serguei, et al (1998) Egg parasitoids of H.C. Florida Entomologist 81:2 241-243

Triapitsyn, Serguei, Phillips (2000) First record of GAnatocerus triguttatus (Hymenoptera: Mymaridae) from eggs of Homalodisca coagulate with notes on the distribution of the host. Florida Entomologist 83:2 200-203

Turner,W. F., and H. N. Pollard (1959) Life histories and behavior of five insect vectors of phony peach disease: USDA Tech. Bull 1988:28

University of Florida Institute of Food and Agricultural Sciences; Department of Entomology and Nematololgy. (2003) Glasswinged sharpshooter (*Homalodisca coagulata)* Retrieved on 12-6-2003 *http://creatures.ifas.ufl.edu/fruit/glassywinged_sharpshooter.htm*

Wagner, Herst, Sohmer (1990) Manual of the Flowering Plants of Hawaii Volume I and II. University of Hawaii Press, Honolulu

Whistler W, Arthur (1980) Coastal Flowers of the Tropical Pacific: A Guide to Widespread Seashore Plants of the Pacific Islands. Oriental Publishing Co., Honolulu, pp 25,41,43,46

# Factors influencing survivorship of larval *Culex roseni* in the carbonate platform pools of Mo'orea, French Polynesia.

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ABSTRACT. *Culex roseni* is a relatively unstudied mosquito species endemic to French Polynesia. Larval populations were observed living in karst pool formations on the carbonate platforms of Mo'orea, French Polynesia. This study sought to identify the factors influencing survivorship of *C. roseni* in these salt-water pools, including ability to survive high densities, salinity change, and desiccation. The average density of 4 chosen pools on the Tiahura motu during three weeks of sampling, was 3927 larva per $m^2$ or 53636 larvae per $m^{23}$. In a lab-based trial, *C. roseni* can inhabit water with salinity levels ranging from fresh water (0 ppt) to salt water measuring 60 ppt. *C. roseni* can osmoregulate within this range to adapt to abrupt or gradual change in salinity. In a heat shock trial, *C. roseni* survived water temperature up to 49° C. In lab-based trials, *C. roseni* endure 2 hours, 20 minutes without water during tidal fluctuations as long as they remain slightly moist.

## Introduction

High densities of *Culex roseni* (Belkin) were found living in the salt water pools on Tiahura motu. At times, the larvae appeared to darken the water with their intense biomass. This density was not only visually stunning but also of scientific interest as *C. roseni* has been previously recorded as a fresh-water organism. (Belkin 1962, Riviere et al. 1986a) Fluctuating salinity, water temperature and tide levels make the pools these larvae inhabit a severe and dynamic environment. For this reason, I was amazed to find these "fresh water organisms" not only surviving but thriving in high densities.

This study sought to quantify the densities of these larvae and the physical parameters of their natural habitat. It also sought to determine the extent of *C. roseni's* tolerance to extreme salinities, high temperature and desiccation.

I hypothesized that in lab-based tests, *C. roseni* larvae would survive even more variable parameters than those observed in the field. If my hypothesis is true, it may account for the abundance of larvae.

## Methods and materials

### *Site location*

The Tiahura motu is located off the northwestern coast of Mo'orea, French Polynesia (17° 30' S 149° 50'). A motu is a small island formed by coral debris depositing through storm activity on the barrier reef of a larger island. On the Tiahura motu the island formed its own reef which was cemented to a "platform" over time and then exposed to air during global changes in sea-level. The pools used for this study are formed in this exposed carbonate platform. They are situated on the northern side (Figure 1) of the motu. (17° 29.179' S 149° 54.723' W)

*C. roseni* larvae take advantage of a geological formation on the carbonate platform of the Tiahura motu. The geological formations in which these larvae live have been described as karst pools. This is because these formations are formed by the dissolution of calcium carbonate, called the karst process. On the motu, these "karst pool" formations are carved out of the vadose and phreatic layers. These two layers have a porous layer in between them which subterraneously connects the karst pool to the ocean. (Figure 2) (Waljeski, pers. comm.) Larvae are not at risk of being sucked into the ocean because a sandy substrate protects them from this porous layer.

Karst pools, with subterranean ocean connections, have several advantages for the *C. roseni* larvae. (These karst pools will be referred to as "pools" for the remainder of the paper.) The pools are not connected to the ocean above ground, except through occasional wave swells, and therefore possibly avoid being colonized by larvivorous tide-pool fish during day to day tidal variation. The pools also never dry completely, as equally sized "closed system" pools do in Mo'orea's hot weather. Pool permanency has a notable affect on the type and density of larvae that are able to live in that environment (Laird 1988, Russell, pers. comm.). As well, these pools are uncolonized by other mosquito larvae, as other mosquitoes on Mo'orea are incapable of withstanding such high salinities in their larval stage. (Navarro 2003, Riviere 1987, Patrick et al. 2001)

Four pools were used for this study. The pools were chosen for roughly equal size (about 2m by 4m and 20 cm deep) and the presence of *C. roseni* larvae. The pools were all within 100m of each other and averaged about 13 meters from the ocean shore.

*C. roseni* larvae were not studied on other parts of the Tiahura motu or Mo'orea. *C. roseni* is not as abundant as other mosquitoes on the island. An earlier paper on ovipositioning preference noted that *C. roseni* was only present in 1% of the egg rafts collected throughout Mo'orea. (Nguyen 2002)

*Larval Density Sampling*

To quantify the larval density in the 4 pools, a sub-sampling technique (Russell, per. comm.) was used. First, the surface area of the pools was calculated. All pools were roughly elliptical with sloping floors. The equation ($ab\pi$) was used. With a and b being the foci measured on the surface of the pool. (figure 3).

The surface area was then divided by two, giving me the number of times I would sample mosquito larvae from each pool. The pools were sampled at roughly 12 p.m. for five days. These sampling days were each about three days apart.

For each individual sample, mosquito larvae were calculated with "fish tank" style nets with a "mouth" measuring 15 cm by 12.5 cm. These nets were submerged and quickly dragged roughly 15 cm through the water parallel to the surface.

The volume of the water sampled for larvae with each pass was calculated (equation: volume=(height)(width)(length)) to be approximately 0028 m³. The larvae were placed into a bucket with water and taken back to the lab for counting.

Population density of each pool was then extrapolated using the larval counts from the sub-sampling and the pool volumes. ($1/3((ab\pi)(c))$) (See figure 3. a=foci b=foci c=height)

Density was measured as the number of larvae per meter squared of surface area, because access to air is a limiting factor for the larvae. (Resh, pers. comm.) Density was also measured in meters cubed for comparison to other pertinent larval density studies.

*Physical characteristics of natural populations*

*Larval salinity tolerance*

In order to determine the level of salinity tolerable by *C. roseni* larvae, I transferred larvae from a pool with salt concentration 30ppt water to experimental cells with salinities ranging form 0ppt to 90 ppt, in steps of ten. Salinity was measured using a "Lecia" hand-held refractometer. Experimental cell salinity was prepared by dilution or heat-assisted evaporation of ocean water collected at the study site, except in the 0 ppt cells. 0 ppt concentration was obtained using non-chlorinated tap water. 40 cups were prepared with 20 larvae in each experimental cell. (Figure 4)

The volume of water in each cup was 40 ml so that larvae had adequate living space. (Russell, pers. comm.) Larvae were used that had been collected from pool 3 for density measurements. On the day of collection, pool 3 had a salt concentration of 30 ppt. The larvae from this sample were subdivided into four larval instar stages. Instar stages were determined by size.

Cell maintenance was performed daily in the following manner:

1. Larvae were fed an aliquot of yeast and water
2. Cell salinity was measured with the hand held refractometer and adjusted to compensate for evaporative losses.
3. All dead larvae were removed.

On density sub-sampling days the salinity of each pool was measured.

The range of natural salinity fluctuations occurring at the study site were determined by taking salinity measurements at 2 hour intervals for 24 hours on November 5th.

*Larval temperature tolerance*

The range of natural temperature fluctuations occurring in the field were determined by recording pool temperature at 1 hour intervals for 24 hours. Pool temperature was recorded at the top and bottom of the water column. Ambient temperature was also recorded.

In order to determine the temperature tolerance of *C. roseni* larvae, heat shock tests were performed using five larvae from each of the four instar levels. These groups of five were placed in a beaker containing water of given temperature. The desired water temperature was kept constant for at least a minute. Upon total survival ($LD_0$), a new larval group was utilized and the temperature increased by 1°C. The highest temperature in which all larvae survived was recorded as the tolerance of *C. roseni.*

*Larval desiccation tolerance.*

During low tide, significant decreases in the water level in the tidal pools were observed. At very low tide, such as that occurring on November 5, 2003, nearly half the volume of each pool drained into the ocean leaving larvae stranded on the side of the pool. To characterize the ability of the larvae to tolerate such desiccation, controlled experiments were conducted. The bottom of 18 trays were filled with sediment from the natural pools. The trays were filled with sea water (salinity = 35 ppt) and 20 larvae (5 from each instar). The trays were slowly drained and then placed in the sun. Every 20 minutes for 3 hours 1 of the trays was rehydrated and relocated to the shade. Larval survival was recorded upon rehydration and once again after a 24 hour recuperation period.

## Results

*Larval density sampling*

The highest larval density sampled at a pool on any given day was 11,711/m², the lowest 104/m², and the (mean) average 3928/ m². (figure 5)

An analysis of variants (ANOVA) test found no statistically significant difference between densities of samples on the five sampling days. (P = 0.5389) (chart A)

An analysis of variants (ANOVA) test found no statistically significant difference between the densities of a pool (larvae per m²) and pool's surface area.( m²) (P = 0.1245) (chart B)

An analysis of variants (ANOVA) test found no statistically significant difference between the densities of a pool (larvae per m³) and pool's volume.( m³) (P =0.0545) (chart C)

*Larval salinity tolerance*

All instar stages placed in the salinities ranging from 60 ppt to 90 ppt died within the first day.

Stage 1 instars, (figure 6) were the most susceptible to salinity change.
A Kolmogorov-Smirnov test was run on the larval salinity tolerance data which showed that the larvae experienced significantly different mortality rates between fresh water and 50 ppt, (P = .059) and 30 ppt and 50 ppt (P = .059). There was also a nearly significant difference between 50 ppt and 10 ppt (P= .003) and 50 ppt and 20ppt (P = .023) This developmental stage experienced higher rates of mortality than the other three stages. For stage 2 instars (figure 7), the larvae in the 50 ppt water had significantly different survival rates (P = 0.0) than the other salinities. (P = 1.0) In stage 3 instars (figure 8), there was no significant difference in survival between the salinities.

For stage 4 instars, (figure 9) the larvae in the 50ppt had significantly different survival rates (P = .023) than the other salinities. (P = .954)

The salinity of pool 2 during the 24 hour trial (figure 10) varied by 1 ppt throughout the day in connection to the tide, with higher salinity when the tide came in.

*Larval temperature tolerance*

Average pool temperature (of the 4 pools) measured at the top of the water column varied between 23 and 34 °C. Average pool temperature at the bottom of the water column varied between 23 and 34 °C.

During the 24-hour temperature measurements on November 5th and 6th , the thermometer was accidentally broken with 5 hours left to go. Therefore, the 24-hour measurements for temperature became a 19-hour measurement.

Ambient temperature was observed as being consistently lower than pool temperature. (figure 11) As the tide went out the temperature on the top of the pool was higher. As the tide came in the temperature on the bottom of the water column was higher.

