The 1995 Mo'orea Class upon arrival at the Gump Biological Laboratory, September 23, 1995

**Standing:** Kohina, Hinano, Frank and Terava Murphy, Pam Jutte, Ryan Houston, Andy Johnson, Camille Nowell, Dr. Brent Mishler, Dr. Jere Lipps, Dr. Ferenc de Szalay, Nathan Vaziri.

**Sitting:** Dr. William Alevizon, Michael Schafler, Lena Brook, Tina Liu, Maya Skubatch, Peter Elston, Betty Lin, Lindsay Dinn, Eric Collisson, Ken Greenberg, Abinash Achrekar, Nicola Acutt
Cat for
Bios
## Table of Contents

<table>
<thead>
<tr>
<th>Title</th>
<th>Author</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Introductory remarks</td>
<td>Jere H. Lipps</td>
<td>1</td>
</tr>
<tr>
<td>Predictability in a coral reef fish community: a fixed lottery?</td>
<td>Lindsay Dinn</td>
<td>2</td>
</tr>
<tr>
<td>Habitat distribution and population structure of territorial damselfish, <em>Dascyllus aruanus</em>, in Teavaro lagoon, Moorea, French Polynesia</td>
<td>Maya Skubatch</td>
<td>9</td>
</tr>
<tr>
<td>Habitat partitioning and susceptibility of <em>Sargassum sociale</em> to herbivory by sea urchins</td>
<td>Nathan Vaziri</td>
<td>16</td>
</tr>
<tr>
<td>A description of the spatial and temporal distribution of <em>Paracalanus sp.</em> (Crustacea: Copepoda) in Cook’s Bay (Moorea, French Polynesia)</td>
<td>Ryan M. Houston</td>
<td>25</td>
</tr>
<tr>
<td>Niche partitioning in two species of tropical nudibranchs at Moorea, French Polynesia</td>
<td>Camille Nowell</td>
<td>34</td>
</tr>
<tr>
<td>Comparison of sensory cues in <em>Octopus boky</em> by introduction of predator and prey organisms</td>
<td>Andy Johnson</td>
<td>44</td>
</tr>
<tr>
<td>Establishment of <em>Rhizophora stylosa</em>, an introduced mangrove on Moorea, French Polynesia</td>
<td>Nicola J. Acutt</td>
<td>52</td>
</tr>
<tr>
<td>Behavior of the male short-tailed cricket, <em>Anurogryllus muticus</em> de Geer, affecting reproductive success in Moorea, French Polynesia</td>
<td>Betty Y. Lin</td>
<td>68</td>
</tr>
<tr>
<td>Factors affecting the distribution of freshwater gastropods on Moorea, French Polynesia</td>
<td>Tina Liu</td>
<td>76</td>
</tr>
<tr>
<td>Succession of epiphyllous liverworts and lichens in the Opunohu Valley of Moorea, French Polynesia</td>
<td>Peter A. Elston</td>
<td>90</td>
</tr>
<tr>
<td>An ethnopharmacological study of possible anticancer and antimicrobial plants on Moorea, French Polynesia</td>
<td>Abinash P. Achrekar</td>
<td>98</td>
</tr>
<tr>
<td>Species concepts in the <em>Echinometra mathaei</em> complex</td>
<td>Eric A. Collisson</td>
<td>106</td>
</tr>
<tr>
<td>Benthic Foraminifera from mangrove lagoonal environments of Moorea, French Polynesia</td>
<td>Lena Brook</td>
<td>117</td>
</tr>
<tr>
<td>Variation in flow and sediment transport across Vaipahu reef-flat, Moorea, French Polynesia: a comparison of back-reef morphology</td>
<td>Ken Greenberg</td>
<td>125</td>
</tr>
<tr>
<td>Taphonomy of the coral reef conglomerate platform, Moorea, French Polynesia</td>
<td>Michael Schafler</td>
<td>133</td>
</tr>
</tbody>
</table>
Fifteen undergraduates, two faculty and two Graduate Student Instructors struggled through the tidal channel to reach the Mo‘orea’s reef crest. The tidal rush was just about too much, we thought we thought we would all be swept away. We nearly lost Betty, but Brent saved her. We all made it, and we learned something we had not expected. We were a group and we had to look out for each other. So started our stay in paradise.

Every day we experienced a good deal more than the biology and geomorphology of the tropical South Pacific island of Mo‘orea in French Polynesia. We discovered a lovely people with fascinating ways, we found heat and humidity, strange plants and even stranger animals. We learned about ourselves and each other (and the other animals that shared our houses), close living, and collaboration between students, Graduate Student Instructors, and Faculty. Each moment was an adventure during the Fall 1995 "The Biology and Geomorphology of Tropical Islands", a very special undergraduate course. Students in five majors were selected by application and interview for the course. It was a unique, wonderful, and exceptional experience that deeply affected all of us, especially our students, as indeed it should have.

The academic part of the course began at Berkeley with four weeks of introductory lectures, library research on tropical biology and geology, building a library for our work, travel documents, equipment assembly and logistics planning. Each student was involved in all of this. We spent two days at the University’s Bodega Marine Laboratory in Northern California learning field methods and studying the biota to contrast to what we would see in the tropics. Finally we were ready to go to Mo‘orea.

Field trips all over Mo‘orea introduced the biology and geology, as well as its history and native peoples. Special trips to Tahiti and Tetiaroa added other study opportunities that exposed us to the variety of tropical islands. Most of the nine-week stay at the Gump Station focused on original research projects. Students developed and pursued their own interests, with occasional guidance from the instructors. The results of this research were presented at a symposium at Berkeley in December and in the papers reproduced in this volume. We are proud of these papers—the students came a long way during this course, from uninitiated university science majors to budding research scientists!

The course is not an easy one to instruct. Distances are long, living is different, even rigorous, and resources are scarce. Everyone involved with the course made it a fantastic learning time. As instructor in charge, I thank my colleagues who helped make the course a success again. My colleagues--Brent Mishler, Vince Resh, and Roy Caldwell, each a world-renowned expert in tropical biology--gave truly outstanding instruction in Mo‘orea and at Berkeley. Other experts gave lectures at Berkeley too--Professors Carla D’Antonio, David Lindberg, and Werner Loher. The Graduate Student Assistants, Pam Jutte and Ferenc de Szalay, worked hard to handle the logistics and provide much of the instructional support. Special thanks go to Frank Murphy, Gump Station Manager, and his wife, Hinano, for helpful arrangements and courtesies that gave the students many unique experiences and made their lives more comfortable at the Station. We thank Professor Werner Loher, Director of the Gump Station, and the College of Natural Resources, the managing college for the Station, for the opportunity to conduct this course. Julie Meyer and Dorothy Tabron made the class possible with much administrative support from the office of Integrative Biology.

Jere H. Lipps, Professor
Department of Integrative Biology
ABSTRACT. The structure of fish assemblages residing on isolated patches of *A. formosa* was investigated within the lagoon of Moorea, French Polynesia. Fishes observed were classified as residents or visitors, based upon fidelity to particular patches. Five resident species were identified, four of which occurred on every patch observed. These four occurred in consistent relative proportion on all 10 patches investigated. This finding contrasts sharply with the general observation of unpredictability in resident coral reef fish community structure on the scale of small patch reefs. It suggests that in some coral environments deterministic factors are primarily responsible for community structure.

Introduction
Numerous studies have been conducted on reef fish communities and fish assemblages on patch reefs (Sale 1980; Ogden and Ebersole 1981; Sale and Steel 1986; Alevizon and Brooks 1975; Sale and Dybdahl 1978; Anderson and Ehrlich 1981). There are two distinct views concerning coral reef fish community structure that have come from these studies. The first view supports the idea that no characteristic structure can be found in the distribution of fishes within particular habitats. A study by Sale (1994) obtained results supporting earlier reports indicating a lack of persistent structure in assemblages on patch reefs. In addition, this view claims that the structure of fish communities cannot be predicted (Gladfelter 1980). This non-equilibrium view says that fish inhabit an area without any related pattern, and distribution occurs mostly by chance (Sale and Dybdahl 1978). The contrasting, deterministic view, is supported in studies done by Greenfield and Johnson (1990), Alevizon et al (1985), and Smith and Tyler (1975). The deterministic idea suggests an equilibrium situation in which fish occur in a distinct pattern in those habitats that they distinguish (Alevizon et al 1985). These studies suggest that adaptive choice of habitat leads to the ordered structure of reef fish assemblages (Ogden 1982).

Another important aspect of this debate is the scale on which the research is conducted. Usually, studies conducted on small patch reefs have been unable to find a stable, equilibrium assemblage, while those conducted on larger reefs have generally supported an equilibrium view (Greenfield and Johnson 1990). However, data from large scale studies have only been able to show that community structure is more constant than the community structure on a small scale. The data is not adequate enough to indicate equilibrium communities (Sale 1980).

Branching corals of the genus *Acropora* are common in the Indo-Pacific (Patton 1994). *A. formosa* is a light colored branching coral and is often called staghorn coral because of its antler-like appearance. The *Acropora formosa* habitat is highly uniform and structurally simple, remaining highly predictable from patch to patch. It grows on a sand base and its light skeleton enables it to grow rapidly. This in turn often makes it a dominant species of lagoons (Veron 1986). Though it may be dominant it is limited in its distribution around Moorea. We only observed it at two locations of those examined on the north shore, and so it is therefore a limited resource for animals as well.

The goal of this study was: 1. determine whether a resident fish assemblage existed in a habitat dominated by isolated patches of *Acropora formosa*; 2. if a resident assemblage was found then determine if those fish existed in a
predictable proportion among different coral patches.

Materials and Methods

Study Sites

Field work was conducted on Moorea (17° 32' S, 149° 50' W) in French Polynesia, from October to November, 1995. The two study sites, the Temae lagoon and the lagoon by Motu Fareone (Figure 1) were chosen based on their accessibility and the presence of Acropora formosa. The first site was located on the northeast corner of Moorea in the lagoon immediately offshore the Sofitel Hotel at Temae (Figure 2). The lagoon here is dominated by patches of Acropora formosa, isolated from one another by open sand. Individual patches average 6-12 meters in maximum diameter, although some exceed 20 meters in size. Water depth ranges from about 1-4 meters, although most A. formosa is found at 1-3 meters. Smaller heads of Pocillopora species and Porites sp. were also interspersed throughout the lagoon. Beyond the channel, the coral becomes denser and broader and characteristic of the algal ridge. The currents flow to the southwest the majority of the time. The average temperature of the lagoon was ~23°C.

A second study site was located on the northwest corner of Moorea in the lagoon on the south edge of Motu Fareone. Here, A. formosa is less common and only two large patches were observed. The substrate is characterized by rubble covered sand with considerable algal growth. The bases of the A. formosa branches were generally found to have more algal cover than at site 1. The patches are larger in size (25-45 meters in maximum diameter), and are present at shallower depth (~.5 m). This lagoon has faster currents flowing west and is shallower (.5-1 meters). No Porites corals were observed at this site.

Methods

In order to begin quantifying fish assemblages associated with patch reefs, I swam randomly chosen 50 meter transects and surveyed A. formosa patches to obtain an initial idea of the size range of the corals and the fish that might be present. From these observations, ten isolated patches of Acropora formosa of similar size (from 6-12 m in length) and depth (1.5-2 meters) were randomly chosen. Eight out of the ten patches were singular patches surrounded by sand. The other two were areas of 6-12 m in length selected from the large uniform patches. To determine if the fish preferred one habitat over another, ten Porites species were then randomly chosen at similar depths. These were found in different sizes than the A. formosa patches.

Visual fish censuses were done five times on five non consecutive days on all twenty coral patches. This repetition was necessary to measure the fidelity of the fish to the patches. Each patch was observed by swimming in a zigzag pattern and all fish seen within a 180 degree radius were counted and recorded on an underwater slate. Fish species were recorded until two minutes went by without a new species appearing. The time spent on each patch varied according to size and fauna present (from 2-10 minutes). Only those fish hovering above the coral, living in the coral, or feeding on the coral were recorded. At the motu, patches were observed in a similar fashion, but only for presence or absence of those fish in the assemblage at Temae. Twenty additional patches were randomly chosen at Temae and surveyed in the same fashion for presence or absence of fish seen at the original ten patches. Some of these patches were singular while some areas surveyed were sections of uniform patches.

Fishes were determined to be residents of a particular coral patch if they were present on that particular patch in >90% of the samples. Other fish present <90% of the time were considered visitors. Densities from all five days were averaged for each coral and then relative proportions were estimated. Median values were calculated from these numbers and a goodness of fit test was performed to test whether the proportions were correlated. Density counts from the A. formosa and the Porites habitats were averaged and compared to show habitat preference.
Figure 1. Map of Mo'orea. Both study sites are indicated with arrows.

Figure 2. Overhead view of lagoon at the Sofitel La Ora Moorea Hotel. Dark areas in lagoon are patches of *Acropora porosa*.
Results

Resident Species

Four fish were seen >90% of the time in Acropora formosa and were defined as resident species. Resident fish included two damselfish, Dascyllus aruanus and Stegastes nigricans, one butterflyfish, Chaetodon citrinellus, and one surgeonfish, Zebrasoma scopas. Dascyllus aruanus was the most abundant fish, followed by S. nigricans, while the other two have very similar abundance (Figure 3). Three other fish, Mullolidichthys flavolineatus, Thalassoma hardwickei, and Halichoeres trimaculatus were all observed >90% of the time on the A. formosa patches, however, they were observed wandering between patches during censusing, and were defined as visitors. About 25 other fish observed during censusing were present <90% of the time. While schools of grunts were not present on every patch, they were present on the same three patches in 100% of the censuses. Therefore, they may be considered residents of Acropora formosa, but they are not included in statistical analysis due to their absence in the majority of the patches.

Figure 3. Mean number of fish of the four resident species. Bars are one St. Err. Abundances are averaged from counts of ten Acropora patches sampled on five days. Note: Little variation was observed in the replicate Acropora patches (indicated by small error bars)

Habitat Preference

Density counts on both Acropora formosa and Porites indicated a significant difference in abundance of all fish on the two different habitats. Those fish seen on Porites corals were more variable in number and presence from patch to patch. The four fish determined to be residents of the A. formosa were in much higher abundance on the formosa and were virtually missing from the Porites corals. Dascyllus aruanus and S. Nigricans were absent on Porites and the densities of both C. citrinellus and Z. scopas were an average of one fish per coral.

Predictable Structure

The data indicate that the numbers of each species of fish on each patch remained relatively constant throughout the duration of the census (Table 1). In addition, the data show that there was a
relatively constant abundance throughout all *A. formosa* patches (Figure 3, Table 2). Most importantly, the calculated proportions of the four fish indicate that the fish exist in similar proportion to one another from coral to coral. A goodness of fit test performed on these numbers indicates that the proportions are constant on all patches (Chi-squared test, P>0.05).

Table 1. Consistency of fish abundance from day to day. These numbers indicate how regular fish numbers were from day to day on one particular patch of *A. formosa*, supporting the idea of fidelity. HU=Humbug; BR=Brushtail; GR=Gregory; BU=Butterflyfish

<table>
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<tr>
<th>DAY</th>
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Table 2. Consistency of average fish abundance from patch to patch. Throughout all 10 patches fish had similar average abundance indicating a predictable community structure. HU=Humbug; BR=Brushtail; GR=Gregory; BU=Butterflyfish

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<tr>
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Discussion
Coral reef fish communities are extraordinarily diverse and complex with a wide range of life history strategies (Sale 1994). While there is not an abundance of information available about reef fishes, there is some knowledge about their characteristics. These characteristics allow fish to coexist in the same habitat. In the *Acropora formosa* habitat, there are two representatives of the Pomacentridae family. *Dascyllus aruanus*, the most abundant of the resident fishes, is a mid-water planktivore. It hovers in schools above the coral patch, defending a territory, and escapes into the shelter of the coral when threatened. *Stegastes nigricans*, the other damselfish, is an herbivore, feeding on the algal patches that it defends. Like the *D. aruanus*, it hovers above its territory and retreats into the patch in danger. *Chaetodon citrinellus* is a carnivore, feeding on coral polyps. This species of butterflyfish uses the *A. formosa* habitat as a food source, grazing on the branches of the patch. Its small size enables it to maneuver easily through the coral. Like *S. nigricans*, *Zebrasoma scopas*, a fish from the family Acanthuroidei, is an herbivore. This species scrapes algae from the coral with its small mouth and its laterally compressed body allows it to move easily through the branches of *Acropora formosa* looking for food.