Larvae of all stages withstood a maximum temperature of 49° C ($LD_0$) in the lab for a full minute. At 50° C they experienced total mortality. ($LD_{100}$)

*Larval desiccation tolerance*

Larvae seemed to survive well for about two hours in the sun. Larvae showed a notable drop in survival (figure 12) as sediment temperature reached 37° C and ambient temperatures reached 39° C. (figure 13) As long as there was visible moisture on the larvae they were able to survive but once they were dried, mortality was imminent.

**Discussion**

*Laval density sampling*

The larval density of these pools is relatively high for mosquito larvae, although other mosquito species have been recorded in higher densities, notably *Culex sitiens* and *Aedes vigilax*. (Webb, pers. comm.)

Of the 5 days at the 4 pools, the highest density measurement for any pool was 11,711/m², the lowest 104/m², and the (mean) average 3928/ m². What natural parameters aide support high larval density?

An ANOVA test suggested no correlation between surface area and density (chart A) or pool volume and density (chart B). Analysis of variants (ANOVA)(chart C) suggested that larval density remained constant regardless of date sampled. One might construe from this information, that the *C. roseni* population in the study area is fairly stable.

Why does *C. roseni* live in such high densities? Perhaps this is a sign that it is thriving in this environment. However, a high density environment can also cause stress for the individual leading to stunted growth, depleted health and increasing competition for food. Unfortunately, tests of percentage survival within the pools were not conducted and therefore it is difficult to say whether the high densities are detrimental to the individual larvae. However, possible strategies for survival can be considered from observations in the field and in the lab.

For example, how does this population self-regulate if density becomes too high? Is the availability of food a problem? One observation in the lab brought up an interesting possibility. The phenomenon of "clustering" was observed several times in the lab but not in the field. Clustering was often observed when larvae were left out in buckets with no food as they awaited counting. Several times, a large number of larvae would congregate in a relatively tight cluster in one corner of the container. When closely observed the larvae were seen working their mouthparts over each other in continuous movement.

Perhaps what I observed was the larvae feeding on other larvae. When the clusters scattered in response to my movement, several dead larvae could be found remaining behind. The clustering larvae might have been eating these dead larvae or the bacteria attracted to their remains. Indeed, *C. roseni* larvae have been observed in the lab opportunistically eating other weak or dead larvae.

The larvae might also cluster in order to feed off of each others' molted skin.
An interesting combination of both actions has been observed in crayfish populations. (*Orconectes rusticus*) *O. rusticus* have been recorded clustering around a molting individual of their same species. They sense this individual by olfaction and take advantage of their weakened condition to attack and eat the individual. (Adams 2000)

Perhaps a similar behavior is happening among *C. roseni* larvae.

If *C. roseni* are indeed cannibalistic, it is possible that the larvae actually benefit nutritionally from high densities. Many other animal young have been known to eat their brothers and sisters in response to stressful environments such as high density. For example, the young Tengmalms owl, *Aegolius funereus*, will eat their brethren when a large clutch is raised in an inadequately sized hole (Korpimaki 1984) In addition, Post-larvae *Macrobrachium rosenbergii*, a species of crawdad, are never packed in high densities for shipment to fisheries due to extensive cannibalism. (Alias, 1988)

In the pools on the Tiahura motu, cannibalism has the possibility of being a large source of nourishment in a seemingly nutrient-limited environment.

*Larval salinity tolerance*

*C. roseni* has been most commonly recorded as a fresh-water organism (Belkin 1962, Riviere et al. 1986a) However, the larvae in the (karst) pools were capable of surviving at salinities ranging from fresh to 65 ppt.

Some *C. roseni* larval stages are more susceptible than others to salinity changes. Among the larvae that underwent the salinity trial, the first level instars fared significantly poorer than the other larvae. This was expected as the young stage of many mosquito species are commonly the least resilient. (Belkin 1962)

From these salinity trials it appeared that larvae could not survive the threshold from 30 to 60 ppt or higher. However, the test situation which utilized a sudden transfer from one salinity to another, was not realistic to the natural environment. Therefore, *C. roseni* larvae were also left in trays of 30 ppt water to acclimatize to the salinity as the water naturally evaporated. Some larvae in these trays were capable of surviving from 30 ppt to 65 ppt. Possibly the survival of the larvae is more limited by the sudden transfer than the level of the salinity.

Indeed, gradual changing is more relevant to what I observed in the field. During the 24 hour trial, the salinity of pool 1 was observed to fluctuate from 30 ppt as the tide came in, to 29 ppt as the tide went out.

The highest salinity observed in the field was 45 ppt and the lowest salinity was 8 ppt; in lab observations, the larvae were more than capable of surviving these two extremes.

But why does a "fresh water organism" (Belkin 1962, Riviere et al 1986) why to survive so well in salt water? Perhaps these salt water pools exclude interspecies competition. Of the other mosquito species present on Mo'orea, none were able to survive in salt water except *A. polynesiensis*. (Navarro 2003, Riviere 1987, Patrick et al 2001) *A. polynesiensis* shows some ability to live in salt water (crab holes) near the ocean. However the limit for these larvae was 30 ppt (Riviere 1987) which is commonly surpassed in the carbonate platforms pools inhabited by *C. roseni*.

These parameters, and the knowledge that *C. roseni* has previously been found in freshwater habitats lead one to speculate that perhaps *C. roseni* has chosen this ecological niche out of interspecies competition. However, no experiments were conducted with larval competition, so this is only a guess. Regardless, *C. roseni* has "capitalized" on a habitat which is possibly inhospitable to other local mosquito species.

*Larval temperature tolerance*

In the lab, *C. roseni* larvae were capable of surviving temperatures up to 49° C. Upon pouring the 49° C into their container they were stunned and went stiff for about six seconds before slowly twitching back to normal behavior. However water temperature in the field never measured to exceeded 37° C so *C. roseni* are more than physiologically equipped for handling these temperatures. *C. roseni* showed a greater ability to survive heat than most mosquito larvae which can commonly tolerate 34° C. (Benedict et al. 1991), (Russell, pers. comm.)

In the field, *C. roseni* was only seen emerging and laying at night. Perhaps this behavior is temperature dependent. Other mosquito species show similar temperature dependent growth. In *Culiseta incidens* populations, molting has been observed to be temperature-dependent, with higher temperatures accelerating development and molting. *C. incidens* larvae and pupae experience lower mortality and higher molting success at lower temperatures. (Su, 2001). In *Culex inornata* the time of day when emergence occurred was found to correlate strongly with fluctuations in water temperature. (Barnard et al. 1977)

*Larval desiccation tolerance*

Tidal fluctuation at the field site was observed to leave part of the pool substrate exposed for up to eight hours. In the lab, *C. roseni* larvae experienced total death ($LD_{100}$) after 2 hours and twenty minutes of exposure. Of course the length of survival also has other factors besides exposure to air. Larvae left in a covered container without water were capable of surviving more than 24 hours.

It also must be noted that larvae were not commonly observed stranded on the pool sides. When the larvae were seen stranded they often fell prey to ants. At low tide at pool 3 on November 6th the exposed parts of the pool were crawling with small red *Solenopsis geminata* ants. This fire ant is invasive throughout the tropics. (Foltz, pers. comm.) These ants would pull *C. roseni* larvae of their own size out of the tiny indentations of water. *S. geminata* were also seen climbing out onto algae mats and clearing away compacted filamentous algae at the pool surface. After they had cleared a small area they would pull out the larvae trapped in the "net" of algae.

Ants have previously been observed pulling mosquito larvae directly from the water (Clarke 1995) and capturing newly stranded larvae. (Laird 1988)

### Conclusion

The physiology of *C. roseni* larvae seems to be well suited to the karst pool formations on the Tiahura motu. *C. roseni* were observed in statistically constant densities over time which suggests that they are able to maintain their population in the area despite salinity fluctuations, high temperatures, desiccation and the densities themselves. *C. roseni* can survive wide salinity ranges and higher and faster salinity changes in the lab than what they commonly encounter in the field environment. They can survive temperatures higher than the field conditions I observed, and may lay and emerge at night to ovoid these high temperatures. Larvae are rarely stranded, but when they are, they can survive exposure to air fairly well especially in the absence of intense heat or larvivorous ants.

### Future Research

Future research might include examining rates of successful emergence from karst pools; do the high densities effect growth and survival?

Interspecies competition trials between *Ae. polynesiensis* and *C. roseni.* could lead to interesting observations on mosquito niche habitats.

Increasing the pool density of *C. roseni* larvae artificially may lead to enlightening observations on "clustering," cannibalism and population health.

### Acknowledgements

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## LITERATURE CITED

Adams (2003) Attraction of conspecifics to molt signals in crayfish. American Zoologist 40: 925

Alias (1988) The effect of packing density and habitat material on survival of *Macrobrachium rosenbergii de man* post-larvae. Aquaculture and Fisheries Management 19: 39

Barnard, Mulla (1977) Temporal patterns of pupation and emergence in the mosquito *Culiseta inornata (Dipteria Culicidae)* The Canadian Entomologist 109: 1387

Belkin JN (1962) The mosquitoes of the South Pacific. 203:87

Chapman, (2003) Population structure and dispersal of the freshwater mosquitoes *Culex annulirostris* and *Culex palpalis* (Diptera: Culicidae) in Papua New Guinea and northern Australia. Journal of Medical Entomology 40: 165

Clarke (1995) Culex Roseni: systematics, biology and distribution.Journal of Tropical Ecology. 2: 489

Crans (1996)The blood-feeding habits of *Aedes sollicitans* (Walker) in relation to eastern equine encephalitis virus in coastal areas of New Jersey: II. Results of experiments with caged mosquitoes and the effects of temperature and physiological age on host selection. Journal of Vector Ecology 21:1

Kay (1986) Autogeny in *Culex-annulirostris* from Australia. Journal of the American Mosquito Control Association 2: 11

Korpimaki (1984) Clutch size and breeding success of Tengmalms Owl *Aegolius funereus* in natural cavaties and nest boxes. Ornis Fennica 61: 80

Laird M (1988) The natural history of larval mosquito habitats. Academic Press Limited London pp 15, 131

Mwandawiro (1999)Host preference of Japanese encephalitis vectors in Chiangmai, Northern Thailand. Eisei Dōbutsu 50: 323

Navarro (2003) The potential attractant or repellent effects of different water types on oviposition in *Aedes aegypti* L. (Dipt., Culicidae). Journal of Applied Entomology. 127: 46

Nguyen, Alice (2002) Preferencial Breeding Habitats of Mosquitoes in Mo'orea, French Polynesia. IB 158 Student Research Papers 2002 11:31

Olejnicek , Gelbic (2000) Autogeny in *Culex pipiens quinquefasciatus Say*. Journal of Vector Ecology 25: 118

Patrick, Gonzalez, Bradley, (1987) Sodium and chlorideregulation in freshwater and osmoconforming larvae of *Culex* mosquitoes. The Journal of Experimental Biology 204: 19

Riviere (1987) *Mesocyclops aspericornis copepoda* and *Bacillus thuringiensis-var-israelensis* for the biological control of aedes and culex vectors *Diptera culicidae* breeding in crab holes, tree holes and artificial containers. Journal of Medical Entomology 24: 425

Riviere, Sechan & Kay (1986a) *Culex roseni* larvae in crab holes. The Culicidae of the Australasian Region . pp 153

Su (2001) Effects of temperature on development, mortality, mating and blood feeding behavior of *Culiseta incidens (Diptera: Culicidae)*. Journal of Vector