The physical structure of *Acropora formosa* is consistent among patches; its branches are similar in length and size, and patch size does not vary greatly. Most patches are uniform, with an occasional patch of dead coral or piece of another species of coral in the center of the patch. Structure of individual patches is simple, consisting of a few branches stemming from each base. In contrast, *Porites* colonies found in the Temae lagoon are much more variable in size and shape. While these two habitats differ greatly in composition, they are often found within close proximity to one another. Interestingly, these two habitats have different compositions of fish communities despite being located near one another. Greenfield and Johnson (1990) demonstrated that different habitats can be adjacent to each other and have distinctive blennioid fish assemblages, and apparently, this was also observed in this
A. formosa community structure is structured not by location, but by habitat type. Fish may choose to live in Acropora formosa because it has certain attributes that are beneficial, i.e. open spaces for hiding or maneuvering and surface area for feeding or territory. The resident fish respond to those qualities and prefer to live in this type of habitat. The data collected suggest that this is the case in this study because the four fish are virtually absent from the Porites habitat while they are abundant in Acropora formosa. Furthermore, the fact that these four fish were found at two separate locations, Temae and Motu Fareone, also indicates that it is not just a particular lagoon that is desirable to these four fish, but the Acropora formosa habitat itself.

A deterministic view of reef community structure is one that supports the idea that there is a characteristic, predictable structure to the community (Alevizon, 1985). These results indicate that certain species of fish remain faithful to particular patches of coral and they appear on the same type of coral in more than one location. These facts indicate that a distinct assemblage of fishes exists in Acropora formosa. Sale and Steel (1986) stated that if fish abundance is consistent from one census to another, there is a constant structure to the community. In this study, the four resident fish appeared in the same relative abundance and proportion to one another from patch to patch throughout the censusing, supporting the idea of a predictable equilibrium fish community structure on a small scale.

Conclusion
Further study is necessary due to the short duration of the study and the limited mechanisms used to collect data. Studies using marked fish to determine whether they are truly faithful to a specific coral patch are particularly needed. Additional studies on a broader scale examining fish densities could add greatly to the data suggesting a predictable proportion of fish from patch to patch. A search for additional patches of Acropora formosa in other areas would increase the validity of the idea that the coral maintains a characteristic assemblage of fishes. If Acropora formosa is the preferred habitat for these fish, it is important to preserve this area. Because it is an important resource for the fish and it is limited in availability, this habitat must be managed carefully. Attention should be paid to the fact that a characteristic, predictable community structure was indeed observed on a small scale.

Acknowledgments
Special thanks to Professor Bill Alevizon for his ideas, encouragement, and patience. Many thanks to Maya Skubatch for her company, moral support, and for telling me it was okay not to get in the water at 5 AM in the pouring rain. Thanks to all the other professors for their enthusiasm, interest, and helpfulness. Thanks to Mike Schaffer for choosing a project that gave me more than one opportunity to go diving. Also, thanks to Nate Vaziri for helping me get an early morning start on my field work. My gratitude goes out to Pam Jutte and Ferenc de Szalay for their patience, hard work, and friendship. Thanks to Frank Murphy for the use of the facilities at the Gump Station (especially the diving equipment). And thanks to the rest of the 1995 Moorea class for making this such an unforgettable experience.

LITERATURE CITED


Habitat distribution and population structure of territorial damselfish, Dascyllus aruanus in Teavaro lagoon, Moorea, French Polynesia

Maya Skubatch
Department of Molecular and Cell Biology
University of California at Berkeley
Berkeley, CA 94720

ABSTRACT. This study examined the habitat distribution and population structure of territorial damselfish, Dascyllus aruanus, in the Teavaro lagoon, Moorea, French Polynesia. Three different branched coral habitats were used by D. aruanus in the lagoon. The habitats were distinguished according to coral species and size. They were identified as Acropora formosa-patch (>2m²), Acropora formosa-head (<2m²), and Pocillopora damicornis-head (<1m²). The physical structure of each habitat was compared by measuring average distance between branches. The population structure of D. aruanus in each habitat was compared for size, density, and home range. General observations were made in the lagoon for migration patterns, as well as the abundance and distribution of juveniles and adults. Data revealed a trend of habitat distribution associated with fish size and density. Juveniles were found at high densities in narrow gaps of P. damicornis coral heads, while adults at much lower densities over staghorn A. formosa-patches. I conclude from this study that there is a non-random habitat distribution of D. aruanus in the lagoon, in which juveniles and adults use different coral species for shelter and protection. These observations could be a possible outcome of a population-limitation process.

Introduction
Coral reefs form a complex and diverse set of unique coral microhabitats. Coral habitats are an important resource for many reef fish that use the coral for shelter, feeding and mating (Sale 1972; Shulman and Ogden 1987). Habitat distribution of reef fish varies according to choice of larval settlement and survival after settlement (Sale 1984). This study focuses on one reef fish, Dascyllus aruanus, and its unique habitat distribution in the Teavaro lagoon, Moorea, French Polynesia, where it is found associated with branching corals, Acropora formosa and Pocillopora damicornis.

D. aruanus, also known as the three-banded humbug, is a small damselfish easily distinguished by its three vertical black stripes upon a white background. Juveniles can be visually distinguished from adults by a bright blue line on their pectoral fin. D. aruanus occupies branched corals in shallow waters from the Red Sea to the Indo-East Pacific, with the exception of the Hawaiian archipelago, Pitcairn Island and Easter Island (Planes et al. 1993).
1988). There is also a general tendency to have higher recruitment to corals which have been previously occupied (Sweatman 1990, 1983; Forrester 1990; Jones 1987; Sale 1976).

After settlement, *D. aruanus* begins its second sedentary life phase. Humbugs live in groups on a single 'home' coral colony for periods of seven months or more (Sale 1976). Studies have shown positive intraspecific competition between fish occupying the same coral. Aggressive behavior has also been noted between adults and juveniles (Jones 1987).

*D. aruanus* has a very limited home range. Movements are restricted to a distance of less than 1m from the 'home' coral (Sale 1971). *D. aruanus* uses this distance for feeding zooplankton in the water column by hovering over the coral head while facing the current. *D. aruanus* food consumption has been related to individual size, social rank as determined according to size, and group size. Larger individuals feed more, and cover larger distances than smaller fish. Coates (1980) suggests that higher ranked fish restrict the movement of lower ranked fish to gain access to food.

This study will examine the habitat distribution and population structure of *D. aruanus* in the Teavaro lagoon. Three different habitats are selected and compared in terms of their physical structure and population structure of resident *D. aruanus*. Population are described according to the following criteria: fish size, density, home range, and migration patterns.

Materials and methods

Study site

This study was conducted at Teavaro lagoon, Moorea, French Polynesia (lat 17°31’S, long 149°47’W) (Figure 1) in front of the Sofitel Hotel. Water depth was generally shallow (1-2m) and water currents were slow in the mornings and increased in the afternoons with increasing wind speed.

Data collection

Data was collected from October to November 1995. Snorkeling equipment was used to make all observations. Branching coral species were identified as *Acropora formosa* and *Pocillopora damicornis*. Coral habitats were subdivided into three categories, *P. damicornis*-heads, *A.
formosa-heads, and A. formosa-patches. Coral heads were defined as one coral colony. P. damicornis heads were usually ~0.3m in length, while A. formosa <2m. The A. formosa patches were large groups of corals ranging in length between 2-12m and located mostly north of the pier.

Six corals from each habitat category were chosen randomly and marked using flags for a total of 18 marked corals. Fish counts, size, and densities were made using visual observations, a ruler, and a measuring stick.

Habitat Distribution

Habitat distribution of D. aruanus was compared between branching and non-branching (boulder) corals. The total number of resident of D. aruanus on ten branching and ten non-branching corals was measured. Corals were chosen with random line transects from the pier.

Population structure

The length of resident, D. aruanus was measured on the eighteen marked coral samples. Fish size was defined according to length: small (<2cm), medium (2-5cm), and large (>5cm). The percent composition of fish size was calculated for each coral.

Density was measured as the total number of fish per coral area. Measurements were taken all marked corals. Patch densities were estimated by counting the number of on a 1m² area.

Home range was defined as the farthest distance traveled by D. aruanus from the ‘home’ coral. Measurements were taken on the three farthest fish at four different times of the day. Average home range was calculated for each coral sample.

Migration patterns were observed by offering three coral species to D. aruanus resident on both A. formosa and P. damicornis. The distribution of fish with the new, vacant corals was observed for five minutes. All vacant corals were placed equidistant from home coral, ~5 cm. Also, an artificial reef built between large patches of A. formosa in September was monitored and fish abundance measured again in November.

Data analysis

Density and percent composition of fish size were tested with ANOVA and Tukey’s test.

Results

Habitat distribution

The lagoon had large patches of A. formosa in the north, approximately 8-10m long, and small heads of P. damicornis, 0.3m long, and A. formosa, <2m long, in the south. No D. aruanus were ever observed on boulder, non-branching coral in the Teavaro lagoon. The average number of D. aruanus on ten random branched corals was (X(SE)=3(1.2)). Four of ten branched corals had no D. aruanus inhabitants. Almost all P. damicornis observed in the lagoon were occupied with humbugs. There were some small A. formosa heads with no humbugs.

In comparing the physical structure of each microhabitat, there was a (P<.05) significant difference in branching space of the three coral habitats. Both A. formosa patches and A. formosa heads were different than P. damicornis (Figure 2), but A. formosa heads and patches were not different.

Population structure

Fish size varied greatly between each coral habitat (Figure 3). Ninety-seven percent of small (<2cm) D. aruanus were found living on P. damicornis and none on A.
formosa patches. It should be noted that all fish in the category small were juveniles and large were adults.

The density of *D. aruanus* on *P. damicornis* was significantly higher (p<3.67) than on both *A. formosa* habitats (Figure 4). There was a ten fold increase in the number of fish per coral area in *P. damicornis* (X(SE)=187(22)) than in *A. formosa* (X(SE)=17(5)).

Greater distances were traveled by *A. formosa* residents than *P. damicornis* residents at all times of the day. (Figure 5). Maximum distance was observed at noon on both coral species. No activity was observed at 10 p.m, which indicates a diurnal activity pattern. The average home range of *D. aruanus* is 27.1 cm on *A. formosa* and 6.4 cm on *P. damicornis*.

Observations made on fish migration patterns revealed that more fish were likely to visit a similar coral species as their 'home' coral than visit a new different coral species. No humbugs were ever observed traveling or visiting a boulder coral. Two large humbugs were observed to be residents on the artificial reef built in September.

Discussion

The use of coral resources by *D. aruanus* is highly specific. By choosing an optimal coral micro-habitat, *D. aruanus* can avoid predation, defend a feeding environment, and possibly increase fecundity. Larvae settlement and post-recruitment is highly correlated to the habitat structure and population.

There is a general pattern of smaller fish, <2cm, living at higher densities and on smaller branched corals, such as *P. damicornis*, then larger fish >5cm (Figures 2 and 3). There are several possible explanations for this. One explanation is that staghorn *A. formosa* offers more protection to larger fish than *P. damicornis* or that juveniles actually benefit from
living in higher densities. A previous study (Booth 1995) indicates that there is an increase in survival rate of juvenile reef fish living in larger groups. A second explanation can be attributed to a limited amount of space in the lagoon for juveniles due to the small number of *P. damicornis* corals.

Finally, it is possible that *A. formosa* is the more highly preferred coral in the lagoon and that adults are simply outcompeting smaller fish from these patches in order to maintain the lower densities for increasing food abundance. This type of intraspecific behavior between adults and juveniles has been reported (Doherty 1982; Jones 1984; Forrester 1990) for *D. aruanus* and other reef fish in other locations. This hypothesis also agrees with the 'population limitation theory' which states that intraspecific competition can be used as a biological mechanism to maintain a population below carrying capacity (Wellington 1988; Roberts 1991; Doherty 1994; Doherty et al. 1994). In order to know if the population of *D. aruanus* in the Teavaro lagoon is below carrying capacity further studies and measurements should be done. This type of behavior knowledge can be useful for future constructions of artificial reefs as well as promotion of reef fish populations.

Conclusion

Several conclusions can be made from the study of the habitat distribution of *D. aruanus* which can pertain to future work of reef fish habitats and behavior. First, *D. aruanus* uses specific corals throughout its life for protection. The fish will stay on individual corals for observed periods longer than two months. Second, the specific specie of coral used by the humbug for protection is directly relates to the size of the fish. This is seen clearly in the Teavaro lagoon where there are only two types of distinct branching corals: staghorn *Acropora formosa* and highly branched *Pocillopora damicornis*. The segregation of fish according to size and the different population structures and densities found on each coral hint at the possibility of intraspecific competition behavior in which larger adults control the vast *A. formosa* corals. This type of behavior, also seen in other species, is described by the population limitation theory.

Future research project are needed to compare the habitat distribution of *D. aruanus* at Teavaro lagoon to other sites. This study shows the importance of preserving a variety of corals in the lagoon, which is found near a major tourist site. The destruction of any of the branching corals can potentially eliminate the entire population of *D. aruanus* at Teavaro. On the other hand, a correct reef management program can help preserve the lagoon environment and maintain the reef fish in the lagoon.

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LITERATURE CITED


Habitat partitioning and susceptibility of *Sargassum sociale* to herbivory by sea urchins

Nathan Vaziri  
Department of Integrative Biology  
University of California, Berkeley, CA 94720

ABSTRACT. The susceptibility of *Sargassum sociale* to herbivory was studied on the barrier reef of Moorea, French Polynesia. *Sargassum* was removed from the reef flat where it is naturally abundant, measured, and placed back onto the reef flat and in the lagoon area where it is not normally found. Half of the replicates were caged in each habitat. *Sargassum* replicates were left in the field for ten days, at which time they were collected and re-measured. Uncaged lagoon replicates sustained the most plant loss due to herbivory, while the uncaged reef flat replicates sustained less plant loss. Caged replicates in both habitats sustained little or no loss of plant matter. Three urchin species common in the area were fed *Sargassum sociale* in captivity to determine which were possible herbivores. *Diodema savigni* and *Tripneustes gratilla* consumed nearly all of the portions given to them, while *Echinometra mathaei* showed did not consume the seaweed. Densities and distribution patterns of these three urchin species were measured at the site and superimposed on those of *Sargassum*. *Echinometra mathaei* occurred in both habitats, while *D. savigni* and *T. gratilla* were only found in the lagoon. It is thus concluded that herbivory by *D. savigni* and *T. gratilla* is likely to be a major factor determining the distribution of *S. sociale*.