## Appendix

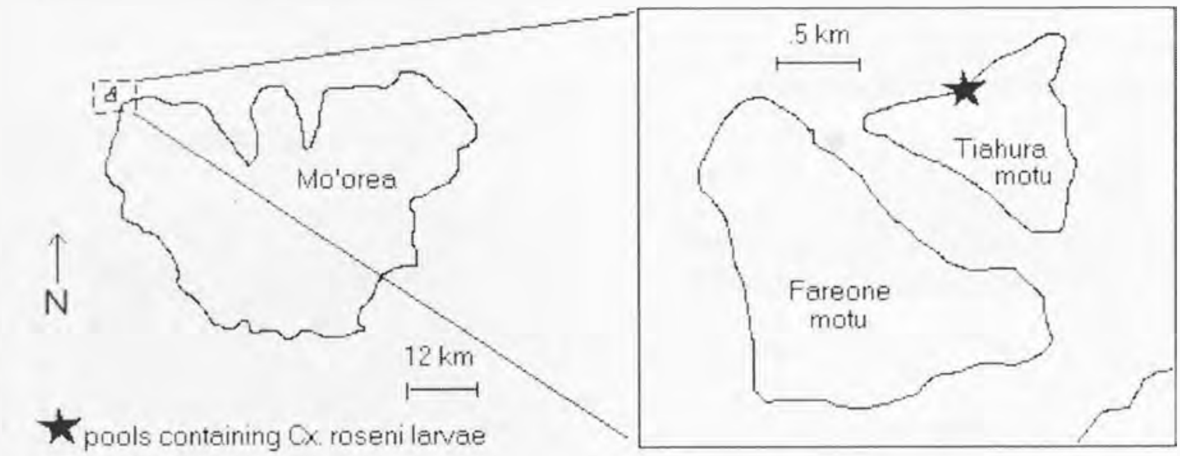

**Figure 1**. Location of the pools containing *C. roseni* larvae: (17° 29.179' S 149° 54.723' W)

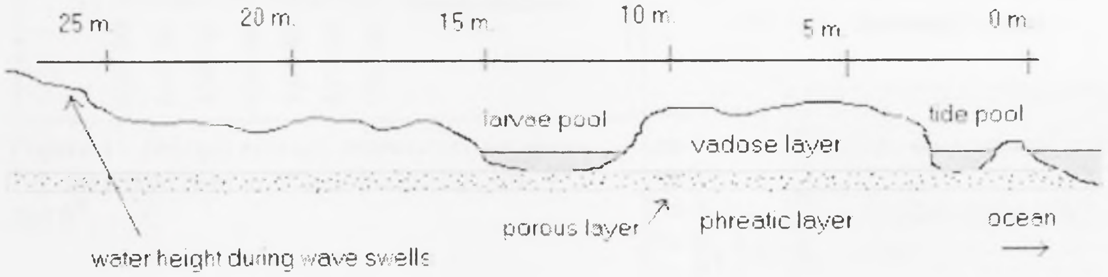

**Figure 2**.simplified cross section of carbonate platform showing layering and connection to ocean. *Note: the porous layer has been increased in size so that it is visible on the chart.*

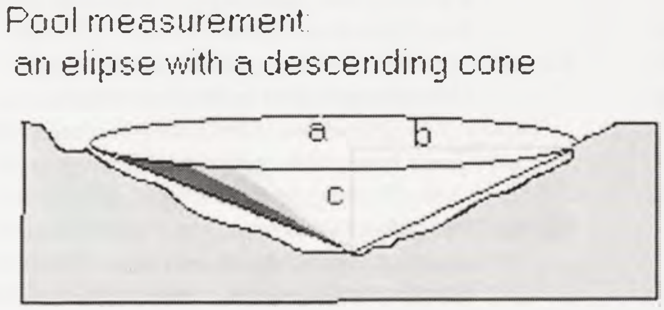

**Figure 3**. pools were measured as being elliptical with a cone descending from them

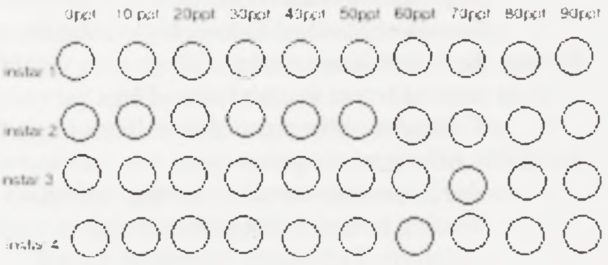

**Figure 4**. experimental cells used to test instar survival in various salinities

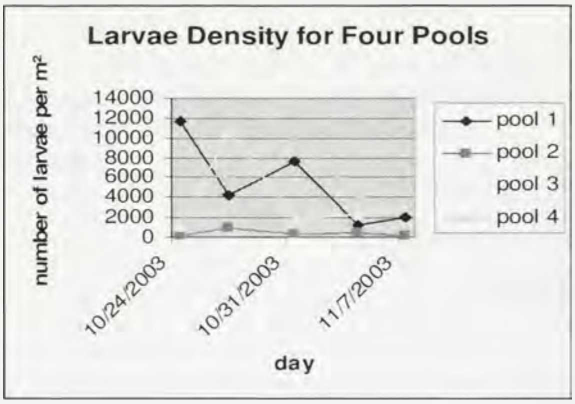

**Figure 5:** larval density on five sampling days

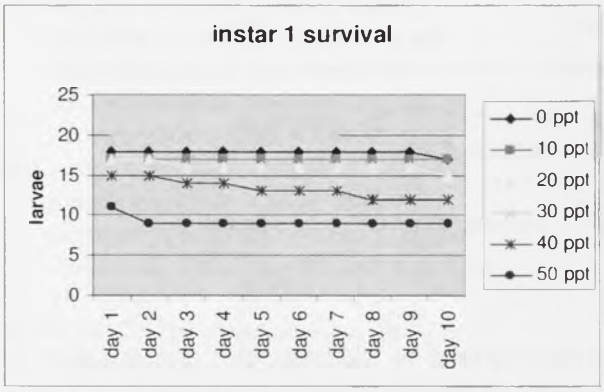

**Figure 6**: Instar 1 survival in variable salinity concentrations

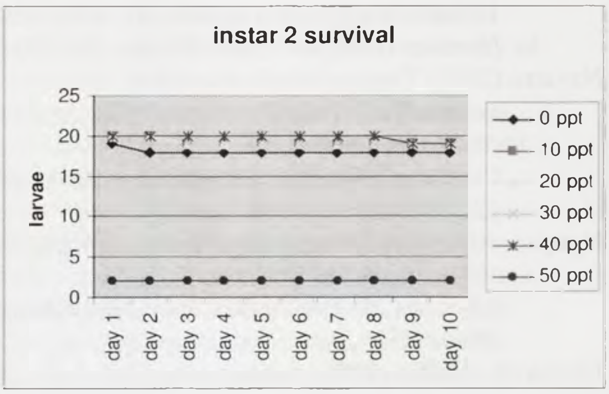

**Figure 7**: Instar 2 survival in variable salinity concentrations

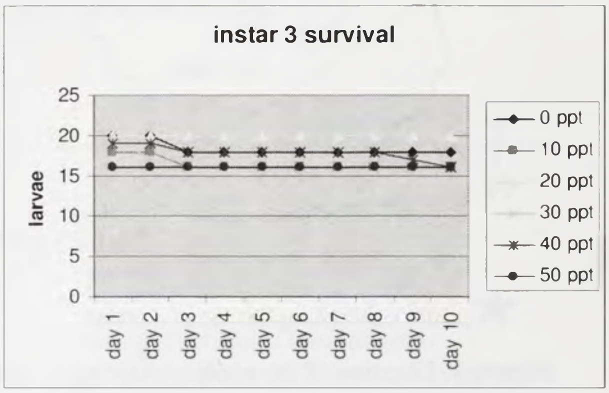

**Figure 8**: Instar 3 survival in variable salinity concentrations

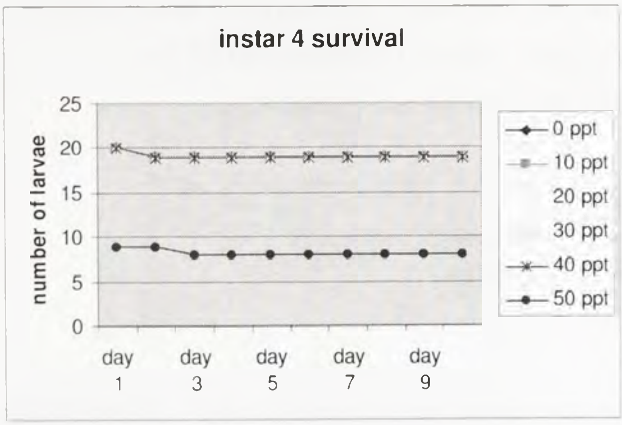

**Figure 9**: Instar 4 survival in variable salinity concentrations

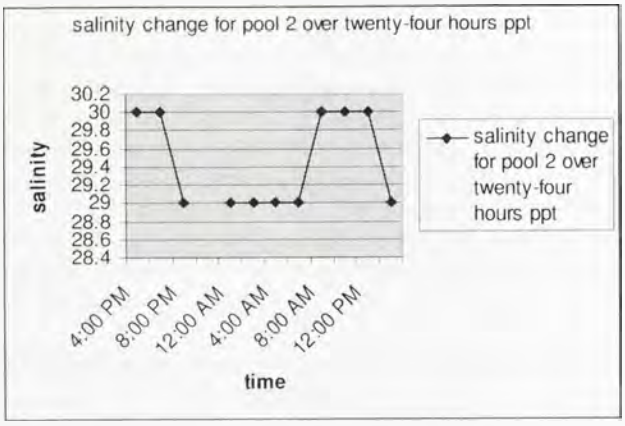

**Figure 10**: Salinity variance over a 24 hour period measured on Nov. 5th and 6th

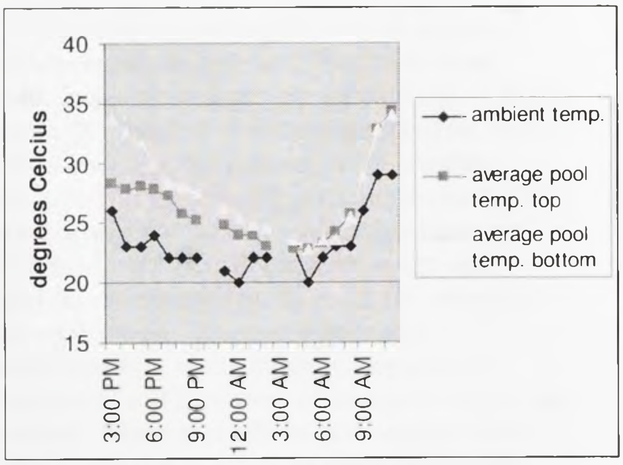

**Figure 11**: (Mean) average temperature for pools 1-4 measured over a 19 hour period on Nov. 5th and 6th

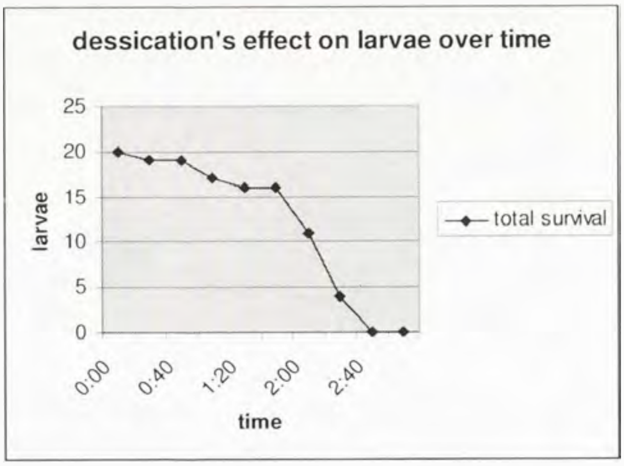

**Figure 12**: Larvae survival over time during the desiccation trial. Note that each "dot" represents the survival of a unique set of larvae.

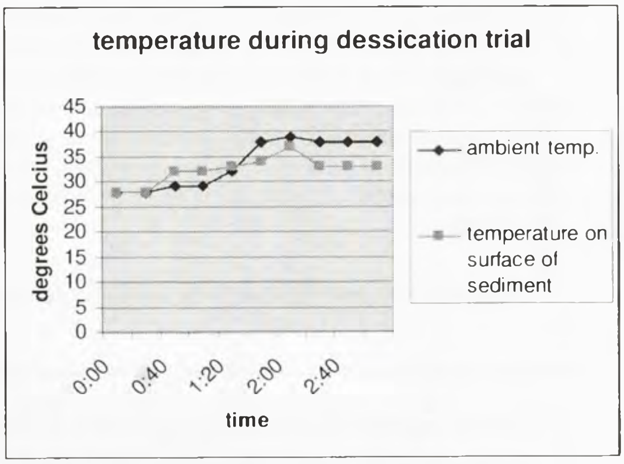

**Figure 13:** Ambient temperature in degrees Celsius during larval desiccation trial

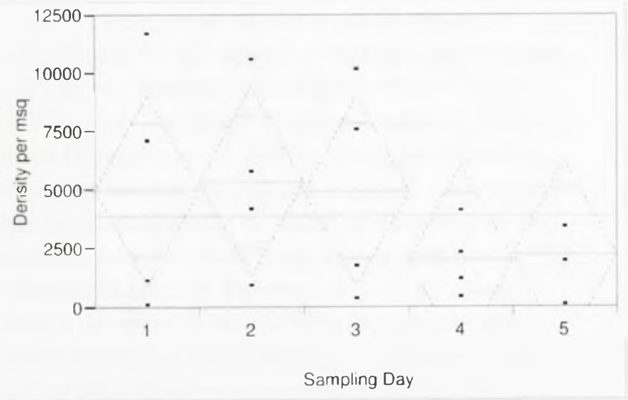

**Chart A**: Oneway Analysis of Density per M² By Sampling Day

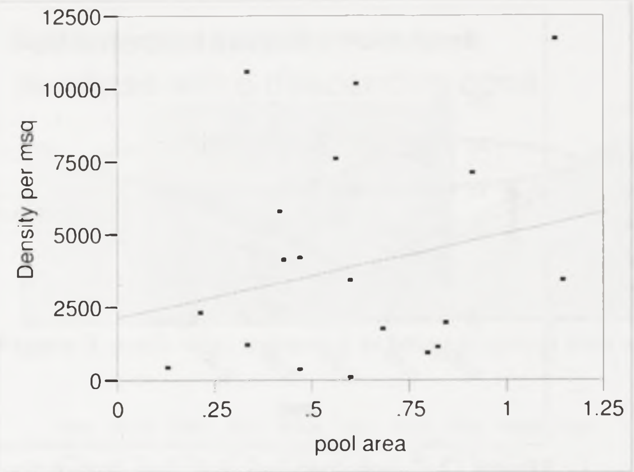

Chart B: Bivariate Fit of Density per M² By pool area

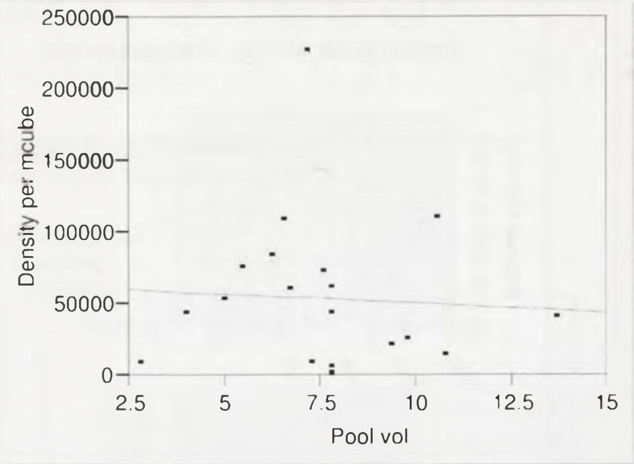

Chart C: Bivariate Fit of Density per M³ By Pool volume

# Attractant Response, Species Distribution, and Diurnal Activity Levels of Mosquitoes (*Aedes aegypti, Aedes polynesiensis, Culex quinquefasciatus)* in Mo'orea, French Polynesia

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**ABSTRACT.** Mosquito-borne diseases such as malaria, dengue fever, and yellow fever kill millions of people each year. Efforts to understand and control these diseases hinge on reliable and effective methods to monitor the mosquitoes that serve as vectors. This study explored the population distribution of mosquito species on Mo'orea, French Polynesia and the response of these species to commonly used attractants. Three trap treatments, containing the attractants carbon dioxide and octenol alone and in combination, were set at seven locations to investigate mosquito species distribution and preference for attractants. ANOVA revealed a significant response to attractant type but not site by *Aedes polynesiensis*. Carbon dioxide-baited traps collected significantly more *A. polynesiensis* than octenol-baited traps, while the results from the combination of $CO_2$ plus octenol were statistically indistinguishable from either attractant alone. These results were not supported by laboratory dual-port olfactometer tests, in which *A. polynesiensis* showed no significant attractant preference. A follow-up study on the diurnal activity patterns of *A. polynesiensis* revealed a mid-day peak with the highest activity at 1400 h and the lowest activity from 0600-0800 h and 1600-1800 h. A comparison of human-bait aspiration and attractant-baited traps showed a significant increase in the numbers of *A. polynesiensis* captured by aspirator over traps. Similar studies on attractant response and species distribution should be undertaken during periods of increased precipitation to maximize catches and better understand the mosquito species on Mo'orea.

**KEYWORDS:** *Aedes aegypti, Aedes polynesiensis, Culex quinquefasciatus*, carbon dioxide, octenol, diurnal, olfactometer.

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## Introduction

As vectors for pathogens such as malaria, yellow fever, dengue, and West Nile virus, mosquitoes are responsible for millions of deaths per year. Billions of dollars are spent on control efforts, such as the destruction of breeding habitats and the use of pesticides, to combat the transmission of these diseases (Spielman and D'Antonio 2001). In order to design and implement effective methods for the control of mosquito-borne diseases, a thorough understanding of the habitats, population dynamics, and behaviors of mosquito vectors are needed. Many past efforts at mosquito control have failed due to a lack of knowledge of the basic biology of mosquito species. This was seen in a study by Focks and Sacket (1976), which found that *Toxorhynchites amboinensis*, an introduced mosquito with predatory larvae, was ineffective in the control of the disease vectors *Aedes polynesiensis* and *Aedes aegypti*, due to a difference in breeding habitats. Reliable information concerning habitat distribution, disease prevalence, and activity patterns can allow public health officials to design control efforts which accurately target disease vector mosquitoes. Effective surveillance methods are necessary in order to gain an understanding of mosquito populations.

A common method for adult mosquito surveillance is the use of attractant-baited traps, such as the Encephalitis Vector Surveillance (EVS) and Center for Disease Control (CDC) traps (Kemme *et al.* 1993). Attractant-baited traps are used to gather information concerning species distribution, population abundance, and disease prevalence in mosquito populations. The attractants used in the traps mimic airborne chemical cues by which female mosquitoes locate hosts for bloodfeeding. Carbon dioxide, in the form of dry ice, is used to mimic the $CO_2$ contained in the exhaled breath of animals. Octenol, formally 1-octen-3-ol, is a volatile emanation isolated from human sweat and from ox breath (Clements 1999). Studies in Queensland, Australia and Florida, USA have shown the effectiveness of traps baited with $CO_2$ and octenol in capturing various mosquito species (Kline *et al.* 1991, Takken and Kline

1989, Van Essen *et al.* 1994). These studies found that the addition of octenol to $CO_2$-baited traps caused a significant increase in the capture of three species in the *Aedes* genus: *A. funerus*, *A. vigilax*, and *A. taeniorhynchus*. No such effect was seen for mosquitoes in the genus *Culex*.

The island of Mo'orea, French Polynesi a is home to seven mosquito species. The three most abundant species in larval studies by Becker (1994) and Nguyen (2002) were *Aedes polynesiensis*, *Aedes aegypti*, and *Culex quinquefasciatus*. The most abundant species, *A. polynesiensis*, is diurnally active and is known to transmit the filarial parasite *Wuchereria bancrofti*, responsible for elephantiasis (Jochowski and Otto 1951). Laboratory results have also shown that *A. polynesiensis* is an effective vector for Ross River Virus, the agent of epidemic polyarthritis, a disease in Australia and Fiji (Mitchell and Gubler 1987). *Aedes aegypti* is a nocturnally active species, known to breed in containers near human dwellings. *Aedes aegypti* is the vector for yellow fever in many parts of the world and carries dengue fever in French Polynesia. The final species in this study, *C. quinquefasciatus*, is a nocturnally active species,also known to transmit *W. bancrofti* (Debenham 1987).

Research was conducted on the island of Moorea, French Polynesia between October 11th and November 11th, 2003. This study investigated the response of three mosquito species to attractants commonly used in mosquito surveillance. Attractants were tested and compared both in baited traps and in laboratory trials. This study also investigated differences in mosquito species distribution and abundance among different sites and habitat types on Mo'orea. Finally, the diurnal activity patterns of the dominant species on Mo'orea, *A. polynesiensis*, were examined.

## Materials and Methods

### *Sample Sites*

Seven sample sites were arrayed along the northern portion of Mo'orea, encompassing a variety of habitat types. Sampling was conducted at sites such as inland, coastal, urban, salt marsh, and high altitude. Site locations and descriptions are shown in Table 1 and Figure 1.

| # | Site | Habitat | Description | GPS Coordinates |
|---|---|---|---|---|
| 1 | Gump Station | Coastal | Hibiscus and Coconut | S 17°29.425'<br>W 149°49.596' |
| 2 | Microbial Mats | Trees bordering marsh | Coconut and Mangroves | S 17°28.840'<br>W 149°46.113' |
| 3 | Paopao Valley | Inland | Inocarpus, heavy understory | S 17°31.322'<br>W 149.49.915'<br>Elev. 94 m |
| 4 | Morai Temple | Inland | Inocarpus and Hibiscus | S 17°32.257'<br>W 149°49.731'<br>Elev. 176 m |
| 5 | Opunohu | Coastal | Hibiscus and Coconut, heavy understory | S 17°30.586'<br>W 149°51.079' |
| 6 | Motu | Coastal | Coconut, Hibiscus, near coral platform | S 17°29.179'<br>W 149°54.723' |
| 7 | Paopao | Urban | Coconut and Hibiscus | S 17°30.303'<br>W 149°48.924' |

**Table 1.** Table of sites, descriptions and GPS coordinates.

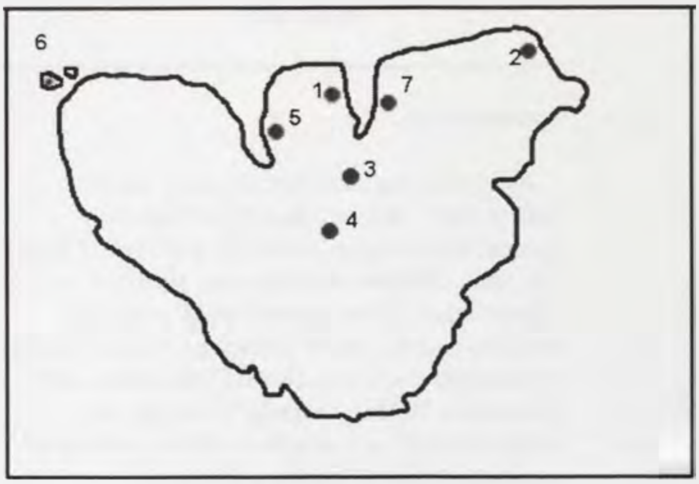

**Figure 1.** Map of Mo'orea, French Polynesia, indicating locations of seven study sites.

*Response to Attractant-Baited Traps*

Three attractant treatments were tested at each site. Traps were placed 30 m apart and hung from a tree branch to a height of 1 m off the ground. Traps were arranged perpendicular to any detectable wind to avoid interaction between attractant odor plumes (Van Essen *et al.* 1994). Battery-powered EVS and CDC traps, operated without a lightbulb, were used with the following attractant treatments: (1) EVS trap with $CO_2$, (2) EVS trap with $CO_2$ and octenol, and (3) CDC trap with octenol . Traps were operated for two nights per site, and trap position was rotated so that each trap occupied a different linear position from the previous night. Traps were run overnight from 1600 to 0900 hours in order to capture both nocturnally and diurnally active species.