Introduction

The abundance and distributions of many seaweeds commonly follow distinct and predictable patterns. Such patterns have been referred to as habitat partitioning (Hay 1985; Carpenter 1986), and result from several abiotic and biotic factors. Abiotic factors influencing seaweed distributions include light intensity (Paula 1994), water velocity and wave action (Doty 1971a; Gao 1991), water salinity and temperature (Paula 1994), and substrate type and topography. Biotic factors include gamete/germling dispersal (Kendrick and Walker 1991) and establishment (Hruby and Norton 1979), competition for substrate with other algae species (Deyscher and Norton 1982), and herbivory by fishes and sea urchins (Hay 1985; Lewis 1985; Foster 1987; McClanahan et al. 1994). The impact of grazers has a large effect on preexisting algae assemblages and the maintenance of spatial mosaics of algae distributions on many coral reefs (Hay 1985). Grazing intensity is directly influenced by herbivore mobility, abundance, and foraging range (Carpenter 1986). These factors are often dependent on abiotic habitat conditions such as flow, depth, and reef topography. Herbivore morphology and behavior greatly influence which habitats they may occur in, and subsequently algal distributions are often influenced by the habitat partitioning of herbivores.

*Sargassum sociale* is a seaweed common to the coral reefs of Moorea and Tahiti (Setchell 1926). Its distribution is restricted primarily to the reef flat, and it is the dominant vegetation type in that zone. *S. sociale* disappears rapidly in the back reef and outer slope portions of the barrier reef, where low growing (<2cm in height) filamentous and crustose forms of green (Chlorophyta) and coralline red (Rhodophyta) algae dominate. However, *S. sociale* is occasionally found in lagoon areas growing on the tops of large coral heads that reach the water surface, and is rarely found in depths greater than 0.5m. Previously published discussions regarding the cause for the distinct distribution pattern of *Sargassum* have only suggested that abiotic factors such as turbid water flow and periodic exposure to air are the possible factors that limit its distribution to near the water surface (Galzin and Pointier 1985; Payri 1987). It has been suggested that higher dissolved oxygen levels on the reef flat may create more favorable living conditions for *S. sociale*. Morphological adaptations such as a strong
holdfast and leathery blades suggest that *S. sociale* maintains a competitive advantage over other less durable algal forms on the highly turbid reef flat. No experimental studies have been performed to determine if other possible factors such as herbivory, germling establishment, or competition with other algae are influencing the distribution of this alga. By conducting a transplant and caging experiment, this study examines the susceptibility of *Sargassum sociale* to grazing by herbivorous fish and sea urchins as a possible factor in creating its distinct distribution pattern. In addition, three sea urchin species found in Moorea were examined with regard to habitat preference and their ability to consume *Sargassum sociale*.

Materials and Methods

*Site Description*

The experimental site was located on Moorea, French Polynesia (17°29'S; 14°50'W) at Point Aroa, Temae (Figure 1). The site was selected for transplant experiments due to the close proximity of the reef flat to the conglomerate platform (~70m). Nearest to the shore lies a cemented, conglomerate platform formed from remnants of hurricane deposits. Between the conglomerate platform and the reef flat lies a lagoon channel (Figure 2), which ranges in depths from 1 to 2m. The reef flat portion of the barrier reef is exposed during most low tides and submerged during most high tides. This zone is constantly facing high water velocities from waves impacting on the fore reef portion of the barrier reef. The topography, geomorphology, and biological zonation of this portion of the barrier reef has been well documented (Galzin and Pointier 1985).
Transplant and caging experiment

Twenty samples of S. sociale were collected from the reef flat by removing dead coral pieces (15-20 cm in diameter) with a chisel and hammer. Algae were brought back to the laboratory and kept in seawater tanks for three days in order to complete initial measurements. For each replicate, S. sociale was measured in three ways: 1) average stipe length of ten randomly selected stipes, 2) average number of blades/2cm of stipe, and 3) volume displacement of the entire plant. Each measured stipe was marked with labeled flagging tape.

Rocks were re-cemented to the reef substrate using Z-spar™ underwater marine epoxy and wire. Ten randomly selected replicates were placed onto the reef flat; five of these were enclosed with 30cm x 15cm wire (0.5cm x 0.5cm mesh)cages. The remaining ten rocks were attached to randomly selected dead coral heads in the lagoon. Five of the lagoon replicates were also enclosed with wire mesh cages. Replicates were left in the field for ten days, at which time each was brought back to the laboratory for final measurements. Voucher specimens were collected and sent to the UC Berkeley Herbarium for identification and preservation.

Sea urchin feeding experiments

Individuals of the dominant urchin species seen at the experimental site were collected for captive feeding experiments. Species examined were Echinometra mathaei, Tripneustes gratilla and Diadema savignyi. Three seawater tanks were set up with two urchins of each species in each tank. 3-4g amounts of S. sociale were weighed, attached to stones with wire, and placed in each tank. Observations were made for a 24-hour period to determine if the Sargassum was ingested by the urchins. After this period, final algal weights were recorded. The experiment was replicated six times, with new urchins for each replication.

Site ambient conditions, urchin and Sargassum habitat partitioning

Surface flow and depth measurements were taken on the reef flat and the lagoon using a floating buoy (6-11cm) attached to two meters of string and a stopwatch for flow measurements. A meter stick was used to measure depth. Data was collected during two high and low tide periods. Urchin and S. sociale densities were measured by visual counts and percent cover estimates, respectively. Two transect lines were laid down in each zone, perpendicular to the shoreline. Along each line, ten quadrats were measured using a random number table to determine quadrat placement.

Statistical analysis

A two-way ANOVA was used to analyze data from the transplant/caging experiment. This statistical test was selected in order to determine if the effects
of caging and habitat were significant. Depth and flow measurements were analyzed for both habitats with an independent t-test to detect statistical significance between habitats.

Results

Transplant and caging experiments

For all three plant parameters (mean stipe length loss, blade loss, and volume loss) the uncaged lagoon treatment sustained the greatest loss of plant matter (Figures 3,4,5).

Within three days from the start of the experiment, *T. gratilla* urchins were observed consuming some uncaged lagoon replicates. Uncaged reef replicates sustained the second largest amount of plant loss, however urchins were never seen feeding on any reef flat replicates. Caged treatments in both habitats sustained the least amount of plant loss, and actually increased in size for two of the three measurements (Figures 3,4). Variability among replicates was most prevalent for the mean stipe length loss (Figure 3), as is shown with the relatively large standard error for this parameter. Results from the statistical analysis for the three variables examined are shown below:

• Habitat variable

  The effect of habitat on plant loss was analyzed for all three plant parameters. For mean stipe length, there was a general trend of habitat on plant loss although statistically insignificant at $p<0.2$. Mean stipe length was reduced more in the lagoon than on the reef flat (Figure 3). The blade portions of lagoon replicates were reduced more than on the reef flat (Figure 4).

For volume, a trend was found to exist between lagoon and reef habitats, however statistically insignificant. Overall, more plant loss was observed on lagoon replicates than reef flat replicates (Figure 5), irrespective of caging.

• Caging variable
The effect of caging on plant loss was analyzed for all three parameters. For all three parameters, caging had a significant effect on plant loss. The net effect of caging was that plant loss was reduced in both habitats (Figures 3,4,5).

- Habitat and Caging interaction variable

The interaction of caging and habitat on plant loss was analyzed for all three plant parameters. For mean stipe length, no interaction was found between habitat and caging (Figure 3). For number of blades/2cm of stipe and volume displacement, statistically significant results (p<.001) were observed (Figures 4,5). This interaction variable shows that the difference between caged and uncaged treatments was significant within and between habitats.

Sea urchin feeding experiments

Only two of the three urchins studied preferred to consume *S. sociale* while in captivity. *Tripneustes gratilla* and *D. savigni* consumed nearly 100% of all portions presented to them (Figure 6).

These two species were observed feeding on the plant assays placed in the tanks. Plant assays given to *E. mathaei* showed no biomass loss for any of the six replicates, and these urchins were never observed to be eating any of the algae placed in the tanks. Observational data was also collected on plant part feeding preferences. When large portions (>30g) were given to *T. gratilla* and *D. savigni*, feeding preferences were observed. *Diadema* would grab the plant with its tube feet, and consume only blades as it moved up and down the plant vertically, leaving the stipes and holdfast of the plant intact. *Tripneustes gratilla* was observed consuming plant parts lower on the plant, and eventually ripping stipes from the holdfast. Field replicates seen being consumed by *T. gratilla* were denuded of all vegetation.

Site ambient conditions, urchin and Sargassum habitat partitioning

Depth and flow measurements were statistically different between habitats during the two tidal periods (Figures 7,8).
Mean depth was much higher in the lagoon than on the reef flat at high and low tide, is limited to a 3-5m band on the reef flat and it rapidly declines in abundance in the back reef and lagoon areas (Figure 9). The mean density of *D. savigni* was 7.1/m², and its distribution was limited to the lagoon channel. The distribution of *T. gratilla* was limited to the shoreward portion of the lagoon channel at a mean density of 1.6/m². *E. mathaei* was found in both the lagoon channel (5.6/m²) as well as on the reef flat (1.6/m²).

Discussion

Some of the variability in mean stipe length loss can be attributed to variable feeding behaviors by different herbivores. Some uncaged lagoon replicates were completely consumed, and others had only sustained blade loss while retaining stipe length. This is explained by the feeding preferences observed of the two

Mean flow was significantly higher on the reef flat than in the lagoon. Quadrat data for *S. sociale* showed that its distribution possible herbivores *T. gratilla* and *D. savigni*. Both of these urchins have been widely studied and consume many species of seaweeds and kelps in other areas of the Pacific (Harrold and Reed 1985; Foster 1987; McClanahan et al. 1994). Fish were never observed consuming *Sargassum* in the field, and the role of herbivory by fish was not analyzed in the laboratory.

Data suggests that the presence of a cage in both habitats significantly inhibited plant loss. The absence of a cage consistently led to greater plant loss with regard to the stipe length and blade number parameters. In the case of volumes, it is possible that intense wave action could have torn some unmarked plant portions off of the rocks, giving the result of more plant volume loss in the caged reef flat replicates than in uncaged reef flat replicates (Figure 5). However, when comparing each habitat individually it is evident that the absence
of a cage on the reef flat has less effect on plant loss than in the lagoon. Also, plant loss was greater in uncaged lagoon replicates than in uncaged reef flat replicates, suggesting that habitat plays a role in determining the amount of grazing that occurs within different areas within the site. The results of the statistical analysis show a significant relationship between habitat and caging. This may be because of the distributions of potential herbivores, *S. sociale*, and the degree of grazing pressure exerted in each habitat.

The fact that depth and flow were significantly different between the two habitats probably affected the habitat partitioning of sea urchins. The only urchin found on the reef flat was *E. mathaei*. *Echinometra mathaei* is a relatively small burrowing species with short spines. Its ability to survive on the reef flat as well as in the lagoon is probably due to its behavior and morphology, as it may find areas of refuge from intense waves in small burrows it creates in dead coral rock. However, the presence of *E. mathaei* on the reef flat should have no effect on the abundance of *S. sociale* in this zone because this urchin did not consume this seaweed in captivity. Larger urchins such as *D. savigni* and *T. gratilla* are not able to withstand the intense energy found on the reef flat, as increased drag may pose a risk of spine damage (Dart, 1972; Denny et al., 1985). Thus the distribution of the two possible urchin herbivores of *Sargassum sociale* is restricted to the lagoon area. The absence of these urchin herbivores from the reef flat may allow *S. sociale* to maintain dominance on this portion of the barrier reef. In other areas of Moorea, *Sargassum* is found growing at the tops of large coral heads at the water surface. It is possible that in these areas wave action keeps out herbivores and permits *S. sociale* to occur lagoon habitats.

*Sargassum* germling dispersal and establishment has been studied in depth. Studies involving other *Sargassum* species show that germlings of this genus can tolerate a wide range of abiotic factors such as light intensity, salinity, and current speed (Paula 1994; Gao 1993). This suggests that *Sargassum* is essentially a generalist in the habitat in which it may occur. However, increased rates of oxygen evolution in adults and juvenile plants have been detected in areas of faster flows (Gao 1991). Hruby and Norton (1979) found that *Sargassum* germling dispersal distances and rates of establishment generally have a localized (within 1 m of parent) distribution, although some germlings have been known to settle as far as 1 km from the parent. Beds of *Sargassum* are quite localized due to this localized establishment pattern. Long range establishment has been observed with drifting pieces of plant material that travel long distances (Kendrick and Walker 1991).

Previous studies have also shown that interspecific and intraspecific competition for bare substrate greatly affects the mortality of germlings, and that thallus regeneration is common in maintaining algal beds in some species of *Sargassum* (Hruby and Norton 1979). Competition with quickly colonizing algal species in the lagoon habitat combined with *S. sociale*’s inability to regenerate from preexisting beds in the lagoon could offer another explanation for its absence from this habitat. The absence of *S. sociale* from the fore reef habitat could possibly be a result of its inability to withstand the intense impact of waves on the outer slope due to its relatively long stipe length. It is probably outcompeted by low growing forms of coralline red algae which thrive in this habitat.

**Conclusion**

This study demonstrates that herbivory is a factor influencing the distribution of *S. sociale*, and that *D. savigni* and *T. gratilla* are two consumers of this alga. However, further studies involving the biology of *Sargassum sociale* should be done in order to fully understand the ecological niche that this alga fills. Future studies needed include: analysis of photosynthetic rates under various conditions, patch dynamic studies of germling dispersal and establishment, interactions with other algal species, and chemical analysis of possible secondary...
metabolites as a possible deterrent to herbivory by fish. Understanding the role of fish herbivory on this seaweed is key in understanding the trophic relationships of herbivores and predators with respect to algal assemblages in Moorea.

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Payri CE (1987) Zonation and seasonal variation of the commonest algae on Tiahura reef (Moorea Island, French Polynesia). Botanica Marina. 30:141-149
A description of the spatial and temporal distribution of *Paracalanus sp.* (Crustacea: Copepoda) in Cook's Bay (Moorea, French Polynesia)

Ryan M. Houston
Department of Environmental Science, Policy, and Management
University of California, Berkeley 94720

**ABSTRACT.** The spatial distribution of *Paracalanus sp.* (Crustacea: Copepoda) was examined in Cook’s Bay (Moorea, French Polynesia) at five locations within the bay, Avaroa Pass, and the nearby lagoon during October and November 1995. At each of the five sites, the number of small individuals (<1.25 mm length) and large individuals (>1.25 mm length) per sample was counted and used to describe the surface abundance throughout the study area. Changes in surface abundance throughout 24 hour cycles were observed by sampling at one location every three hours during four 24 hour periods. Small plankters were found in increasing abundance from the head of Cook’s Bay to Avaroa Pass, but in lower abundance in the lagoon. Large plankters were observed in increasing abundance from the head of Cook’s Bay to the mouth, but in decreasing abundance in Avaroa Pass and the lagoon. During temporal distribution studies, large and small plankters were observed in greatest surface abundance between 9 pm and 12 midnight. Large plankters were found in low abundance at all other times throughout the day whereas small plankters were observed in gradually increasing abundance from 6 am to 12 midnight. Observations suggest the spatial distribution of *Paracalanus sp.* was most likely caused by the patterns of the local surface currents. The observed differences in surface abundance over 24 hour periods may have resulted from differential predation pressures on large and small plankters.

**Introduction**

There have been many studies describing the distribution and vertical migrations of zooplankton near Pacific islands and tropical lagoons (Sale et al. 1976; Renon 1978; Champalbert 1993). However, in the lagoon of the high island of Moorea, French Polynesia, there have been few zooplankton studies. Early taxonomic studies focused on cataloging and describing zooplankton in the lagoon (Gray 1930; Rose 1953). Recent studies have focused on species richness around the island (Lefèvre 1985) or the specific behavior of zooplankton in the lagoon at the north-west corner of the island (Renon 1989). No studies on Moorea have focused on copepods or either of the two prominent bays on the north side the island.