The $CO_2$ bait for EVS traps was released from an insulated container situated above the trap opening, filled with 1 kg of dry ice. Octenol bait was released from a microreaction vial, modified with a 2-mm hole drilled in the top. A cotton wick was inserted through the hole and extended 7-8 mm outside the vial to release octenol into the air (Kemme *et al.* 1993). The microreaction vials were attached to both CDC and EVS traps with tape.

*Laboratory Attractant Response*

Laboratory trials were conducted, using a dual-port olfactometer, to investigate the response of *A. polynesiensis* to the attractants $CO_2$ and octenol (Clements 1999). The dual-port olfactomer was constructed from 10 cm diameter PVC piping (Figure 2). Collections of approximately 20 *A. polynesiensis* were released into the entrance from a plastic collection cup. Mosquitoes flew from the entrance towards two possible collection cages containing different attractants.

In the first set of laboratory trials, $CO_2$ was compared with octenol. 50 g of dry ice was placed adjacent to Exit A and a piece of tissue paper doused with octanol was placed adjacent to Exit B. A notebook was used to fan the attractants into the pipes, and 5 minutes passed before the mosquitoes were released into the apparatus. After 30 minutes, the cages were placed in a deep freezer, and the mosquitoes were counted. Four trials were run, and the position of the attractants was alternated between exits A and B to account for any directional preference of the mosquitoes. An hour passed between successive trials in order to allow residual attractants in the olfactometer to dissipate.

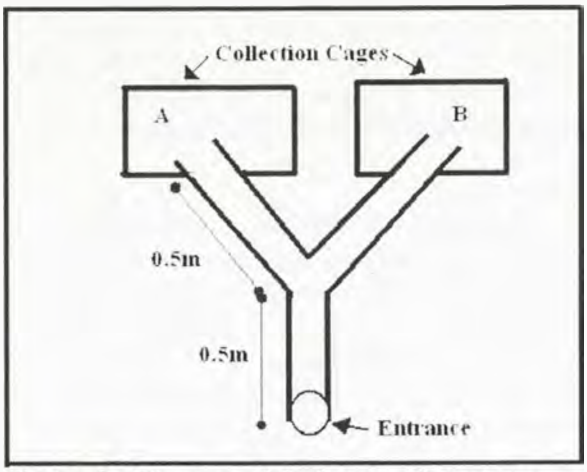

**Figure 2.** Diagram of dual-port olfactometer used in laboratory trials.

In the second set of trials, $CO_2$ alone was compared with $CO_2$ plus octenol. The same procedures from the first set of trials were followed, except 50 g of dry ice was placed in one cage, and the combination of 50 g of dry ice and an octenol-soaked tissue was placed in the other. Four trials were run, alternating attractant position.

*Diurnal Activity Levels*

Human-bait aspirator collections were made at the Gump Station site, a forested area dominated by coconut and hibiscus trees. Collections were conducted by one investigator, wearing clothing to cover the upper body completely, and shorts to expose the legs and feet. Mosquitoes were collected as they landed on the investigator, using a breath-powered aspirator (Rakai *et al.* 1974). Mosquitoes were deposited in a container and frozen, after which species were identified using a reference text by Belkin (1962) and counted. Only *A. polynesiensis* totals were recorded.

Aspirator collections were conducted on four days at the Gump station site, on October 26th, and November 2nd, 8th, and 11th. Aspirating was conducted for 15 minute increments beginning every hour, on the hour, from 0600 to 1800 h.

*Aspirator and Trap Comparison*

To compare attractant-baited traps with human-bait aspirator catches, trapping was conducted from 0600 to 1800 h at the Gump Station site on November 6th and 8th. The same procedures from night trapping trials were followed, altering only the time at which the traps were operated. The total yields from the three traps over two days were compared with aspirator catches from the diurnal activity research on November 2$^{nd}$ and 11$^{th}$.

*Data Analysis*

The data from 14 nights of trapping was square-root transformed and analyzed using a two-way ANOVA test. Attractant treatments were compared using a Tukey-Kramer test of pairwise mean differences. The results from the 4 days of human-bait aspirating trials were analyzed using a repeated measures analysis. The numbers of mosquitoes captured via human-bait aspirating and attractant-baited traps were compared using a t-test. All statistical analysis was done using Systat 7.0.

## Results

*Response to Attractant-Baited Traps*

A total of 82 mosquitoes were caught during 14 nights of sampling. Three species of mosquito (*C. quinquefasciatus, A. aegypti*, and *A. polynesiensis*) were captured (Figure 3, 5). *Culex quinquefasciatus* and *A. aegypti* were found only at the urban site, while *A. polynesiensis* was found at all sites. Of the three species captured, only *A. polynesiensis* was captured in numbers sufficient for statistical analysis. Therefore, the following statistical results refer only to *A. polynesiensis*.

Two-way ANOVA (Table 2) revealed a significant effect of attractant treatment ($F_{2,21} = 6.613$; $P = 0.006$), but not site ($F_{6,21} = 1.865$, $P = 0.135$) and no site-treatment interaction ($F_{12,21} = 1.234$ ; $P = 0.325$).

A Tukey-Kramer test of pairwise mean differences between attractant treatments revealed that $CO_2$ caught significantly more than octenol (p=0.002), and that $CO_2$ plus octenol was indistinguishable from either attractant alone.

*Laboratory Attractant Response*

A paired samples t-test revealed that *A. polynesiensis* exhibited no significant preference in dual-port olfactometer trials comparing $CO_2$ vs. octenol or $CO_2$ vs. $CO_2$ plus octenol (p= 0.678, p= 0.219, respectively).

*Diurnal Activity Levels*

Repeated measures analysis of daytime aspirator data revealed a statistically significant correlation between the numbers of *A. polynesiensis* captured and the time (p=0.001). Examination of total mosquito collections from four aspirating trials clearly demonstrated increased activity between 0900 and 1600 h, with a peak at 1400 h (Figure 6, 7). A decrease in activity was seen near dawn and dusk, from 0600-0800 h and 1600-1800 h. The highest total number of *A. polynesiensis* was collected on November 2$^{nd}$.

*Aspirator and Trap Comparison*

A t-test confirmed that a significantly larger number of mosquitoes were captured via human-bait aspirating than by attractant-baited traps (p = 0.05). A total of 296 mosquitoes were caught over two days using a human-bait aspirator, while daytime trapping with attractant-baited traps captured 22. The average catches for both methods are shown in Figure 4.

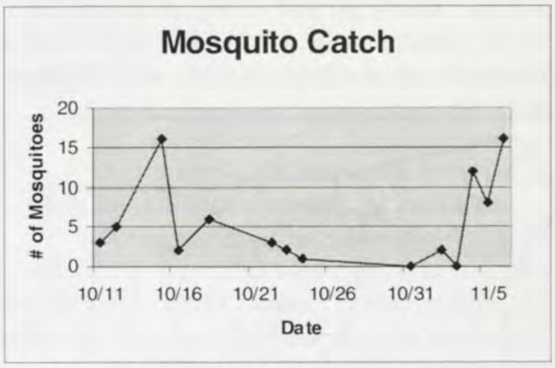

**Figure 3:** #of mosquitoes (*A. polynesiensis, A. aegypti, C. quinquefasciatus*) caught in all three traps by date

| Source | SS | df | MS | F | P |
|---|---|---|---|---|---|
| Site | 2.944 | 6 | 0.491 | 1.865 | 0.135 |
| Treatment | 3.480 | 2 | 1.740 | 6.613 | 0.006 |
| Site & Treatment | 3.897 | 12 | 0.325 | 1.234 | 0.325 |
| Error | 5.526 | 21 | 0.263 | | |

**Table 2.** Results from two-way ANOVA comparing sites, attractant treatments, and interactions between these factors.

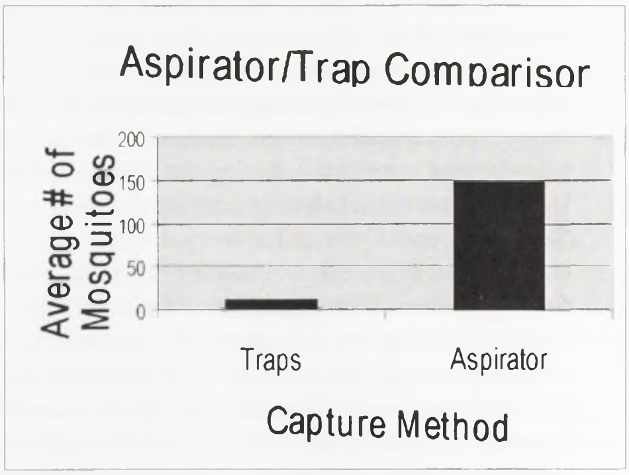

**Figure 4.** Average # of mosquitoes caught per day by traps and by human-bait aspirator.

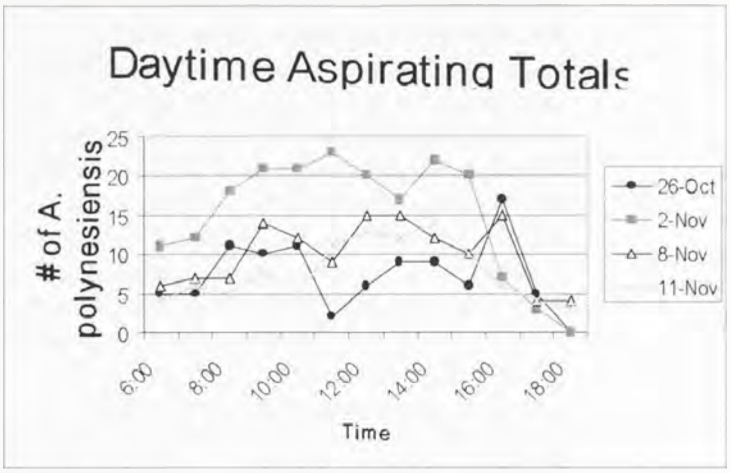

**Figure 6.** Hourly aspirating totals from 4 days of aspirating trials.

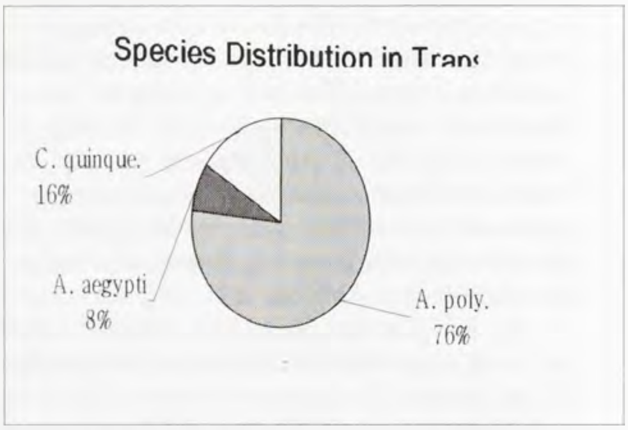

**Figure 5.** Average # of mosquitoes caught per day by traps and by human-bait aspirator.

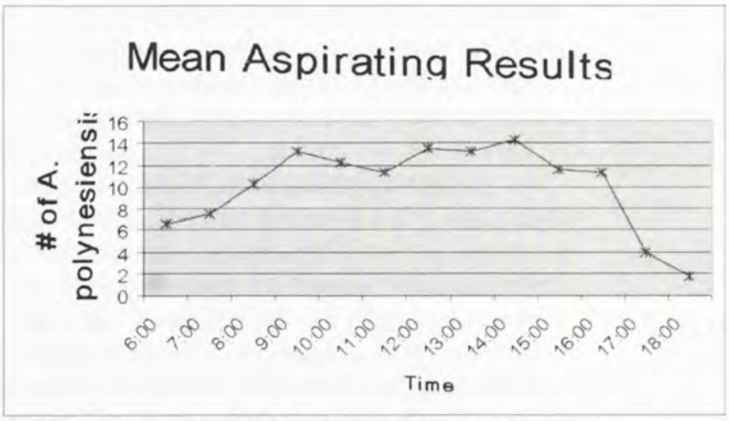

**Figure 7.** Mean results from aspirating trials.

## Discussion

The results from this study revealed that carbon dioxide is an effective attractant in surveillance of *A. polynesiensis*. Octenol, however, is ineffective as an attractant. Traps baited with octenol alone did not catch a single mosquito throughout the course of this study. Contrary to a prior study on mosquitoes in the *Aedes* genus (Kline and Wood 1991), the addition of octenol to $CO_2$-baited traps did not cause a significant increase in the numbers of *A. polynesiensis* captured. A slight decrease in catch numbers was actually seen when octenol was added.

*Aedes polynesiensis'* lack of response to octenol may be due to an anatomical deficiency of specific chemical receptors. Mosquito species responsive to octenol have been found to contain octenol-sensitive neurones in the peg sensilla of the maxillary palps (Clements 1999). It is possible that *A. polynesiensis* lacks these neurones or that they are specialized for the detection of other chemical cues. Further studies involving anatomical comparison to species sensitive to octenol could determine the validity of this hypothesis.

Due to the availability of traps at the Gump Research Station, two trap types, EVS and CDC, were used in this study. It is possible that trap type could have affected the numbers of mosquitoes captured. However, steps were taken to minimize trap differences. Both traps were operated without a lightbulb, as the light strength differed between traps. Both traps use a simple fan to capture mosquitoes. Future studies should use only EVS traps, to avoid any confounding variables.

Site location was not shown to have a significant effect on the numbers of *A. polynesiensis* captured during this study. These findings are in agreement with Nguyen's (2002) larval study, in which she failed to find a significant effect of site on larval species distribution. Mo'orea may be too small (130 $km^2$), to observe appreciable habitat differences between inland and coastal sites, or diminished populations may have made any differences difficult to detect.

While small catches of *Aedes aegypti* and *Culex quinquefasciatus* precluded formal statistical analysis, it should be noted that these species were only found at the Paopao urban site. This was expected, as both species are known to be anthrophillic and to live near dwellings (Debenham 1987). The urban site contained a number of containers with standing water, the preferred ovipositioning locations for both of these species. Future studies should include a number of urban sites to test if this trend is seen throughout Mo'orea.

The results from the habitat preference and attractant response sections of this study should be interpreted with caution, as mosquito populations were small during the course of the study. Dry weather during the months of September and October led to an absence of standing water and thus a lack of larval habitats for mosquitoes (Nguyen 2002). While larval numbers tend to increase soon after a rainfall, it may take months for adult mosquito populations to increase substantially. This is due to a larval maturation time of two weeks for most species. It often requires several generations of adults before a large population increase is observed (Russell pers. com.). As the rainy season in Mo'orea begins in November, it is likely that the mosquito populations lacked the time to reach large proportions. The diminished mosquito population may have led to the small trap catches seen in this study. The lack of mosquito abundance caused difficulties in statistical analysis, thus limiting the predictive power of this study. Future studies conducted during periods of increased rainfall should yield more conclusive results regarding habitat distribution and attractant preference.

The dual-port olfactometer experiments failed to reveal a significant attractant preference of *A. polynesiensis*. The clear preference of *A. polynesiensis* for $CO_2$ over octenol seen in the field could not be recreated in the first set of laboratory trials. The results from the second set of trials, $CO_2$ vs. $CO_2$ plus octenol, were consistent with trap data, as *A. polynesiensis* failed to show a significant attractant preference. It seems likely, however, that this agreement was coincidental, as the dual-port olfactometer did not appear to effectively mimic natural conditions. In a natural setting, mosquitoes locate hosts through trace, wind-blown scents given off by the host (Clements 1999). In the olfactometer, little fresh air flowed into the pipes and both octenol and $CO_2$ may have been present at concentrations repellant to mosquitoes (Russell pers. com.). Thus, the results of these trials may reflect mosquitoes attempting to escape from the experimental apparatus, rather than flying towards a particular attractant. Further studies, using larger-diameter pipes, a controlled air flow system, and an adjustable attractant release should be used to test the attractant response of *A. polynesiensis* under more realistic conditions.

The low catch numbers from overnight trapping led to an investigation of the daytime activity levels of the mosquitoes on Mo'orea. The results from daytime aspirator trials revealed a mid-day peak in the diurnal activity of *A. polynesiensis*. A previous study by Jachowski and Otto (1951) had revealed a diurnal activity pattern in *A. polynesiensis*. However, the results of the present study contradict Jachowski and Otto's findings that biting activity was highest near dusk and dawn, with peak activity between 1500 and 1800 h. The present study revealed lower activity near dusk and dawn, with a peak between 1200 and 1400 h (Figure 6, 7). The number of mosquitoes captured increased in the hours following dawn, stayed relatively stable, and began to decline at 1500h. Fluctuations were seen between hours on individual days, generally corresponding to wind or the presence of light rain. This was seen clearly on October 26th, when high winds from 1100 to 1300 h caused a severe dip in the number of mosquitoes captured. Despite these fluctuations, the overall trend remained clear.

A possible source of error in the human-bait aspirating trials was the practice of conducting catches in consecutive hours throughout the day. Local depletion of the mosquito population could have taken place, since mosquitoes were captured and removed as they were caught. It is possible that the decreased number of mosquitoes at the end of the day was due to a lack of available specimens in the area, not a decrease in activity. Conversely, returning to the same site throughout the day may have allowed mosquitoes from the surrounding area to become localized to the study site, thereby increasing mosquito density. To verify the results of this study, aspirator catches should be conducted at random times throughout the day, over a longer period of time, in order to account for any local depletion or localized population increases.

In this study, human-bait aspirating was shown to be a significantly more effective method for capture of *A. polynesiensis* than attractant-baited trapping. These results are not surprising, as a human host emanates numerous chemical cues that mosquitoes have evolved to detect. The mosquito *Anopheles gambiae*, for instance, has been shown to respond to over 15 chemical constituents in human sweat (Cork and Park 1996). The attractant-baited traps in this study used only two chemical cues, $CO_2$ and octenol. Mosquitoes also use sight and heat sensing for host location. It is likely that the combination of chemical cues, heat production and appearance make a human host much more attractive to mosquitoes than the traps. Another factor that could account for a discrepancy in mosquito catches is the capture mechanism. The traps use a small fan, requiring mosquitoes to fly close to the fan before they can be captured. In aspirator collections, however, the mosquito needs only land on the researcher in order to be aspirated and captured.

While human-bait aspirating was clearly the most efficient method for mosquito capture in this study, the utility of this method must be weighed against possible health risks. During times of disease outbreak, it may be unsafe to conduct human-bait aspirator collections, as this could expose researchers to an elevated risk of disease contraction. The local prevalence of disease and the risks of increased exposure should be considered before human-bait aspirator trials are conducted.

## Conclusions

In attractant-baited trapping of the species *Aedes polynesiensis*, carbon dioxide was found to be an effective attractant. The addition of octenol to $CO_2$ –baited traps did not cause a significant increase in the numbers captured. Human-bait aspirating was found to be significantly more effective at capturing *A. polynesiensis* than attractant-baited trapping. *Aedes polynesiensis*, a diurnally active species, displayed an activity peak in the afternoon, with decreased activity near dusk and dawn. A similar study conducted during the wet season could reveal the habitat preferences and attractant responses of the other mosquito species on Mo'orea.

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# LITERATURE CITED

Becker, J. (1995) Factors influencing the distribution of larval mosquitoes of the genera *Aedes, Culex,* and *Toxorhynchites* (*Diptera: Culicidae*) on Moorea and the relative importance of coconuts on roadside trash as breeding sites. Journal of Applied Entomology. 119:527-532.

Belkin, J.N. (1962) The Mosquitoes of the South Pacific (Diptera, Culicidae) Volumes 1 and 2. University of California Press, Berkeley, California.

Clements, A. N. (1999) The Biology of Mosquitoes Volume 2. CABI Publishing, New York, New York.

Cork, A. and Park, K. C. (1996) Identification of electrophysiologically-active compounds for the malaria mosquito, *Anopheles gambiae* in human sweat extracts. Medical and Veterinary Entomology. 10: 269-276.

Debenham, M. L. ed. (1987) The Culicidae of the Australasian Region Volumes 4 and 7. Autralian Government Publishing Service. Canberra. 48-68, 201-213.

Focks, D. A., Sackett, S. R. (1976) Some factors affecting interaction of *Toxorhynchites amboinensis* with *Aedes* and *Culex* in an urban environment. In: Mosquito ecology: field sampling methods. Ed. By Service, M. W. New York: Wiley.

Kemme, J. A., Van Essen, P. H. A., Ritchie, S. A., Kay, B. H. (1993) Response of mosquitoes to carbon dioxide and 1-octen-3-ol in Southeast Queensland, Australia. Journal of the American Mosquito Control Association. 9(4):431-435.

Kline, D. L., Wood, J. R., Cornell, J. A. (1991) Interactive effects of 1-Octen-3-ol and carbon dioxide on mosquito (Diptera: Culicidae) surveillance and control. Journal of Medical Entomology. 28(2): 254-258.

Mitchell, C. J., Gubler, D. J. (1987) Vector competence of geographic strains of *Aedes albopictus* and *Aedes polynesiensis* and certain other *Aedes* (Stegomyia) mosquitoes for Ross River Virus. Journal of the American Mosquito Control Association. 3 (2): 142-147.

Nguyen, A. (2002) Preferential Breeding Habitats of Mosquitoes (*Aedes aegypti, Aedes polynesiensis, Culex quinquefasciatus, Culex atripceps, Culex roseni, Culex annulirostris, Toxorhynchites amboinesis*) in Mo'orea, French Polynesia. Biology and Geomorphology of Tropical Islands, Student Research Papers. University of California, Berkeley. 31-37.

Rakai, I. M., Naserua, J. D., Macnamera, F. N., Pillai, J. S. (1974) Mosquito-Borne Infections in Fiji: Part IV: Biting times for village mosquitoes and human filarial transmission potential of *Aedes polynesiensis* and *Aedes pseudoscutellaris.* Journal of Medical Entomology. 11 (5): 588-594.