The present study describes the spatial and temporal surface water distribution of *Paracalanus sp.* in Cook’s Bay, Avaroa Pass, and the nearby lagoon. The purpose was to test two general hypotheses: 1) *Paracalanus sp.* in Cook’s Bay, Avaroa Pass, and the nearby lagoon are distributed in predictable patterns; 2) large (>1.25 mm) and small (<1.25 mm) *Paracalanus sp.* will be observed in different patterns of surface abundance throughout the 24 hour cycle.

A calanoid copepod was chosen for this study because calanoid copepods are major food sources for many reef fishes and corals (Hobson 1991), are abundant throughout the lagoon of Moorea (Lefèvre 1985), and often comprise 60-85% of the total zooplankton in tropical lagoons (Champalbert 1993). *Paracalanus sp.* was chosen because it is an established resident of the lagoon of Moorea (Renon 1989) and is present throughout Cook’s Bay in two distinct size categories: individuals >1.25 mm carapace length (‘large’ individuals), and individuals <1.25 mm carapace length (‘small’ individuals). Different size zooplankters are often found in different distributions and patterns of vertical migration within tropical bays and lagoons (Hobson et al. 1978). Studying these two size categories may provide data that can be used to make generalized conclusions about the behavior and distribution of both large and small copepods in Cook’s Bay, Avaroa Pass, and the nearby lagoon.
Site, Materials and Methods

Study site

Cook's Bay is located on the northern side of the island of Moorea, French Polynesia (17° 30' South, 149° 50' West) (Figure 1). The bay is 2.5 km long from head to mouth and 1 km wide at the widest point. Directly north of the mouth is Avaroa Pass. The depth of Cook's Bay is 10 m near the head, 30 m in the central bay, and 45 m in the pass. A lagoon is located east and west of the bay and its width varies from 400 m to 900 m between shoreline and reef crest. The lagoon is shallow (1 m to 10 m deep) except for the region closest to the mouth of the bay (15 m to 25 m deep) (Galzin et al. 1985).

Spatial distribution

Sampling was conducted to determine Paracalanus sp. distributions within Cook's Bay, Avaroa Pass, and the nearby lagoon. Samples were collected at five sites within Cook's Bay, the pass, and the lagoon at 6:00 am, 12:00 pm, and 6:00 pm on 15 non-consecutive days for a total of 90 tows (Figure 2). Site 1 was located near the head of the bay, approximately 200 m from the inlet stream near the town of Pao Pao. Site 2 was located near the geographic center of the bay. Site 3 was located near the mouth of the bay. Site 4 was located at the southern boundary of Avaroa Pass. Site 5 was located within the deep-water area of the lagoon at the eastern edge of the mouth of Cook's Bay.

Temporal distribution

Additional sampling was conducted to determine the temporal distribution of Paracalanus sp. in the surface water of Cook's Bay. A total of 72 plankton tows...
were collected during four non-consecutive 24 hour periods at site 2. Each day, two duplicate samples were taken every three hours from 6:00 am on the first day of collection to 6:00 am the following day for a total of 18 samples per 24 hours.

Sampling methods

All field studies were conducted during October and November, 1995. Samples were collected with a conical 202 μm plankton net with a circular opening (diameter = 25 cm). During each sampling session, the net was towed 12 m behind a small skiff at approximately 2 km/hr for 5 minutes. Tows were made into the prevailing current (usually north-east). No samples were collected during periods of extremely high winds or waves. Each tow was about 200 m long and sampled approximately 9.8 m² of water. Depending upon currents and waves, the sampling depth ranged from 1 m to 3 m below the surface of the water. Samples were immediately transferred to plastic jars and the net was thoroughly rinsed between samples. During each sampling day, the air temperature, wind speed and direction, wave height and direction, cloud cover, solar radiation, tide, previous 24 hour precipitation, and lunar phase were recorded. General surface water current directions were recorded at each of the five sampling sites by observing the movement and orientation of plastic flags attached to a stationary rope.

*Paracalanus sp.* were counted with a dissecting scope in two size categories: 'small' plankters with carapace length <1.25 mm, and 'large' plankters with carapace length >1.25 mm. If the number of *Paracalanus sp.* in a sample was <50, counts were completed for the entire sample. If the number of *Paracalanus sp.* was >50, samples were transferred to a 250mL graduated cylinder and thoroughly mixed. Using a large pipet, a volumetric fraction (1/5 to 1/10 of the total sample) was removed and the *Paracalanus sp.* individuals in each size category were counted within the sub-sample. The number of individuals in the sub-sample were multiplied to estimate the total number of individuals in each size category for the total sample (Lefevre 1985).

Data analysis

For both large and small *Paracalanus sp.*, data from 6 am, 12 pm, and 6 pm samples were combined for statistical analyses because relative distributions between the five sampling sites did not differ between the three sampling times. Statistical differences of large and small *Paracalanus sp.* abundance between sampling sites in spatial distribution studies were determined using two one-way ANOVA's and accompanying Tukey’s tests with log₁₀(x+1) transformed data.

The temporal distribution patterns of large and small *Paracalanus sp.* were compared using Chi-square (X²) with the average abundance at each sampling time. Differences between the abundance at each sampling time were determined using a one-way ANOVA and accompanying Tukey’s test with log₁₀(x+1) transformed data.

Results

In Cook’s Bay, secchi disk visibility varied from 10 m at the head of the bay to 16 m in Avaroa Pass. Surface water temperature was between 26° C and 27.5° C. Surface currents measured to a
depth of 3 m changed with wind direction; during the dominant north-eastern wind, currents traveled generally into Cook's Bay whereas during infrequent periods of south-eastern winds, surface currents traveled generally out of Cook's Bay into the open ocean (Figure 3).

Spatial distribution
The average abundance of large *Paracalanus* sp. in all sites did not change significantly between 6 am, 12 noon, and 6 pm samples. At 6 am, 12 pm, and 6 pm, large *Paracalanus* sp. were observed in increasing abundance from site 1, through site 2, to site 3 (Figure 4). In sites 4 and 5, the observed surface abundance of large individuals was lower than in site 3. *Paracalanus* sp. concentrations between sites were significantly different (*p* < 2.3 X 10^{-14}, df = 4). Concentrations in site 1 and site 5 were significantly different than all other sites but concentrations observed in site 2 and site 4 were not. Concentrations in site 2 and site 3 were also not different.

Small *Paracalanus* sp. in the combined results from 6 am, 12 pm, and 6 pm samples were present in the lowest average abundance in site 1 and in increasing abundance through sites 2 and 3 to a peak in site 4. Site 5 had a lower abundance than site 4. *Paracalanus* sp. concentrations were significantly different between sites (*p* < 5 X 10^{-14}, df = 4). Abundance measured in sites 2, 3, 4, and 5 was not significantly different. The abundance in site 1 was significantly different than all other sites.

No clear correlations were found between the distribution and abundance of *Paracalanus* sp. and air temperature, cloud cover, solar radiation, tide, precipitation, lunar phase, or turbidity. A change in large and small *Paracalanus* sp. abundance and distribution was observed in all five sites with changes in wind direction and the accompanying surface currents. In three samples taken at each sampling site during south-eastern wind, both large and small *Paracalanus* sp. were absent from site 1, in very low abundance in sites 2, 3, and 4, but in significantly higher abundance in site 5. Concentrations of large and small *Paracalanus* sp. were significantly different between sites (*p* < 1.4 X 10^{-6}, df = 4; *p* < 2.5 X 10^{-8}, df = 4, respectively) (Figure 5).
Temporal distribution

Large and small *Paracalanus* sp. individuals were present in significantly different patterns of abundance even though the greatest abundance of both size classes occurred between 9 pm and 12 am ($X^2 = 135.45, df = 8, p < 0.001$) (Figure 6). Large *Paracalanus* sp. individuals were observed in the greatest abundance at 9 pm, with a significantly lower abundance at 12 am and 3 am ($p < 3.5 \times 10^{-4}$, df = 8). The lowest abundance was observed at 6 am and 6 pm with a slight increase in abundance observed between 9 am and 3 pm. Small *Paracalanus* sp. individuals were observed in increasing abundance from 6 am, gradually throughout the day, to the greatest abundance at 12 am ($p < 7 \times 10^{-15}$, df = 8). After 12 am, small *Paracalanus* sp. abundance decreased until 3 am.

Discussion

Spatial distribution

In most tropical lagoons, oceanic plankton are carried into the lagoon by currents flowing over the barrier reef
(Champalbert 1993; R. Galzin pers. com.). Plankton distributions within a bay or lagoon are often controlled by the movement of local surface water currents and zooplankters tend to concentrate in areas of moderate water flow but are often absent from areas of extremely high or low water flow (Hobson et al. 1978). Therefore, interpretations of the observed distributions of Paracalanus sp. in Cook's Bay, Avaroa Pass, and the lagoon must consider the dominant north-east surface currents present during sampling (Figure 3a).

Large Paracalanus sp. individuals were observed in low abundance at the head of Cook's Bay (site 1), with increasing abundance through the center portion of the bay (site 2) to the mouth (site 3). Lower abundance was observed in Avaroa Pass (site 4) and the lagoon (site 5) than in the mouth of Cook's Bay (site 3) (Figure 4a). The north-eastern surface currents probably carried oceanic plankters across the barrier reef east of Cook's Bay, west through the lagoon toward the mouth of Cook's Bay, and across Avaroa Pass. Surface currents suggest that some plankters could be carried into Cook's Bay and become concentrated within the mouth of Cook's Bay, resulting in the high concentrations of large Paracalanus sp. observed in sites 2 and 3. Currents in Avaroa Pass and the lagoon were probably too strong for the concentration of significant numbers of plankters, thus resulting in the low observed large Paracalanus sp. abundance. At the head of Cook's Bay, the low abundance of large and small Paracalanus sp. could be caused by several factors. Very little oceanic water circulated within shallow region of the bay near site 1. Therefore, surface currents may rarely carry oceanic plankters deep enough into Cook's Bay to reach site 1 in any significant concentrations. Furthermore, the increased turbidity, variations in salinity, and other changes in water quality associated with a shallow estuary region like that near site 1 may be intolerable for oceanic copepods and result in high plankter mortality and the low observed abundance.

When the wind and surface currents in Cook's Bay changed directions and originated in the south-east, Paracalanus sp. distributions were different than observed during north-east winds and surface currents. During south-eastern winds, surface currents flowed from the head of Cook's Bay, through the mouth, and into the open ocean via Avaroa Pass. In the lagoon, the prevailing surface currents were from the north-east, creating a...
distinct boundary between incoming north-east currents and out-going surface water exiting Cook’s Bay from the south-east.

During south-eastern winds, large and small Paracalanus sp. were observed in similar patterns. Very few Paracalanus sp. were found in Cook’s Bay or Avaroa Pass whereas a high concentration of plankters was found in the lagoon. The observed distribution pattern is probably a direct result of the south-eastern surface currents flowing north out of Cook’s Bay and into the open ocean. Surface currents probably carried the majority of the surface plankters, normally present in the bay during north-easterly currents, through Avaroa Pass and into the ocean. The incoming plankters crossing the barrier reef into the lagoon probably became highly concentrated in the circulating eddies created by opposing currents at the boundary between the lagoon and the north-eastern corner of Cook’s Bay.

The distinct changes observed in the distribution of Paracalanus sp. during periods of north-easterly and south-easterly surface currents suggest that surface currents have significant impacts upon the distribution of plankters in Cook’s Bay, Avaroa Pass, and the lagoon. However, other factors that have been discussed in the current literature may have contributed to the observed distribution patterns. Increased zooplanktivorous fish predation in shallow near-reef regions (Hobson 1991), changes in water quality in shallow bays (Champalbert 1993), and high variations in salinity within tropical bays and lagoons (Gabrie et al. 1985) may have increased plankter mortality in some regions of the study area and contributed to the observed distribution patterns. More research should be conducted to examine the effects of these factors.

**Temporal distribution**

Both large and small Paracalanus sp. were observed in high surface concentrations between 9 pm and 12 am and low concentrations at 6 am. However, the observed distributions of large and small plankters between 6 am and 9 pm were significantly different. Large plankters were observed in low abundance between 6 am and 6 pm but increased significantly at 9 pm. Small plankters were observed in increasing abundance from 6 am to 12 am before decreasing to 6 am.

The observed changes in surface abundance can be attributed to diel vertical migration, an anti-predator defense (Lampert 1989) used to escape predation by zooplanktivorous fishes (Loose 1994). During the day, downward migration minimizes the risk of predation by visually orienting zooplanktivores present in the surface water (Hobson 1991, Kerfoot 1985). However, downward migration reduces the efficiency of growth and reproduction, so plankters migrate to the surface at dusk when predation risks are low (Lampert 1989, Loose 1994).

Plankters must balance the risk of predation associated with remaining in the surface water with the costs in growth and fecundity associated with downward migration by altering vertical migration behaviors (Loose 1994). The precise behaviors that minimize predation risk and maximize growth and fecundity are different between zooplankters (Loose 1994) based on differences in size, pigmentation, and biology (Hobson 1991). Consequently, highly variable vertical migration behaviors have been observed between zooplankters that experience different relative risks of predation while present in the surface water (Loose 1994).

Large Paracalanus sp. may experience greater risk of zooplanktivorous attack than small Paracalanus sp. for two reasons: 1) larger size allows easier detection by visually orienting zooplanktivorous fishes, and 2) large zooplankters are often more heavily pigmented than smaller zooplankters, thus more easily detected (Hobson et al. 1978, 1991). Precise timing in vertical migrations may be more important in large Paracalanus sp. than in small Paracalanus sp. because large individuals are more easily detected by zooplanktivorous fishes. Therefore, the distinct periods of increased and decreased surface abundance in large individuals would be expected as observed. Small individuals may not encounter serious predation risks because they are too small to be seen by zooplanktivorous fishes.
(Hobson 1991) so vertical migrations may not be as important for survival in small individuals as in large individuals. The different predation risks encountered by large and small Paracalanus sp. may allow the vertical migration patterns in small individuals to be more gradual, and less precise, than in large individuals.

Suggestions for future research

A continuation of the present study could examine the distribution of a variety of zooplankton in Cook's Bay to determine if the patterns observed in this study are similar to those observed in other types of zooplankton. Also, the patterns observed in this study could be compared to patterns observed in the future in Opunohu Bay or bays with similar characteristics on other tropical islands.

Previous studies have shown that plankton distributions around patch reefs significantly influence the activity of zooplanktivorous fishes (Hobson et al. 1978). On a larger scale, it would be interesting to determine if the zooplankton distributions within a tropical bay or lagoon influence fish distributions.

Conclusions

The predictable distribution of large and small Paracalanus sp. in Cook's Bay, Avaroa Pass, and the nearby lagoon suggest the patterns are closely tied to surface currents. However, there may be many other untested factors that are important in creating this distribution pattern which should be considered in the future. The changes in surface abundance of large and small plankters over time were observed as expected and supported by previous research. The difference between the patterns observed for large and small Paracalanus sp. was probably a result of different predation pressures experienced by large and small zooplankters. The results from the present study provide preliminary information which should encourage future zooplankton research on the island of Moorea.