Russell, R. C. Personal Communication. 15-30 October 2003.

Spielman, A., D'Antonio, M. (2001) Mosquito: A Natural History of Our Most Persistent and Deadly Foe. Hyperion. New York, New York. 49-137.

Takken, W., Kline, D. L. (1989) Carbon dioxide and 1-octen-3-ol as mosquito attractants. Journal of the American Mosquito Control Association. 5: 311-316.

Van Essen, P. H. A., Kemme, J.A., Ritchie, S. A., Kay, B. H. (1994) Differential responses of *Aedes* and *Culex* mosquitoes to octenol or light in combination with carbon dioxide in Queensland, Australia. Medical and Veterinary Entomology. 8: 63-67.

# Factors Influencing the Fate of Prey in Communal Webs of *Cyrtophora moluccensis* and the "Kleptoparasitic" *Argyrodes argentatus*.

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ABSTRACT. Two species of spiders, *Cyrtophora moluccensis* and *Argyrodes argentatus*, coexist on the communal webs spun by the former. The prey capture behavior of both species was investigated by means of a field experiment that introduced prey items of varying size and vigor into communal webs occupied by both species. The experiment was carried out over the period 4 Oct 2003 to 15 Nov 2003 on the island of Mo'orea, French Polynesia. In general, active prey items were recovered by *Cyrtophora moluccensis* (24/25) and passive prey items were recovered by *Argyrodes argentatus* (25/38). *Cyrtophora moluccensis* readily recovered passive prey items by responding to signals generated by attempted *Argyrodes argentatus* recoveries. In this way the relationship between the host and "kleptoparasite" showed mutualistic qualities.

## Introduction

Certain spiders of the orb-weaver family build large communal webs (). These webs provide a large surface area which facilitates other species of spiders as possible competitors. In the case of *Cyrtophora moluccensis*, two different species have been reported to use this surface area in different ways: Pholcid, Argyrodes (Keeney, 2002)

Due to these various spiders living in close proximity, the communal webs become a very interesting place to study symbiosis and ask ecological questions concerning the interaction and impact between species.

There are three different types of symbiosis one can examine here: mutualism, commensalisms, and parasitism. Let us, for the purposes of this paper, define mutualism as the symbiosis in which both parties benefit (+/+). Commensalism then shall be defined as the symbiosis in which one party benefits and the other is unaffected (+/0). Finally, Parasitism shall be defined as the symbiosis in which one party benefits and the other is harmed in some way (+/-).

"Kleptoparasitism" is a unique form of parasitism and is defined as the phenomena in which one partner in a symbiosis benefits from the other by stealing its food or other resources." (Keeney, 2002). *A. argentatus* has been classified as a kleptoparasite, but the relationship between *A. argentatus* and *C.moluccensis* is very complex and dynamic. Their relationship has even been shown to be plastic, changing from kleptoparasite/host to predator/host. The exact nature of their relationship is not clearly defined and the affect of the kleptoparasite on the wellbeing of the host has been identified as an area that deserves attention (Whitehouse et al. 2001). This study aims to investigate the nature if their relationship.

The inspiration for this study developed out of an interesting initial observation at the study site:

> I first noticed that the majority of entangled prey items were recovered and consumed by the host species, *C.moluccensis*. The one exception to this trend was

an instance where a particularly small prey item, a juvenile leafhopper, became entangled and lay static in the web (generating little disturbance). This prey item was initially ignored by the host and a retrieval attempt by the kleptoparasite, *A.argentatus*, soon ensued. Somewhere in its retrieval process, the kleptoparasite created a disturbance and alerted the host to its position. The host then moved in on the leaf hopper, chased the kleptoparasite away, and recovered the prey item.

Based on this interaction the following questions arose: Are the two species directly competing for food or is there a difference in food types sought by each (i.e. niche partitioning)? If there is a difference in food types, what is this difference based on?

To begin to answer these questions it became necessary to chose possible prey characteristics that could provide a basis for niche partitioning. Since a survey of every possible prey type by order, size, and vigor was far out of the scope of time and resources allotted for this study, I chose to focus on a single order of prey and simply examine the effect of prey size crossed with vigor. I hypothesized that the distribution of resources was not random, that the mechanism allowing these two species to coexist was resource partitioning (Wise, 1993), and that the basis of the partitioning lay in some combination of the prey characteristics chosen for this study.

## Experimental Design: Materials and Methods

The basic experimental design was the introduction of test prey items of different characteristics to look for evidence of niche partitioning. The characteristics varied were size (small, medium, and large) crossed with vitality (active and passive).

### *Prey Item Size Categories*

The introduced prey items were split up into three size classes: small, medium, and large. Small prey items were defined as those flies that measured 2-4 mm in length*. Medium prey items were defined as those flies that weighed between 0.003 – 0.014 g, measuring between 4-6 mm in length. Large prey items weighed 0.030 – 0.042 g and measured 7-9 mm in length. Note: The three size classes were comprised of three different species of Diptera. The difference in species composition was not determined.

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*The weight of small prey items could not be determined.

### *Vitality: Active/Passive*

Each of these three weight classes were broken up into active and passive subgroups. In the active case, the fly was captured by net at the study site, apprehended, and one wing removed to prevent escape. In the passive case, flies were captured by net and killed.

### *Introduced prey: Diptera*

In regards to introduced prey items I chose to focus on a single order, Diptera, which based on personal observation, comprised the most abundant, natural prey type. I subdivided this order into 3 morpho-types based on quantitative size and qualitative vitality.

### *Study Site*

Preliminary scouting surveys were carried out from 12 Sept 2003 to 26 Sept 2003 around the island of Mo'orea, PF, during which the study population along the Belvedere Creek Trail was located. More extensive surveys, to search out additional populations, were conducted from 1 Oct 2003 to 8 Oct 2003 to no avail. The Viare-Pao Pao trail was traversed and no populations were found despite being previously reported (Keeney, 2002). The Belvedere overlook trail was also traversed, searching several offshoot trails along the way, finding nothing. The Belvedere creek bed (south of the Belvedere Three Coconuts traversed and no additional populations were found.

**Figure 1**. Map of Study Site

### *Study Population*

The population studied was located less than 2 miles from the Belvedere Lookout (UTM coordinates E 199,915.98 N 8,060,539.65) at the intersection of the Belvedere Creek and the Belvedere Creek Trail. The communal webs sat in an open area immediately over Belvedere Creek. The structural strands of the barrier webs were anchored to hibiscus tree branches, spanning a volume of roughly 2m by 3m by 5m. The stream bed below consisted of a basalt substrate covered in moss, littered with hibiscus detritus. The surrounding canopy cover was a mixture of Hibiscus and Tahitian Chestnut, providing approximately 75% coverage.

### *Feeding Observations*

Behavioral observations at the Belvedere Population were carried out from 11 Oct 2003 to 4 Nov 2003, for total period of 80 hours. The observer sat on a rock 2 to 3 m from the base of the colony during daytime hours. Prey items were introduced into the webs by standing atop this rock and allowing the prey item to fall into a chosen orb-web. Orb-webs were varied and chosen at random.

### *Terrarium Observations*

Terrarium observations were carried out from 14 Oct 2003 to 2 Nov 2003. Three juvenile hosts and two kleptos were placed in a terrarium measuring 30 X 50 X 30 cm. After 4 days of acclimating, all three hosts had spun webs. Active prey items were introduced into the terrarium in the morning and checked midday and evening to look for evidence of secondary feeding by kleptos. This was performed in order to obtain long term data on feeding behavior ( post-host feeding).

**Results:**

**Table 1**. Raw Data for host and klepto recoveries when presented with prey items of varying size and vitality.

| | **Active** | | | **Passive** | | |
|---|---|---|---|---|---|---|
| | small | medium | large | small | medium | large |
| 10/11/2003 | H | H | H | | K | H(k),K,K |
| 10/12/2003 | | | | | H(k) | H(i),K,K |
| 10/13/2003 | | H | H,H | | K,K | |
| 10/14/2003 | H | H | H | | | |
| 10/15/2003 | | | | | | |
| 10/16/2003 | | | | | | |
| 10/17/2003 | | H,H,H | H | | | |
| 10/18/2003 | | | | | | |
| 10/19/2003 | | | | H*,K | H(a),K | H(a),K |
| 10/20/2003 | | | | | | |
| 10/21/2003 | | | | | K | |
| 10/22/2003 | H(k) | | | K | H(i) | |
| 10/23/2003 | | H | H | | | K,K |
| 10/24/2003 | H,K | H(k) | | H(k) | | H(i),<br>H(k),K |
| 10/25/2003 | | | | | K,K | |
| 10/26/2003 | | | | | | |
| 10/27/2003 | | | | | | |
| 10/28/2003 | | | | | | |
| 10/29/2003 | H | | H | H(i),K | K | K |
| 10/30/2003 | H | H | H | K | K | |
| 10/31/2003 | H,H | | | | | |
| 11/1/2003 | | | | | | |
| 11/2/2003 | | | | | | |
| 11/3/2003 | | | H | K,K | | K |
| 11/4/2003 | | H | | H(a),H(k) | | |

K: klepto recovery
H: host recovery
H(a): host recovery by active localization
H(i): host recovery on initial impact
H(k): klepto-assisted host recovery

*Statistical Analysis: Chi-Square Test for Non-Parametric Data (performed by Chi-Square Calculator)*

| | Active | Passive | Total |
|---|---|---|---|
| **Host** | 24 | 13 | 37 |
| **Klepto** | 1 | 25 | 26 |
| **Total** | 25 | 38 | 63 |

Degrees of freedom: 1
Chi-square = 21.3921901528014
$p$ is less than or equal to 0.001.
The distribution is significant.

## Discussion

### *Host Recoveries (Active)*

Active prey items are generally recovered and consumed by hosts. For example, 24 of the 25 total introduced active prey items were recovered by hosts. This was observed through all size categories: all of the large and medium active prey items introduced into the webs were recovered by hosts; all but one of the small active introduced prey items were host recovered. All of the naturally occurring prey entanglements observed were also recovered by hosts, with the exception of one leaf hopper*. Although exact times were not recorded for every instance, active recoveries by the host were generally achieved in less than 5 seconds.

*Although the leaf hopper was active, the signal generated by this entrapment was negligible

### *Host Recoveries (Passive)*

Hosts were able to recover passive prey items but only if they could employ the following techniques:

1. **Initial impact signal**: This is where the host was able to use the impact signal generated by the introduction of the passive prey item to locate it. The impact signal generated by the passive prey was strong enough and continued for a sufficient amount of time to elicit investigation and location by the host. This happened more for the large passive prey items. It would have been advantageous to devise a prey introduction method that didn't produce such a significant signal upon impact. This was difficult because some platforms were deep within the web and the only way to get a prey item to them was to allow the prey item to drop from a distance or throw it. Four of the 13 passive prey host recoveries were due to initial impact disturbance signal.

2. **Active Localization**: If *C.moluccensis* was unable to locate passive prey items on the initial impact, it would actively shake the entire web in order to continue and amplify the disturbance signal generated by the static item. Active localization has been previously described by Barth and shown to be a common technique employed by orb weavers (Liesenfeld, 1956). Three of the 13 passive prey recoveries by a host were due to active localization.

3. **Klepto-assisted recoveries**: This is where host would use disturbance signals generated by attempted retrievals by *A.argentatus* to home in on the location of passive prey. This would occur when the klepto made an error its retrieval process: when kleptos would compete amongst each other for a passive item,

or (in the active case) when the klepto would induce movement in an entrapped prey item. Six of the 13 passive prey recoveries by a host were due to klepto-assisted recoveries.