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Niche partitioning in two species of tropical nudibranchs at Moorea, French Polynesia

Camille Nowell
Department of Environmental Science, Policy and Management
University of California, Berkeley, CA 94720

ABSTRACT. Two nudibranch species, Risbecia imperalis and Glossodoris cincta, were studied at Moorea, French Polynesia, in a fringing reef and in aquaria to determine how the niches they occupy are separated. The activity, mate preference, and distribution of both species was observed. Observations of crawling, feeding, mating, egg-laying and stillness showed both species are diurnal. Highest activity levels were found in the morning and mid-afternoon. The predominant daytime activities of Risbecia imperalis were crawling and mating. The predominant daytime activities of Glossodoris cincta were crawling and feeding. Both species were tested in a Y-maze to see if animals prefer known or unknown mates. Results in this test suggested these species do not distinguish between known and unknown mates. Three areas were sampled to determine the distribution of both species, and of the Dysidea sponge, a potential food of Glossodoris cincta. Nudibranchs were found in low densities on a transect along the edge of the fringing reef (0.05/m²), and on a transect 10 meters shore-ward from the edge (0.03/m²). Dysidea was found in all three transects, but in increasing quantities towards the edge of the fringing reef. The three test areas suggested some differences in niche occupation between the species.

Introduction
Coral reef ecosystems are amongst the most diverse habitats on earth (Campbell 1993). Sometimes in these areas, closely related species are found to co-occur. It is not clear how these organisms can maintain stable populations when they are competing for the same temporal and spatial resources. The competitive exclusion principle, formulated by G. F. Gause (1934), states that two species cannot coexist indefinitely on the same limiting resource (Ricklefs 1973). When the same resource is utilized by two organisms, in time, the organism which can secure the resource most efficiently will out-compete the other. Organisms with the most similar resource needs will compete most intensely, so competition between individuals of the same species is usually more intense than competition between individuals of different species.

Nudibranch mollusks, along with most other marine species, have their greatest species richness in the Indonesian Malaysian archipelago. Species richness declines with distance outward from this area but is still high throughout the tropics. The dominant historical model of Indo-Pacific species dispersion states that larval forms of generalist species dispersed from this area, and successfully colonized more remote areas where the species became specialized in time (Lipps, pers. comm. 1995). Species richness of nudibranchs in the Indonesian Malaysian archipelago is estimated to be about 1,000 and decreases to 400 in the south Pacific, where this study was conducted (Gosliner, pers. comm. 1995). Some work has been done on nudibranch systematics in Moorea, French Polynesia (Johnson 1994), but the relatedness of most of these organisms is still unknown.

While much work has been done on the neurophysiological aspects of behavior in opistobranchs, little has been done on behavior and ecology in the field (Kupfermann 1967). Previous studies have been conducted on behavior while using the anaspidean opistobranch Aplysia, rather than with species of nudibranchia (Jacklet 1972; Leonard 1991). Reasons for the limited study of nudibranchia include problems of working in the temperature, turbidity, and depth of water in which most nudibranchs live (Ramos, Rocafort, and Miller 1995). These were not problems at the site chosen in Moorea, French Polynesia, where field sites were in shallow, clear water, and could be linked with laboratory studies.
I chose to study the two coexisting nudibranchs, *Risbecia imperalis* and *Glossodoris cincta* to understand how these organisms are partitioning their environment. I tested several aspects of their behavior and habitat to discover in which ways these animals diverge. The first specific goal of this study was to determine what the predominant activity patterns of *R. imperalis* and *G. cincta* nudibranchs are, and also to determine if these activities display a daily pattern. The second specific goal of this study was to understand when pair associations are made, and if these associations are limited to known animals within the group. Although both nudibranch species used in this study are simultaneous hermaphrodites, and therefore could mate with any other individual, observations suggested that some type of discrimination is employed, and that pair encounters do not always result in copulation. The final specific goal was to determine where both species of nudibranchs are found on the fringing-reef, and with what foods they are associated.

**Materials and methods**

**Study site**

Studies were conducted on the island of Moorea, French Polynesia, (17° 30', 149° 50'), near the mouth of Cook's Bay, on the western side (Figure 1). Laboratory experiments were conducted at the Richard P. Gump Biological Research Station between 13 October and 16 November 1995.

Collection and observation of animals in the field was done on the reef flat and near the edge of the fringing reef which borders the Gump Station on Cook's Bay (Figure 2). The reef flat ranged in depth between 1m and 2m at high tide. After the drop-off the depth of the bay increased to depths exceeding 20m.

**Study organisms**

The two nudibranch species used in this study are both members of the chromodorididae superfamily. Species within this superfamily have elongate bodies with two rhinophores anteriorly that are usually lamellate. The gills are situated posteriorly on the mantle and are usually grouped in a circle about the anus. This superfamily is found throughout tropical waters and is usually brightly colored (Willan and Coleman 1984). *Risbecia imperalis* has a white base color with yellow dots spread over the mantle. The mantle fringe is black. In *R. imperalis* the most anterior portion of the mantle spreads into a spatula shape. *R. imperalis* are between 2-5 cm. *Glossodoris cincta* are larger than *R. imperalis* but are more compressed anteriorly. *G. cincta* have a base color of purple-brown, have a black-purple fringe, and their skin is often lumpy. *G. cincta* range in length between 2-6 cm.
Activity patterns

Laboratory observations

Observations of the daily activity patterns of *R. imperalis* and *G. cincta* were done on separate groups of both species in captivity. Animals were kept in two, 418 gallon cement aquaria which contained circulating ambient sea-water. Aquaria were located outdoors and received natural weather and light conditions. Two independent trials were run with each species. To recondition the aquaria between the trials, all animals and food were removed and the aquaria were flushed with sea-water for two days. For the next trial, new groups of animals and food were brought from the study site. Seven *G. cincta* were put in the aquaria for each trial to approximate densities observed in the field. Seven *R. imperalis* were also kept in each trial to standardize the experiment, although they were never found in this density in the field. Pieces of rubble, covered with the encrusting sponge *Dysidea*, bryozoans and algae, were brought from the nudibranch capture site and placed in the observation tanks to provide food alternatives. The rubble was distributed evenly in the aquarium, covering approximately 30% of the aquarium floor. All nudibranchs were observed for activity every three hours throughout a 24 hour period beginning at 00:00. They were observed within 30 minutes of the selected hours, for a ten minute period. A ten minute observation period was chosen to minimize locomotion measurement error resulting from nudibranch paths overlapping. At the beginning of the ten minute period the activity of each animal was categorized and their locations were marked on the aquarium with a wax pencil. After ten minutes elapsed, the distance crawled was measured and recorded. Observations were made for four discontinuous days.

Field observations

Individual site sampling of nudibranch activity was done by snorkeling a prescribed route that encompassed the study area. Along the route, records of nudibranch sitings were kept on an underwater slate which included, number and species of nudibranchs seen, substrate type, depth, and activity. For movement studies on the reef flat, two areas with populations of five to eight *G. cincta* were marked with buoys. At five times which were spaced evenly throughout daylight hours, the animals present in the marked areas were observed for a ten minute period. After ten minutes elapsed, the distance crawled from the starting point was measured and recorded. Observations were repeated on successive days at the same times until the movement of 21 animals had been measured. As *R. imperalis* was more rare in the field, any individuals located at the selected times were observed for activity and timed to record distance traveled in ten minutes. Data on *R. imperalis* were therefore limited to six observations at each time.

Mate preference

Pairs of each species were collected in the field and housed in aquaria in the laboratory. All pairs were kept in individual aquaria. Several pairs were collected during the same trip from areas in the field site which were separated by at least 3m. Animals were chosen as a pair if they were found within 1 cm or less of each other. Tests in the laboratory were run in a Y-maze constructed of half-circle plastic, which measured 44 cm along each of the three arms, and was 8.5 cm wide (Figure 3).

![Figure 3. Design of the Y-maze used in the nudibranch mate preference tests](image-url)
The Y-maze was filled with fresh ambient sea-water with water depth of 3.5 cm. The two top arms were blocked, 5 cm from the end, with porous paper to block any visual cues. One animal of the pair was placed in the bottom of the Y-maze, while the mate was placed at the top of one arm and an unknown nudibranch in the opposing arm. All animals were placed facing the center of the maze, 3 cm from the end of each arm. The test animal was then observed to see which animal it chose to crawl toward. Trials were run with each individual of ten pairs for both R. imperalis and G. cincta. Individuals were given up to 90 minutes to make their decision. Choice was recorded once the decision animal crawled half way up one of the top arms. Between trials the Y-maze was thoroughly scrubbed to remove the mucus trails of the previous specimens and was reconditioned by flushing with fresh sea-water for 2-3 minutes. Ten trials each were conducted with the known mate in the left arm and in the right arm. Chi-squared analyses were done to compare the results (number of choices of unknown verses known individual).

Distributional survey

Species distributions were recorded while snorkeling a prescribed route along the edge of the fringing reef while doing individual site sampling for nudibranch activities. To supplement distribution observations, measurement of nudibranch density was done by laying three transects parallel to the shore sampling certain areas of the fringing reef (See Figure 2). The first transect was 15m from shore in an area covered in sand and algae. The second transect was run 10m parallel to the edge of the drop-off of the fringing reef. The last transect was laid along the edge of the fringing reef, above depths of 2m. Along each transect 10 lm x10m plots were sampled. The samples were spaced randomly along the transect. Areas within the sample boundaries were thoroughly checked for type of substrate, number of Dysidea and number of nudibranchs.

Results

Activity patterns

Laboratory observations

Results of the laboratory observations showed both R. imperalis and G. cincta are diurnal and spend their active hours doing five activities that were operationally defined and easily distinguishable.

• Crawling. The animal moves at a relatively constant pace along the wall or on the floor of the aquarium. Animals were classified as crawling if they moved 5 cm or more during the 10 min. observation period. While crawling some animals would go up and over successive pieces of rubble without pausing. R. imperalis would often interrupt locomotion to “head wave”, after which it would sometimes change its course. In “head waving” the anterior portion of the animal is lifted off the substrate and the head is moved from side to side in a rhythmic motion. R. imperalis also often moved while “towing” another individual. When “towing”, the second animal would place its oral fold on the posterior part of the first animal’s foot.

• Sponge-feeding. The animal is hunched over the side or top of an area of Dysidea and periodically moves around the Dysidea at a rate of approximately 1 cm/5 min. This activity was almost exclusively identified in G. cincta. To feed the animal must evert its radula through its oral tube then rasp off a piece of material which is then consumed. The eversion of the radula could not be seen, so feeding was not confirmed.

• Mating. Both animals are in a fixed position with the right anterior-lateral portion of their bodies in contact. Contact of the everted penis sheaths was often clearly visible allowing mating to be confirmed without disturbing the animals. Sometimes 3-5 animals would be found in contact with each other while some were mating. All animals in this aggregate were classified as mating.

• Egg-laying. The animal extrudes an egg-mass from its genital aperture on its right side. The nudibranchs would rotate clockwise over the area for several hours until the egg-laying was completed. Animals deposited egg-masses on the wall of the aquarium or on the underneath portion of a piece of rubble. Egg laying
predominantly occurred 1-3 days after the animals were brought into the laboratory.

- Still. No motion can be detected from the animal and the pedal sole is in contact with the substrate. Throughout the night almost all animals were found to be "still" on the wall of the aquarium near the water's edge. In the night the remaining animals would be found "still" while hunched on the highest portion of a piece of rubble or on the aquarium floor. In the daytime the animals that were "still" were normally located on the walls of the aquarium.

Crawling was found to be the dominant daytime activity for *R. imperalis* in trials one and two, and for *G. cincta* in trial one (Figure 4, Figure 5). During the second trial, *G. cincta* was "feeding-sponge" for the greatest portion of the day. Other activities did not display a recognizable daily pattern. Distances moved by both species while crawling changed throughout the day (Figure 6, Figure 7).

Field observations

*R. imperalis* were normally seen alone or in pairs (with one animal "towing" the other) moving over many types of substrate. Less frequently, *R. imperalis* were seen "still" in depressions on the undersides of dead coral heads. *G. cincta* were normally seen hunched and apparently feeding on the top of *Dysidea*. Aggregations of two to five *G. cincta*, in which all animals were in contact or were within 2 cm of each other, were often seen. Egg-laying was occasionally observed in the field on the undersides of pieces of rubble. Egg-laying took between 3 and 6 hours.

Results of the movement studies on the reef flat were compared with those of both species in the laboratory aquaria (Figure 6, Figure 7). In the natural habitat both species were found to crawl less, and when they did crawl they did not move as great a distance as they did in the laboratory.
Figure 5. Distribution of daily activities of *G. cincta* monitored in tanks in the laboratory. Results are a composite of four discontinuous days of observation.

Figure 6. Mean crawling distances of *R. imperalis* throughout the day. Animals crawled a minimum of 5 cm in the ten minute observation period. Results in each of the laboratory trials and in the field survey are a composite of four days.

Figure 7. Mean crawling distances of *G. cincta* throughout the day. Animals crawled a minimum of 5 cm in the ten minute observation period. Results in each of the laboratory trials and in the field survey are a composite of four days.
Mate preference

Results in the mate preference tests showed that these species did not differentiate between known and unknown mates. Chi-squared analyses confirmed these results. Since $X^2_{comp} = 150.7$, $p<.05$ the hypothesis was rejected that almost all *R. imperalis* prefer known mates. Similarly, since $X^2_{comp} = 127.7$, $p<.05$ the hypothesis was rejected that almost all *G. cincta* prefer known mates. Both species often appeared quiescent in the Y-maze container, but would gradually begin to crawl at a slow pace. Some test animals would begin by crawling to the end of their arm of the Y-maze, while others would go partially up one top arm then reverse and go up the opposing arm. Results of both species in the Y-maze experiments are shown in Table 1.

<table>
<thead>
<tr>
<th>Mate Preference</th>
<th>Known</th>
<th>Unknown</th>
<th>No choice</th>
<th>n</th>
<th>$X^2$</th>
<th>Ave.</th>
<th>St. dev.</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>R. imperalis</em></td>
<td>35% (7)</td>
<td>65% (13)</td>
<td>0% (0)</td>
<td>20</td>
<td>150.7</td>
<td>26.4</td>
<td>18.1</td>
</tr>
<tr>
<td><em>G. cincta</em></td>
<td>35% (7)</td>
<td>60% (12)</td>
<td>5% (1)</td>
<td>20</td>
<td>127.7</td>
<td>43.9</td>
<td>19.5</td>
</tr>
</tbody>
</table>

Table 1. Y-maze experiments for mate preference with *R. imperalis* and *G. cincta*.

<table>
<thead>
<tr>
<th>Transect</th>
<th>Nudibranchs/m²</th>
<th>n</th>
<th>Nudibranch Spp.</th>
<th>Dysidea/m²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shore</td>
<td>.0</td>
<td>0</td>
<td>–</td>
<td>.08</td>
</tr>
<tr>
<td>Middle</td>
<td>.03</td>
<td>3</td>
<td><em>G. cincta</em>(3)</td>
<td>.58</td>
</tr>
<tr>
<td>Drop-off</td>
<td>.05</td>
<td>5</td>
<td><em>G. cincta</em>(3), <em>R. imp.</em>(2)</td>
<td>.158</td>
</tr>
</tbody>
</table>

Table 2. Density of nudibranchs and *Dysidea* on fringing reef.

Distributional survey

Field observations conducted on snorkel showed *G. cincta* were most abundant on patches of dead coral rubble and masses of coral which supported growth of small brown algae, bryozoans, and *Dysidea*. Most *G. cincta* were found hunched over the top of *Dysidea*, and totally exposed. Occasionally *G. cincta* were found partially or totally hidden, inside of rubble crevices. The height of the dead coral rubble substrate above the surrounding fine sand, was between 5-35 cm. The dead coral rubble patches were approximately 2 m² and the masses of dead coral, which occur on the edge of the drop-off, were of approximately 2.5 m² at the highest points. *R. imperalis* was found throughout the area moving over many types of substrate. Common species in the vicinity included the holothurid *Bohadschia argus*, several species of pomacentridae, and other fish. Both species of nudibranchs were normally found within 30m shore-ward of the drop-off of this reef, and were found more sparsely at depths along the drop-off exceeding 8 meters.

The transects of the fringing reef showed an absence of nudibranchs towards the shore and low densities along the reef flat and drop-off (Table 2). In the first transect, one predominant substrate was found which was composed of *Padina* and *Fauchea* algae. In the second transect, three substrate types were found. Four samples were laid over patches of dead coral rubble, Five samples were laid over 1m wide live coral heads, and one sample was laid over *Padina* and *Fauchea* algae. In the third transect, three substrate types
were also found. Six samples were laid over dead coral masses, two samples were laid over dead coral masses covered with filamentous algae, and two samples were covered with dead coral rubble. Fine sand was also present in all samples.

Discussion

Activity patterns

The R. imperalis and G. cincta observed in the aquaria were active only during daylight hours and were still throughout the night. There may be many reasons for this diurnal pattern in these species. These animals are aposematically colored (Rosenberg 1991). If their bright coloration warns predators of unpalatability, it would be most effective during hours of light. The predators of these nudibranchs are assumed then to not feed at night. This conclusion corresponds with the nocturnal feeding activity of many species of cryptically colored Aplysia ostitrobranchs (Susswein et al. 1983). Physiological needs may also dictate R. imperalis and G. cincta nudibranchs are inactive during the night. The sustained period of inactivity allows metabolic energy to be utilized for growth and reproductive functions.

The data collected on both species in the aquaria indicates crawling activity is considerably greater during the morning and midday when the animals were probably searching for food and mates. Crawling decreased dramatically between 15:00 and 18:00. The high divergence between movement in the field and in the aquaria may have been the result of a tank effect, in which the animals searched for food or habitat not found in the tank. Similar behavior in aquaria has been observed in Aplysia californica (Kupfermann, 1976). The animals may also have been looking for a way out of the limited aquarium space. One of the main differences between the aquaria and the field is the limited water volume. In the aquaria chemical signals from animals affect all other animals simultaneously and remain in the aquaria environment. These high concentrations of chemical signals may have stimulated greater locomotion (Susswein et al. 1983).

Feeding was observed to be the dominant activity of G. cincta in the field and in the second laboratory trial. Feeding was not observed to be a main activity of R. imperalis, possibly because the preferred food source was not in the aquaria. R. imperalis may also have been feeding in areas on the reef flat which were hidden from view.

The portion of time spent mating varied in both trials in both R. imperalis and G. cincta, but ranged between one and seven percent. In the field, mating was not distinguished from aggregation behavior, but was probably a component of this behavior. A similar aggregation behavior which was coupled with mating with many partners has been found in Aplysia (Susswein et al. 1983). The form of mating observed in both R. imperalis and G. cincta appeared to be simultaneous insemination. This contradicts mating systems theory for hermaphroditic gastropods which predicts in mating encounters the male role will be preferred and cheating is employed as a strategy to achieve this (Leonard 1991). In Aplysia brasili ana opistobranchs, egg-laying animals assume the female role while other free roaming animals take the male role (Blankenship et al. 1983). Egg-laying in this study was never observed to occur simultaneously with mating. Timing of egg-laying did not appear to exhibit a daily pattern but may have been stimulated by relocation from the reef into the aquaria. In the reef flat synchronicity of egg-laying was never observed.

The classification “Still” was found to occupy a small portion of the daytime budget of the aquaria animals in 3 out of 4 trials. In the field “still” was not observed but may have occurred during part of the time that was classified as “feeding-sponge” in G. cincta.

Mate preference

Results in the mate preference test showed R. imperalis and G. cincta exhibit no bias favoring group members when selecting mates. This result is not surprising as it is genetically advantageous in organisms to produce progeny from a diverse
gene-pool. Although familial genetic similarity does not occur within a localized group of nudibranchs, as all organisms settled from planktonic larvae, low numbers of organisms in the group can restrict genetic diversity. By having no mate bias, these species may facilitate greater diversity and adaptability to environmental changes.

Although the Y-maze test results showed no mate preference, the findings may be due to chance. Nudibranch activity in the Y-maze appeared significantly reduced from normal aquarium activity levels. Possibly, the animals were not receiving enough chemical cues from other animals to stimulate them to search. Animals were “still” for long periods (5-90+ min.), and did not go directly towards the mate choices in the top arms. In other containers when nudibranchs were transported in a group all organisms would crawl continuously. When R. imperalis groups (n = 3-6) were kept in a small container all animals would begin “towing”, forming chains of 2-6 animals. For this reason other types of containers should be tried for further tests. Employing a water circulation system may also improve the testing apparatus.

**Distributional survey**

Results of the distribution survey and transects showed that nudibranchs were absent from the landward edge of the fringing reef, but were present in low densities near and along the drop-off. Higher densities of G. cincta seemed to be correlated with the presence of Dysidea. Dysidea is the likely food source for G. cincta so this correlation is logical (Gosliner, pers. comm. 1995). Other factors that may contribute to the distribution pattern of G. cincta and R. imperalis are water depth, temperature and light penetration. The distribution observations and transects did not identify a probable food source or microhabitat for R. imperalis. When R. imperalis were sighted, they may have been migrating between areas with denser occupation and food. These microhabitats may have been inside of coral masses or inside of rubble crevices.

**Conclusion**

The results of the tests conducted indicate there is niche separation between R. imperalis and G. cincta. Activity pattern tests demonstrated that both R. imperalis and G. cincta are diurnal. The predominant daylight activities of G. cincta were crawling and feeding, while the predominant daylight activities of R. imperalis were crawling and mating. In tests with both species for preference of mate the animals appeared to not distinguish between known and unknown animals. This result may be an adaptation for producing large numbers of varied offspring which can succeed in different environmental conditions (Susswein et al. 1983). Finally, surveys of the fringing reef at the field site in Moorea, showed R. imperalis and G. cincta are found in low densities along and near to the edge of the reef flat. The presence of G. cincta may be linked to the presence of Dysidea, which is a likely food source. The food source of R. imperalis is thought to be located inside of rubble or coral head crevices.

This study investigated two apparently co-occurring species of nudibranchs in a tropical fringing reef. Several aspects related to their behavior and habitat were tested and some differences which separate the two organisms were found. The results of this study therefore give support to the competitive exclusion principle.

**Acknowledgments**

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LITERATURE CITED


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Comparison of sensory cues in *Octopus bocki* by introduction of predator and prey organisms

Andy Johnson
Department of Integrative Biology
University of California, Berkeley, CA 94720

**ABSTRACT.** *Octopus bocki* is a pygmy species of octopus that lives in coral reef assemblages on Moorea, French Polynesia in the same habitat as *Gonodactylus* stomatopods and *Pachygrapsus* crabs. Octopuses are known to have some of the most advanced sensory capabilities of all invertebrates. *O. bocki* uses these capabilities to detect crabs and stomatopods in their habitat. Relative size of these two types of organisms determines which one is the predator. *O. bocki* was exposed to test organisms (crabs and stomatopods) and the ventilation rate of the octopus was measured as an indicator of behavioral response in treatments of only visual cues, only chemical cues, and a combination of both. Size classes of large and small test organisms were set up to represent predator and prey. It was found that *O. bocki* uses visual and chemical cues in a similar proportion. Response to crabs and stomatopods was the same and there was no difference between size of the test organism.

**Introduction**

Octopuses are known to be versatile predators (Iribarne 1991). They can also become prey to other predators, such as stomatopods (Caldwell 1979). Octopuses survive in this environment by utilizing their advanced sensory organs. Vision is one sense that is very well developed (Chase and Wells 1986). The functional and structural components of the octopus eye are very similar to that of the vertebrate eye (Wells 1978). When an object is presented, octopuses can use either monocular or binocular vision, depending on the distance and orientation of the octopuses' body to the object being located (Gwyther and Muntz 1988). Once an object is located, octopuses can discriminate fine patterns on the object (Wells 1978).

Many species of octopus are nocturnal (Kayes 1974; Mather 1980), living in locations where light is minimal and vision may not perform optimally. Chemoreception is used by *Octopus* to receive stimuli from the environment in the absence of visual cues (Chase and Wells 1985). *Octopus* can distinguish between dissolved biological compounds in seawater, such as glycine and glutamic acid (Chase and Wells 1985). Extracts from crustaceans and sardines can also be detected (Boyle 1983; Wells 1963). The extent which octopuses use chemoreception is uncertain. The location of the chemoreceptors is not known, but is hypothesized to be in the arms (Chase and Wells 1985).

Although research on chemoreception and vision for some *Octopus* has been done, very little has been done with pygmy octopuses. Pygmy octopuses resemble their larger relatives, but are distinguished by smaller adult size and shorter life span (Hanlon 1983). More research is needed on the pygmy species comparing their biology to the larger species.

*Octopus bocki*, an Indo-Pacific pygmy species (Adam 1945), lives in coral reef assemblages. *O. bocki* exists in the same habitat as other benthic organisms, such as crabs, shrimp, and stomatopods. When these animals interact, the size of the organism can determine whether it is predator or prey to the other. The possession of advanced sensory organs benefit the octopus by allowing it to identify a possible competitor in the area before the competitor can react.

Research was conducted on the response of *O. bocki* to visual and chemical cues from *Gonodactylus* stomatopods and a sympatric species of *Pachygrapsus* crab. Behavioral response was measured by ventilation rate of the octopus, which has been determined to be an accurate measure
of arousal (Boyle 1983). Deviations from normal behavior were used to determine which sensory cue (vision, chemical, or a combination of the two) was more important in predator/prey interactions. The reaction of *O. bocci* was also analyzed to determine if there is a differential response to the two classes of organisms, crabs and stomatopods.

Materials and methods

Study site

The *O. bocci* that were used in this study were collected on the island of Moorea, French Polynesia in October and November of 1995 at three different sites (Figure 1). Moorea is a small, volcanic island in the tropical South Pacific. The island has a barrier reef, lagoon, and fringing reef. The first collecting site was on the barrier reef at the mouth of Cook’s Bay. The other two sites were along the west shore of Cook’s Bay, on fringing reef.

*O. bocci* lives in reef rock, but is collected most easily from pieces of loose rubble. All sites were chosen for their availability of loose rubble. *O. bocci* was extracted from the rubble by placing it in containers. The containers were allowed to sit for 10-15 minutes, while water drained out from the cracks in the rubble. The octopuses would follow the water to the bottom, where they were easily collected.

The test organisms (*Pachygrapsus* crabs and *Gonodactylus* stomatopods) were collected from the bottom of the collection container at the same time as the octopus, from rocks split open by rock hammer, and from rocks obtained by SCUBA.

Experimental procedure

The animals were kept in water tables supplied with a constant flow of sea water from Cook’s Bay at the Richard P. Gump Biological Station Lab. The *O. bocci* were sexed and measured at the time of collection and placed in small plastic cups. Water was changed every day and the octopuses were fed every other day with small crabs. The octopuses were last fed the night before the experiment and were excluded from the experiment if they did not eat. This was to standardize the hunger level among octopuses. The test organisms were measured upon collection and kept in plastic cups. Four classes were created: large crab (15-16 mm carapace width), small crab (5-8 mm carapace width), large stomatopod (34 mm body length), and small stomatopod (19-20 mm body length).
Six identical 12x6x7 inch glass aquariums were used in the experiment. The tank was divided into halves with glass plates: one half for the octopus specimen and one half for the test stimuli. The plates were sealed with silicone to avoid water contamination between the halves and each side of the tank held 1.5 liters. The *O. bocci* were allowed to acclimate to the tanks one hour before the start of the experiment. The experiments were performed at night (18:00-0:30) under red light, due to the nocturnal nature of *O. bocci*. Three treatments were created: Vision (V), Chemical (C), and Vision/Chemical (VC). Eleven octopuses were exposed randomly to each of the four classes of test organisms, performing each treatment once for this experiment (V, C, and V/C).

**Vision**

The glass divider was placed in each tank to allow the octopus to see the test organism, but excluded any physical or chemical cues. The resting rate of the octopus was measured before any tests were made. A crab or stomatopod was randomly introduced to the opposite side of the tank. *O. bocci* ventilation rate was recorded for one minute. The control for this treatment was a small or large rock (depending on the size class used) placed in the tank in the same manner as the test organisms. Resting and reaction ventilation rates were taken again.

**Chemical**

The tanks used for the chemoreception experiment were modified by placing small plastic tubes at each corner on the octopus side of the tank. Before the experiment, the test organism was placed in a cup with 150 ml of fresh seawater for 30 minutes, and then removed. Plastic tubing connected the cup to the aquarium and a ball valve controlled flow at 1ml/min. After a resting rate measurement, the water was allowed to flow into the tank and a reaction ventilation rate was immediately measured. The control was a flow of plain sea water to the system.

**Vision/Chemical**

This treatment is a combination of the vision and chemical tests. The test organism was allowed to sit for 30 minutes in the cup with 150 ml of fresh seawater. The test water was allowed to flow into the tank just as it was in the Chemical treatment and the crab or stomatopod was introduced to the tank at the same time. The control was using plain sea water and introducing an appropriately sized rock.

The resting ventilation rate was subtracted from the reaction ventilation rate to detect any change from basal behavior. The corrected ventilation rate data were analyzed by Wilcoxon matched-pairs signed ranks test and by Friedman’s two-way Analysis of Variance.

**Results**

**Behavioral observations**

Feasibility studies were conducted to record the different behaviors of *O. bocci* and to determine which behavior would be the most appropriate in a sensory cue study. The behaviors that were determined to be most useful to this study were ventilation rate, parallax, use of an arm to probe the environment before moving, color change, large increases of ventilation rate over a short time period, and expulsion of ink. The specimens of *O. bocci* reacted to the observer every time, but these reactions were minimal and each octopus was subject to the same observer in every trial.

**Vision**

The difference from control (rock) to experimental (test organism) ventilation rate was tested using a Wilcoxon matched-pairs signed rank test. There was a significant change in ventilation rate for each organism class (large crab: N=11, T=1, p<0.01; small crab: N=10, T=0, p<0.01; large stomatopod: N=11, T=4.5, 0.02>p>0.01; small stomatopod: N=10, T=3, p=0.01). The experimental ventilation rate in the Vision trials was compared to the Chemical and Vision/Chemical trials using Friedman’s two way Analysis of Variance. The range, distribution of values,
within the 75th percentile, and median of the experimental ventilation rate for each octopus was plotted for each sensory cue in (Figure 2. This test combines results from each treatment (V, C, and VC) and will be mentioned once. No significant difference was detected between the different sensory cues. The experimental ventilation rate was also used to compare the four classes of test organisms to each other, using a Friedman’s test. The results were plotted in Figure 3a in the same manner as the previous figure. No difference was detected between the four groups.

Chemical
Ventilation rates for Chemical and control stimuli were significantly different. There was a significant reaction for large stomatopods (N=11, T=7.5, 0.05>p>0.02) and small stomatopods (N=10, T=4, 0.02>p>0.01). Although no significant differences were found between small and large crabs, the trend was toward significance. Therefore, the data for large and small crabs was included in the rest of the analyses. No significant difference was found between the test organisms for the Chemical trials (Figure 3b).

Vision/Chemical
The control and chemical stimuli ventilation rate were significantly different for 3 of the 4 test organisms (small crab: N=11, T=1, p<0.01; large stomatopod: N=11, T=0, p<0.01; small stomatopod: N=11, T=8, 0.05>p>0.02). O. bocci did not react significantly to large crabs. No significant difference was found between the test organisms for the Vision/Chemical trials (Figure 3c).