*Klepto Recoveries (Active)*

Two instances of active prey recovery by kleptoparasites were recorded: one introduced and one naturally occurring. In both cases, the prey items were small and the generated disturbance signals were negligible. Besides being alive, these prey items were basically passive in the web.

*Klepto Recoveries (Passive)*

Passive prey items introduced into the webs were generally recovered by kleptos: 25 out of the total 38 introduced passive prey items were klepto-recovered. This also occurred through all size categories.

*Passive prey retrieval by Argyrodes argentatus*:

A. argentatus exhibited a highly developed process of passive prey retrieval. This process has previously been described as prey "gleaning" (Whitehouse et al, 2001). I distinguished the following five steps in the gleaning process during my field observations: location, cutting, extraction, tethering, securing, and feeding. These steps are illustrated below:

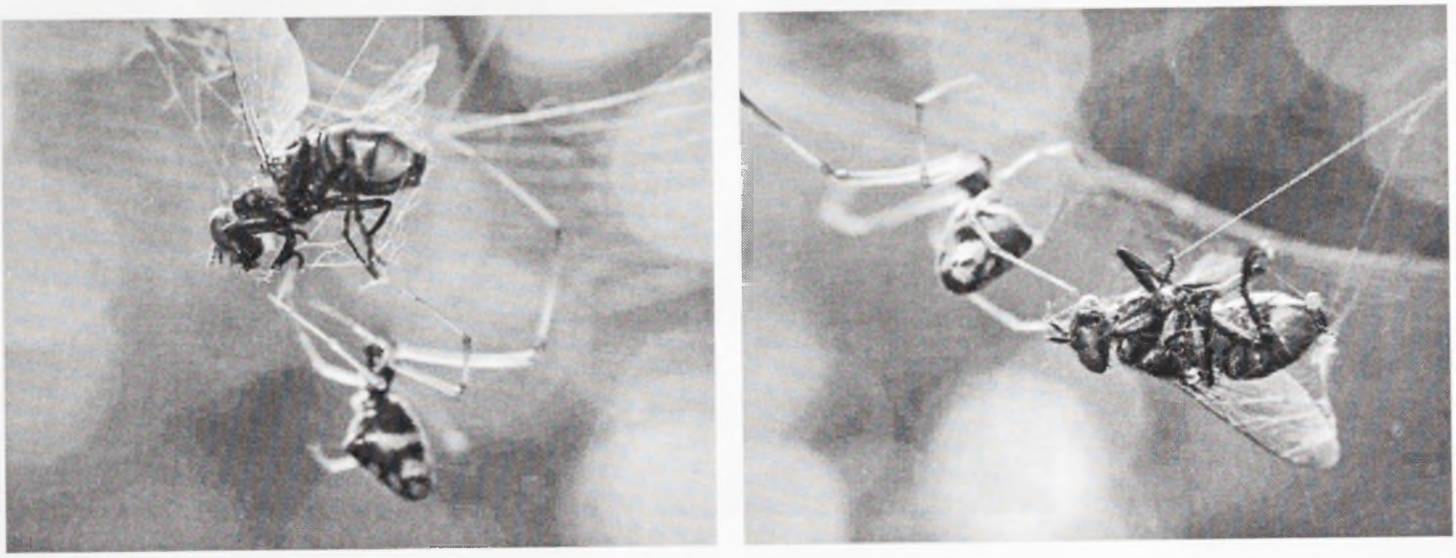
**Location**

**Figure 1.** A. argentatus locating passive prey item. Little is known about what mechanisms A.argentatus uses to locate passive prey. In this experiment, A.argentatus seemed much more able or willing to locate passive prey.

## Cutting

**Figure 2**. A. argentatus will carefully snip the separate mesh sections surrounding the prey. They have been shown to guard against the sudden release of tension by applying an opposing force with its front legs to the cut radius, then slowly releasing (Vollrath, 1979)

## Extraction



## Tethering

**Figure 3 a,b**. A. argentatus extracts the prey out of the orb web.

**Figure 4.** After a successful extraction, A. argentatus tethers the prey item below itself. Perhaps this is to avoid any further transmission of prey-generated disturbance signal (should it be active) to the orb web.

## Securing

**Figure 5.** When the klepto has reached the periphery of the web, it secures the prey item to the structural strands of the communal web with silk of its own.

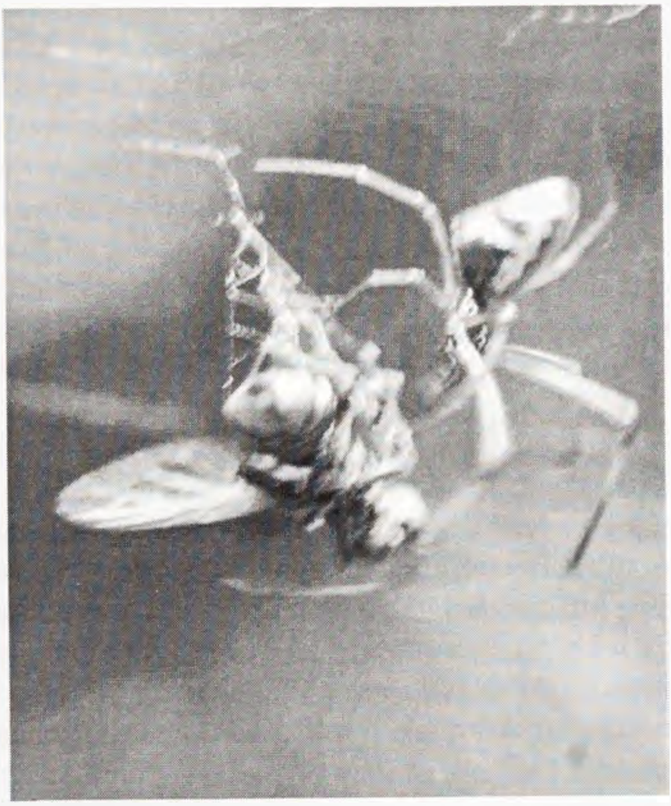


**Figure 6**. *A. argentatus* will then feed on the secured prey item where it is safe.

It is useful to describe these techniques of passive prey retrieval: studying these foraging behaviors can shed light on the evolution of kleptoparasitism by providing a link to spiders that exhibit similar foraging behaviors.

*Dominant Prey Characteristic*

The dominant prey characteristic in determining which species recovered it was the signal generation of the prey item and not size. Active, signal generating prey items were recovered by the host 94% of the time. Passive, non-signal generating preys were recovered by kleptobionts 66% of the time. Those passive prey items that were recovered by hosts were cases in which recovery was achieved on the introductory impact signal or where it was possible to induce some sort of signal from them externally (i.e. active localization or klepto-generated disturbance).

### *Parasitism vs. Commensalism vs. Mutualism*

*A.argentatus* has previously been classified as a kleptoparasite based on the fact that it captures all of its food in webs spun by a host (Li cited by Whitehouse et al, 2001). At the very least, the results of this experiment demonstrate that there is little competition between host and kleptoparasite for active food items in the experimental size and weight ranges for dipteran specimens. The host received 24 of the 25 active prey items introduced into the webs, suggesting that a food niche loosely characterized by active, signal generating prey was exclusive to the host species and basically untouched by *A. argentatus* in this experiment. This would go against the definition of kleptoparasitism suggesting that *A.argentatus* is not derogatory to the well being of the host, and would support a commensal view of their relationship provided adequate availabilities of active prey.

There is, however, competition suggested for passive prey items in the experiment: 25 out of 38 passive prey items were recovered by kleptos; 13 out of 38 were recovered by hosts. The klepto clearly benefits in that it receives food at all from the host's web. Whether or not this competition has a negative effect on the host is open to interpretation. One possible interpretation that follows is that the host is positively affected by receiving prey with the assistance of klepto-generated disturbance signals. I failed to observe any evidence that would support the idea that the host had the ability to eventually locate passive, static prey items. In this regard, the relationship can be interpreted as mutualistic.

### *Conclusions*

Based on the data collected in the field experiment, I conclude that in the active case there was evidence strongly supporting niche partitioning. The kleptoparasitic *A.argentatus* did not directly compete for the active introduced prey items.

While active prey items were generally recovered by hosts, the majority of passive prey items were recovered by kleptoparasites. This implied a difference in food type and its basis was the signal generation of the prey in question. There was clearly no diet overlap between host and klepto parasite in the active case. The diet overlap in the passive case was due to the hosts' ability to either:

1. Interpret passive, non-signal generating prey items as active, signal-generating prey items (as in the case of initial impact recoveries and klepto-assisted recoveries).

or

2. Manipulate the passive prey item into an active, signal-generating prey item (active localization).

Both cases could be interpreted (if one was feeling bold) as the host taking food items characteristic of the kleptos' food niche (passive prey) and manipulating them to be included in the hosts' food niche (active prey). So if one could loosely define food type by vitality alone, this would be a clear case of niche partitioning and could explain the mechanism that permits the coexistence of the two species in communal webs.

To truly explain the real mechanisms, however, one would need to examine the natural prey spectrum coming into these communal webs and document the observed prey distribution. One could then more accurately define the food niche of each species and the degree of diet overlap between the two. This study looked for evidence of niche partitioning in an experimental context. The differences found in food types as they've been defined do not reflect or support niche partitioning in the true sense.

They do however suggest a possible difference in the search behavior or strategies between *C. moluccensis* and *A.argentatus*. In regards to passive prey recovery, where does the kleptoparasites' apparent advantage come from?

### *Future Studies*

Clearly the host will consume passive prey if given the opportunity (evidence: initial impact and klepto-assisted recoveries). So where does the apparent advantage come from? In considering the apparent advantage one may make the following logical speculations as to the possible sources:

1. Differences in resting positions of host and klepto: Tension in the radial threads of the orb web has been shown to vary as one move from the center outward (Barth, 1985). Perhaps the kleptoparasite is able to use its position along the periphery of the orb web to its advantage. Perhaps the slacker, outside lines are better at detecting dead weight in the web.
2. Gross morphological differences: Perhaps the kleptoparasites posses chemo-sensory structures or sight structures that are superior to that of the host.

A possible future study could plot the relative positions of host and klepto during prey recoveries to see if this sheds some light on 1. Gross morphological investigations could be investigated by SEM.

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## Literature Cited:

**Barth FG** eds (1985) Neurobiology of Arachnids Springer-Verlag pgs 221-225

**Foelix, Rainer F.** (1982) Biology of Spiders Havard university Press : pg 138

**Keeney, Brooke** (2002) The Nature of Web Parasitism by Argyrodes argentatus(Araneae: Theridiidae) on Cyrtophora moluccensis ( Araneae: Araneidae) *Biol. Geomorph. Trop.Is.* (2002) 11:47-56

**Vollrath F** (1979) Vibrations: their signal function for a spider kleptoparasite. *Science* 205:1149-1151

**Whitehouse, Mary et al.** (2001) Argyrodes: Phylogeny, Sociality andinterspecific interactions – A Report on the Argyrodes Symposium, Badplaas 2001 *Journal of Arachnology*: Vol. 30, No. 2, pp. 238–245.

**Wise DH (1993)** Spiders in Ecological Webs, Cambridge Universtiy Press: pgs 82-85, 52

## Swimming with the Whales

Humpback whales migrate annually from Antarctic seas to French Polynesia to breed, give birth and care for their calves. They can be seen spy-hopping and jumping off the reef at Moorea during the southern spring. Picture by Victoria Bertics