Discussion
Based on the observational data taken at the beginning of the experiment, ventilation rate was the best choice for measuring the behavioral response of O. bocci. The other behaviors, such as color changing, inking, and probing the environment are just as important to octopus biology, but did not occur frequently enough to compare between test specimens. Ventilation rate, which is physically moving water through the mantle cavity, occurred at all times. It is important to note that ventilation rate only measures how much an octopus is aroused, but does not indicate the cause of the arousal. The observer in the experiment may have caused some of the increases in ventilation rate, but this was minimized in two ways. First, the observer watched in the same place for every replicate and did not move. Preliminary results showed that O. bocci tended to change color and ink only when the observer made sudden moves or startled the animals. Second, resting rates were used because this removed any observer caused increase in ventilation from the final score.

Vision in O. bocci appears to be well-developed. The octopuses reacted to test organisms as soon as they were introduced. The first behavior that was usually seen was parallax. This behavior involves moving of the head to triangulate and get a better discrimination of the distance to the object (Wells 1978; Gwyther and Muntz 1988). The increase in ventilation rate would usually follow parallax, but the behaviors are separate. Parallax was performed whenever O. bocci needed a better view of the object in question. For the Vision trials, O. bocci reacted significantly to every test organism. Although the octopuses were aroused by every test organism, no difference was found between organisms when compared to each other. Therefore, we can not tell whether the octopus considered the test organisms predator or prey. A possible scenario could be that O. bocci forages on the reef, notices another organism, and reacts. The response is a method for preparing the octopus for action.

The experiments for chemoreception suggest that a difference between the control and experimental ventilation rates exists for both classes of stomatopods, but not for crabs. O. bocci reacted less to the crabs, but the pattern was suggesting significance. One possible explanation for the decrease in response to crabs could be that O. bocci does not emit chemicals in the same proportion as stomatopods. An alternative explanation could be O. bocci cannot detect crabs with chemoreception.

O. bocci also showed an interesting behavior when it was tested for chemoreception, both in the control and in
Figure 2: Comparison of Reaction to Sensory Cues for all *O. bocki* (*n* = 11)

Box plots were used to graph data for each of the test organisms (a-d). The vertical bar is the range, the box represents 75% of the values tested, and the horizontal bar in the box is the median. No significant values were detected. Ventilation rate was corrected for resting rate, so negative values were allowed.
Figure 3: Comparison of Reaction to Test Organisms for all *O. bocki* (n=11)

Test Organisms: LC= Large Crab, SC= Small Crab, LS= Large Stomatopod, and SS= Small Stomatopod. Box Plots were used to graph data for each sensory cue (a-c). The vertical bar is the range, the box represents 75% of values tested, and the horizontal bar in the box is the median. No significant values were detected.

Ventilation Rate was corrected for resting rate, so negative values were allowed.
experimental trials. The octopus would occasionally inflate its mantle more than normal and ventilate rapidly. This would last for a short period, up to five seconds. This behavior has been noted in other members of the genus *Octopus* and been termed blowing (Chase and Wells 1986). This behavior is hypothesized to either rid the chemoreceptors of an unpleasant compound or direct a chemical towards its chemoreceptors, where it can be perceived better. *O. bocchi* seemed to perform this behavior at random times, and not as a reaction to test organisms.

*O. bocchi* did not show any kind of additive effect when both vision and chemical stimuli were tested. There was a significant reaction to all the test organisms except for large crabs. When the response to the test organisms was compared to each other for both sensory stimuli, no difference was found between the different species and size classes. The pattern is true for each of the experimental treatments. One possible explanation is that *O. bocchi* cannot distinguish between species. They can only detect the presence of an organism. Another explanation suggests *O. bocchi* can distinguish between species of test organisms, but the size difference between large and small test organisms was not large enough for *O. bocchi* to detect danger. Evidence that supports this is inkling was never observed during the experimental procedure. In contrast, inkling was observed frequently when the observer startled the octopuses because inkling is known to be a predator escape response (Wells 1978). This suggests that the octopuses never considered themselves in danger. A solution could be to use a larger size class to represent predators.

When the octopuses’ reaction to visual and chemical cues was compared to each other, no significant difference was detected. This suggests that *O. bocchi* use vision and chemoreception equally. This explanation seems plausible when you consider the habitat *O. bocchi* lives in. Vision would be useless to *O. bocchi* when hiding in a crack in the coral rubble. An approaching organism could be detected using chemoreception. Upon leaving the crack in the coral rubble, vision could detect the organism. An alternative explanation to why there is no difference between visual and chemical cues is the threshold values for detecting a cue were greatly exceeded. The octopus always react because the cues were so strong. Finer discrimination between use of sensory cues might be detected by reducing the amount of stimuli presented to the octopus. This could be accomplished by moving the visual cue farther away or diluting the chemical cue.

**Conclusion**

*Octopus bocchi* was found to use both vision and equally. When presented with different size classes of stomatopods and crabs, the octopus reacted the same to each test organism. Understanding how *O. bocchi* reacts to possible competitors in their habitat is important to learning about the general behavior of the species and allows comparison with its larger relatives. Most studies on *Octopus* have involved their learning behavior. Future studies on *O. bocchi* could compare their learning rate to *Octopus sp*. Studies such as these will be important in determining the evolutionary significance of pygmy octopuses.

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LITERATURE CITED


Establishment of *Rhizophora stylosa*, an introduced mangrove on Moorea, French Polynesia

Nicola J. Acutt
Department of Environmental Science Policy and Management
University of California at Berkeley
Berkeley CA 94720
nicijane@uclink3.berkeley.edu

ABSTRACT. The objectives of this study were to determine if *Rhizophora stylosa* is increasing its range exponentially and to examine patterns of seedling establishment at different aged stands on the island of Moorea. The distribution of *R. stylosa* was surveyed along the entire coastline of Moorea. The spread of *R. stylosa* was not found to be exponential. Three km of the coastline was found to be colonized and an additional 3 km was determined to be potentially favorable habitat. A decline in *R. stylosa* population density was observed since the last survey in 1987. The primary explanations suggested for the decline are natural distributional limits and human impacts. In regard to the natural distributional limits, patterns of establishment were studied (seedling densities at different aged stands, seedling morphology and the effect of light on seedling morphology). Seedling densities in mature, establishing and newly established stands were shown to be significantly different. The survival from seedling to juvenile stage was examined but not shown to be significantly different; however a pattern of increasing survival from seedling to juvenile stage was observed in establishing stands. Variation in seedling morphology between mature and establishing stands was observed and quantified. Leaf area and stem length were shown to be significantly different. Light, as a potential factor affecting seedling establishment, was examined experimentally for its affect on propagule and newly recruited seedling morphologies. Propagules and seedlings were collected, weighed, measured, tagged and planted in one of two experimental light conditions (sun or shade). Light levels had no significant effect on propagule and shoot morphology. However, experimental light conditions had a significant effect on already recruited seedlings from different age stands. The most dramatic change was seen in biomass and number of leaves in seedlings from mature stands placed under sun conditions. This study suggests that *R. stylosa* seedlings are phenotypically plastic during the initial stage of development. This therefore enables seedlings to adapt to the environmental conditions into which the propagule happens to be dispersed and thus increases the ability to survive in an already harsh environment. This study is thus a foundation for further evaluation of the mechanisms determining success or failure of *R. stylosa* on Moorea.

Introduction

Mangrove forests develop in the intertidal zone along tropical and subtropical coastlines and are dominated by salt and flood tolerant trees (Tomlinson 1986). These habitats play a vital ecological role in maintaining the integrity of the coastal zone. For example, mangrove fringe exerts a breakwater effect in absorbing most of the storm-driven wave energy caused by tropical storms as well as protecting the shoreline and reef system from sediment run off and erosion (Burns 1977). Mangroves also play an important role as a nursery ground for economically important fish and shrimp (Burns 1977).

The mangrove ecosystem is extremely complex and continually adjusts to the changes in the surrounding environment. As a result, mangroves exhibit a number of specialized morphological and physiological adaptations facilitating their existence in an environment that is too harsh for the vast majority of the world’s higher plant flora (Burns 1977). Adaptations include proproots and vivipory. Proproots or aerial roots are necessary for the development of an above ground part of the root system due to the anaerobic nature of swamp substrates and the need for atmospheric oxygen. Viviporous propagules are essentially a developed seedling on the parent tree. Furthermore, viviporous seedlings are a unique aspect of mangrove establishment, especially in the family Rhizophoraceae (Tomlinson 1986).

The word “mangrove” was originally used to define “trees characteristically found in tidal swamps”. The elements of true mangroves were defined by Tomlinson (1986), who also identified the five plant families making
up the major components of true mangroves. The family Rhizophoraceae is pantropical, consisting of 16 genera and 120 species (Tomlinson 1986). The genus Rhizophora is circumtropical in distribution containing 8 species (Tomlinson 1986). Rhizophora is characterized by evergreen scrubby trees, perfect flowers, and extensive aerial stilt roots known as proproots. The seeds of Rhizophora are viviporous. The detached seedling (called a propagule here) is the unit of dispersal. It is composed of a hypocotyle and a plumule (Figure 1). The plumule is composed of a pair of cotyledonary stipules that enclose the first set of leaves. These cotyledonary buds play a significant role in establishment of the seedling. Seed establishment of Rhizophora is a complex process that is still under debate, especially the mechanism of movement of the propagule from horizontal to vertical orientation as it establishes. Seedling establishment occurs when the propagule anchors into the substrate and to resists displacement by tidal fluctuations. Following considerable initial root growth, leaf expansion begins within the plumule.

The biogeographic distribution of mangroves in general is defined by the 25 degree north and south latitude lines. This zone encompasses about 75 percent of the world's coastal fringe (Burns 1977). On islands in the Pacific Ocean there is a decline in the number of species from west to east. The most mangrove development is seen on larger islands in the western and southwestern Pacific (Merrill 1945). The natural distribution of the mangrove species R. stylosa ranges from southern India to Samoa in the eastern Pacific, southward to New South Wales and westward to Indochina (Figure 2). In the western Pacific, Rhizophora stylosa is particularly vigorous and has been known to survive in extreme habitats such as coral reef and rocky coastlines (Merrill 1945).

R. stylosa was introduced to the Society Islands, including Moorea, Tahiti and Bora Bora (Taylor 1980). It has also been reported on Huahini, Tahaa and Raiatea (Woodroffe 1987 and Grenier 1994). R. stylosa was first introduced from New Caledonia to Moorea, at Vaianahae Bay as seedlings in the 1930's and then again in 1935. The purpose of introduction was to cultivate oysters on the aerial proproots. This project failed yet the mangroves established and have dispersed to new areas around the island. Cavoloc (1987) suggested that the mangroves will continue spreading exponentially around the island as there are many unoccupied favorable sites.

Since R. stylosa is an introduced species, the majority of work that has been done on Moorea has involved its impact on native fauna and flora. A majority of this work was done by Cavoloc (1987), who described the ecological consequences of mangrove colonization. Kramer (1992) identified the threat to Paspalum vaginatum and the role of herbivory. Grenier (1994) suggested that the longevity of the mangrove propagules affects potential dispersal around the island.

Mangroves, as a group, have a limited capacity for vegetative reproduction and are thus dependent on successful establishment and survival of seedlings for regeneration and spread (Tomlinson 1986). The seedling stage is a

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**Figure 1.** Rhizophora stylosa (Rhizophoraceae). Flower, fruit and seedling. Re-drawn from Tomlinson (1986).
critical phase in the life cycle of all seed plants (Harper et al. 1965). The seedling establishment phase represents a period of maximum vulnerability to physical changes in the environment (Solbrig et al. 1979). The few known mortality schedules for plant populations have demonstrated that the highest mortality occurs at the seed and seedling levels (Cook 1978). Seedling establishment is crucial for mangroves because of the harsh conditions, unstable and variable substrates and the fluctuations of the intertidal habitat (Tomlinson 1986). Establishment and survival of seedlings directly affects distribution and abundance patterns, yet no studies have been done on the establishment patterns of R. stylosa, with regard to its affect on distribution along the coastline of Moorea.

Plants in their native habitat show great variation in reproductive and vegetative functions (Schaal 1984). It has been suggested that the greater the developmental flexibility of the phenotype, the better a species can cope with environmental uncertainty without genetic reconstruction (Johnson and Cook, 1968). Differences in seedling morphology have been shown to be due to phenotypic plasticity (Bradshaw, 1965).

The objectives of this study are: (1) to determine if the spread of mangroves on Moorea is exponential as Cavoloc (1987) suggested; (2) to describe current establishment patterns and better understand the factors affecting the biology of R. stylosa during the seedling establishment phase of its life cycle. Specific questions addressed are: (1) Does the density of seedlings and juveniles vary at different aged stands? (2) Is there variation in seedling morphology? (3) What is the affect of light on seedling morphology?

My hypothesis is that variation in R. stylosa seedling morphology, after initial propagule establishment, is due to phenotypic plasticity, stimulated by different environmental conditions, specifically light availability. This study, therefore provides a foundation for further evaluation of the mechanisms determining R. stylosa seedling success or failure and potential forest spread and regeneration on Moorea.

Materials and Methods

Distribution survey

A circum-island survey of the distribution of R. stylosa on Moorea was
Distribution survey

A circum-island survey of the distribution of R. stylosa on Moorea was conducted during the months of October and November 1995. The PK (kilometer) markers along the coastal road were used as reference points. Every 500m of the coastline was surveyed for presence of R. stylosa using binoculars or walking along the shore. In areas inaccessible by truck, the coastline was surveyed from the water using a windsurfer board to paddle along the shore. At every 500m stop the substrate and coastal vegetation was ranked as either favorable, moderately favorable, or unfavorable for R. stylosa establishment. These categories were based on observations of habitats in which R. stylosa was seen to occur. Favorable habitat included Paspalum vaginatum, mud flats, brackish waters and protected areas of the lagoon with very organic muddy substrate. Moderately favorable habitat included organic, sandy type beaches and rocky shoreline with still water and algae growth such as Padina. Unfavorable habitat included stone retaining walls, conglomerate platform, fine sand or coral beaches, black sand beaches, dense coastal vegetation such as Hibiscus tiliae groves.

At sites where R. stylosa was observed, the number of trees was recorded. In stands where the number of individual trees was >150 the stand density was estimated using a 10m x 10m plot in which the number of trees were counted. The average number of trees per m² was calculated and the area of the site was measured by pacing the length and width of the stand. The number of trees per m² for the stand was then extrapolated from these measurements. Changes in stand density observed between 1987 to 1995 were classified as either increasing, decreasing, static or no longer exists (based on Cavoloc's survey numbers of 1987).

To test if the distribution of mangroves is in fact spreading as Cavoloc (1987) suggested, the expected number of trees for 1995 was calculated using an exponential model and compared to the actual number recorded in my survey. Cavoloc's data from 1933 to 1987 was fitted to an exponential model using the formula y=Ae^kt, where y=number of mangroves and t=time (time is Year-1933).

Establishment study

Seedling density: Three categories of R. stylosa stands were identified based on stand density and reproductive output. These three categories were: mature, establishing and newly established. Mature stands were characterized by dense, closed canopy and high reproductive output. Establishing stands were characterized by a more dispersed open canopy and trees of reproductive age. Newly establishing stands were characterized by sparse trees, primarily juveniles and with a few individuals of reproductive age.

Density measurements were classified into two age categories based on height. Seedlings were classed as <1m and juveniles as >1m and <3m. The density of seedlings and juveniles were recorded at six different sites of each stand category (mature, establishing and newly established stands). Seedlings and juveniles were counted by laying out a 10m x 30m plot and selecting ten random co-ordinates. A 1m x 1m quadrant was used to sample at each co-ordinate point. Only live seedlings and juveniles were included in the density counts. The plot was placed parallel to the waters edge in each site. The density of seedlings and juveniles at each stand type was analyzed using one way ANOVA. Fisher PLSD test was conducted to test variation in means.

In order to get an approximation of the survival rates from seedling to juvenile stage at each stand category, a ratio between the number of juveniles and number of seedlings at each sample was calculated. The ratio of juvenile to seedling numbers in establishing and mature stands was tested for statistical significance using students T-Test.

Variation in seedling morphology: Field observations of variation in seedling morphology at different stands were made and characterized. These observations included: leaf size, leaf color, internode length, internode width and leaf orientation. Twenty seedlings from an
and leaf area were measured. A T-Test was used to analyze the variation in leaf area and epicotyle length between seedlings from establishing and mature stands.

The effect of light on propagule morphology: The growth of ripe propagules under two experimental light conditions (sun and shade) was tested. An experiment was set up near the south end of the Gump station property, using a hibiscus grove as the shade conditions and an open lawn as the sun conditions. Fifty ripe propagules were randomly collected from the mature stand north of Haapiti. Each propagule was measured for fresh weight, hypocotyle length and epicotyle (plumule) length, then tagged and randomly assigned one of the two experimental light conditions. Propagules were placed upright in plastic containers with soil from the field site and placed in the experimental locations. The containers were filled with 500ml of sea water every day. After four weeks propagules were collected, and re-measured for fresh weight, epicotyle length, root mass, and root number. A root to shoot ratio of propagules under each light treatment was calculated and tested for significance using T-Tests.

The effect of light on newly recruited seedlings: The growth of already established seedlings from mature and establishing stands was tested under the same experimental conditions as described above. Twenty seedlings, with their first set of leaves, were collected from a mature stand and an establishing stand. Ten seedlings from each stand were placed under shade and sun treatment. After two weeks seedlings were collected and measured. The change in fresh weight and leaf number as a result of different light conditions was tested for significance using T-Tests.

Results

Distribution survey

The spread of *R. stylosa* was not found to be exponential as suggested by Cavoloc (1987). The results of the fit of Cavoloc's data to an exponential model clearly showed that the spread of mangroves is not exponential at this point in time (Figure 3). Based on Cavoloc's assumptions of exponential growth, the expected number of individuals was calculated to be approximately 6,000 in 1995. The results of my survey indicate that the actual 1995 numbers are approximately 2,000 individual adult trees.

R. *stylosa* was found to occupy approximately 3 km of the coastline at 18 sites. The extent of colonization is represented in Figure 4. In comparison to
Cavoloc’s map of distribution in 1987 and previous surveys (Figure 5) my survey results indicate that there has been a change in stand numbers. Between 1987 and 1995 nine sites have decreased in density, 7 increased, 3 stayed the same and 6 were found to no longer exist (Figure 4).

Fig 4. Change in Rhizophora stylosa stands since 1987

Of the total coastline surveyed, 11% (6 km) was identified as favorable R. stylosa habitat, 15% (9 km) moderately favorable and 74% (45 km) as unfavorable. (Figure 6 and Figure 7)

Establishment study

Seedling density: The sites where density samples were recorded are represented in Figure 8. The density of seedlings and juveniles at new, establishing and mature stands was found to be significantly different, $P=0.0083$ for seedlings and for juveniles $P=0.005$ (Figure 9). The highest density of seedlings was found in the mature stands. In mature stands, the average density of live seedlings (<1m) was 11.73/m² ranging from 3.3 to 22.7/m², the average density of juveniles (>1m) was 2.63/m² with a range from 1.1 to 5.1/m². In the establishing stand, the average number of seedlings was 2.97/m² and with a range from 0.3 to 8/m², the average density of juveniles was 0.65/m² with a range from 0.02 to 1.4/m². In the newly established stand, the average seedling density was 2.11/m² with a range from 0.7 to 3.7/m², and the average density of juveniles was 0.42/m² and with a range from 0.1 to 1/m². Fisher PLSD test found that in both cases the mean density of seedlings and juveniles at mature vs. new and mature vs. establishing was significantly different. In both juveniles and seedlings at new vs. establishing stands were not significantly different.

The ratio of survival from seedling to juvenile stage for each stand category was not shown to be significantly different from each other ($P>0.05$). The survival ratio of juvenile to seedling stage was recalculated including mortality rate data for mature and establishing stands on Moorea (unpublished data, D'Antonio 1992) (Figure 10) The survival from seedlings to juvenile stage between mature and establishing stands was again not shown to be significant ($P>0.05$). However, a strong suggestion of better success from seedling to juvenile stage was observed in establishing stands in comparison to that of the mature stands.
Figure 5. The spread of *Rhizophora stylosa* on Moorea, French Polynesia over time. Data and Maps copied from E. Cavoloc (1987).

Figure 6. Proportion of the coastline favorable to *R. stylosa* establishment on Moorea, French Polynesia.

Proportion of coastline favorable for *Rhizophora stylosa* establishment. Of the coastline surveyed, 74% was unfavorable, 15% moderately unfavorable, 11% favorable. Of the favorable area, 5.5% was unsuitable established by 4 years.

Fig 7. Potential coastline areas for *Rhizophora stylosa* establishment.
Figure 8. *Rhizophora stylosa* Density Study Site Map

Figure 9. Comparison of *R. stylosa* seedling and juvenile densities at different stand categories on Moorea, French Polynesia.

Figure 10. *Rhizophora stylosa* seedling mortality rates at different aged stands on Moorea, French Polynesia. Unpublished data from 1992 Class, courtesy of C. D’Antonio
Variation in seedling morphology:
Seedlings in mature stands were characteristically long and thin, leaves were larger and darker green in color, and the internodes were thin and extended. In comparison, seedlings of establishing stands were shorter and thicker, leaves were smaller and more yellow, internodes were short and leaf orientation was toward the sun (table 1). Variation in leaf area and internode length between seedlings from mature (shade seedlings) and seedlings from establishing stands (sun seedlings) was significantly different (T-Test P=0.009 and P=0.00006 respectively) (Figure 11).

<table>
<thead>
<tr>
<th>Stand category</th>
<th>mature stand</th>
<th>establishing stand</th>
</tr>
</thead>
<tbody>
<tr>
<td>fresh weight (g)</td>
<td>35.08</td>
<td>31.32</td>
</tr>
<tr>
<td>hypocotyle length (mm)</td>
<td>15.49</td>
<td>26.55</td>
</tr>
<tr>
<td>epicotyle length (mm)</td>
<td>10.38</td>
<td>21.18</td>
</tr>
<tr>
<td>leaf area (mm²)</td>
<td>16.78</td>
<td>2.24</td>
</tr>
</tbody>
</table>

Variation in fresh weight and hypocotyle length is not significant P>0.05. Variation in epicotyle internodes length and leaf area is highly significant P=0.009 and P=0.005 respectively.

The effect of light on propagule morphology: The average hypocotyle length was 35cm ± 1.6cm, the average plumule length was 2.5cm ± 1.4cm. The average propagule fresh weight was 32.1g± 3.5g. There was little variation in propagule establishment under the two experimental light conditions (table 2).

Within 14 days, most propagules had put out shoots, and after 4 weeks 98% had successfully rooted. There was no change in the length of the hypocotyle (plumule). The average root to shoot ratio under each treatment was not significantly different (T-Test P>0.005).

The effect of light on newly recruited seedlings: The effect of light treatments on the morphology of already recruited seedlings from the field varied. The most dramatic effect was seen in shade seedlings, from the mature stand. Almost all shade seedlings wilted or died when placed in the sun. Shade seedlings placed in shaded conditions also wilted slightly.

The effect of light on change in biomass of seedlings from the mature stand (shade seedlings), under both sun and shade treatment was significantly different (T-test, P=0.00268). Seedlings from the establishing stand (sun seedlings) showed a similar decrease in biomass under both light conditions (Figure 12 ).
The epicotyle length of shade seedlings showed an average decrease of 0.2 mm when placed in the sun and an increase of 0.1 mm in shade. Sun seedlings showed an average increase in epicotyle length of 0.91 mm when put in the shade and 0.14 mm when put in the sun.

Leaf area of shade seedlings decreased on average by 11.3 cm² in the sun. There was no change in the leaf area of the shade seedlings.

Shade seedlings in both sun and shade showed an overall decrease in number of leaves. Sun seedlings placed in the sun showed and increase in number of leaves where as those placed in the shade did not change. The affect of light on the number of leaves put on under the two different light treatments was significantly different (P>0.005) (Figure 13).

Discussion

Distribution survey

The survey of R. stylosa on Moorea indicated that the spread in distribution of mangroves is not currently exponential as was the case suggested in Cavoloc's report (1987). The exponential model using Cavoloc's data from 1987 and previous survey data showed that while it may have been increasing exponentially, now the current spread of mangrove distribution is no longer exponential. Assuming the growth of the mangrove population was exponential, then the expected population number would be approximately 6,000. In comparison to the actual numbers calculated for 1995, (approximately 2,000) it is clear that the assumption of exponential growth is not valid. In fact, the 1995 population numbers indicates a declining trend.

My study identified R. stylosa to occur on not more that 3 km of the islands coastline. I found 74% of the coast line to be unfavorable for establishment. This large percentage is primarily due to the extensive stone retaining wall along the shoreline. The moderately favorable areas comprise 15% of the coastline. Individual mangroves have been observed in these areas, yet not in any significant populations. Only 11% of the coastline was determined to be favorable for establishment, of which approximately 5.5% (3 km) has already been established (Figure 6). Only another 3 km of the
coastline is even likely to be colonized (Figure 7). My conclusions contradict those of Cavoloc (1987) who stated that *R. stylosa* occupied one fourth of the coastline, which is equivalent to 15 km. Contrary to Cavoloc’s conclusion that the spread of *R. stylosa* is likely to increase, I found that there has been decline in population numbers. On average, the stand densities at each *R. stylosa* site seem to be maintaining themselves or decreasing.

There are several possibilities to explain this trend. First, distribution is limited to a few sites on the island and second, human impacts limit distribution. I found evidence to support both of these explanations in my field observations as well as from discussions with locals. Distribution of *R. stylosa* appears to be limited primarily to shallow, sedimentous parts of the coastline where the algae *Padina* occurs. *R. stylosa* distribution is also restricted primarily to the protected south west, leeward side of the island and to areas of prolific sediment drainage. These areas are located in the vicinity of Haapiti. Although *R. stylosa* was observed establishing on the conglomerate platform at Temae and the Motus (Tiahura and Fareone) it is unlikely that these individuals will establish extensive populations under such extreme conditions.

*R. stylosa* also appears to be limited by human impacts. In my survey I found 6 sites previously identified by Cavoloc (1987) that have disappeared. In two cases there is clear evidence of human impacts. The site at Baie de Athina (PK 18.5) has been cleared and the site at Teavaro (PK 1.5) filled in for housing development (Figure 4). Personal communications with residents of Baie de Vaianae (PK 21 and 21.5), indicate that locals find *R. stylosa* a nuisance as the extensive prop roots block waterfront access and increases mosquitoes. Land owners actively destroy seedlings as they establish on their property (personal communication from Kiam Chanzi, Vaianae, 1995). Housing development on Moorea is increasing rapidly as population expands. Due to the steep mountainous topography of Moorea, people are confined to the narrow coastal belt and as more houses are constructed, more people are in closer contact with fringing coastal vegetation. Human development is a major factor which will affect not only the distribution of *R. stylosa* but also the other coastal vegetation on Moorea.

**Establishment study**

**Seedling density and survival:** Seedling and juvenile densities at different aged stands showed a pattern of increasing density with increasing age of the stands (Figure 9). Significantly different seedling densities were shown to occur in mature stands relative to establishing/newly established stands. This suggests that the gradient between establishing and new stands is small, this may be due to considerable variation in densities recorded within each stand category. Stand density variation has been show to be a natural phenomena because trees vary in their yearly reproductive status and the majority of propagules are dispersed unevenly (Clark 1993). Also, the variation in density measurements was probably influenced by the seedlings distance from adults. McKee (1994) explained 89-94% of variation in relative density of *R. mangle* seedlings as a result of distance from reproductive adults. Field observations indicate this to be especially significant in mature and establishing stands where the highest densities of seedlings occurred around the parent tree.

Statistical analysis of survival from seedling to juvenile stage at each stand category was not shown to be significantly different. These results may have been due to sampling methods which only included live seedlings in the density counts. An attempt to correct for this was undertaken by using unpublished data (D’Antonio 1992) of mortality rates for seedlings in mature and establishing stands on Moorea. This data indicated about a 20% mortality rate at establishing stands and 55% in mature stands (Figure 10). However, even with the incorporation of this data into my initial density calculations, the ratio of juvenile to seedlings was still not shown to be statistically different. Never the less, other studies have found mortality to be the highest during establishment (Mckee...
Harper, (1977) suggested that mortality increases with increasing density and has a regulating property. It is a negative feedback which acts to constrain population size within narrower limits than the range of starting densities.

The patterns of survival of *R. stylosa* from seedling to juvenile stage, suggest that survival is better in establishing stands where seedling and juvenile densities are less. In establishing stands there appears to less competition for resources such as light, space, and nutrients. The variation in seedling and juvenile numbers at different category mangrove stands suggested to me that the survival from seedlings to juvenile stage was influenced by environmental conditions, specifically the light availability created by different canopy cover in the different stands. Clarke and Allaway (1993), found seedling growth and sapling (juvenile) densities to be greater in canopy gaps. In my study a similar pattern of light availability in different stands was observed in comparison to that of light in canopy gaps. Clarke and Allaway (1993) found that recruitment from seedling to juvenile stage was restricted by light and sediment resources. The observations of my study suggested that light is a factor affecting seedling establishment and survival. Future studies on the establishment of *R. stylosa* on Moorea should however, include several other potential factors affecting seedling establishment some of which include; salinity, nutrients, sediments, herbivory, flooding (Clarke and Allaway 1993).

**Variation in seedling morphology:**

Plant morphology is concerned with external features of plants, as such, must be recognized as one of the principal factors influencing survival. It is one of the corner stones of population ecology (Bell 1984). A study of the morphology of plants considers their form and shape. A plants shape represents its ability to physically fit and expand, in spacial terms, into the environment and therefore its ability to collect light, water and nutrients in the face of competition (Bell 1984). Variation in *R. stylosa* seedling morphologies observed at different mangrove stands may be attributed to the predominant environmental conditions such as light.

Variation in leaf area and internode length of seedlings from mature and establishing stands were shown to be statistically different from each other (Figure 11). These observations suggest that between the propagule stage and juvenile stage of development *R. stylosa* seedlings are phenotypically plastic. In other words, they are able to adapt to the environmental conditions into which they were dispersed, such as shading or light intensity.

Seedlings under the shaded canopy of mature stands had a larger leaf area and thinner leaves than those in the establishing stands. This is a typical response of plants to light stress (Hale and Orcutt 1987). Increased light absorption is possible by an increased number of chloroplasts per unit leaf area (Hale and Orcutt 1987).

Field observations on variation in leaf color can be explained by the greater presence of chloroplasts in leaves from under the shade of the mature canopy in comparison to the sun-leaves from an establishing stand. Shade and sun plants vary in the concentration of chlorophyll present and in the ratio of chlorophyll a to chlorophyll b in the chloroplasts. Light absorption efficiency depends on the amount of chlorophyll per unit leaf area but remains constant over wide ranges of light intensities. The chlorophyll concentration and ratio of chlorophyll a to chlorophyll b of a plant can, however, adapt to changing environmental conditions (Hale and Orcutt 1987).

Different leaf orientation at mature and establishing stands was also noted. The leaves in the establishing stand were orientated toward the sun indicating a response to light intensity (Hale and Orcutt 1987). Leaf orientation as well as leaf color, size and thickness suggests xeromorphic adaptations. Wylie (1949) has shown that leaves developing in high light intensity show a higher degree of xeromorphy than those protected from it. Xeromorphic characteristics are present in many mangrove species and presumably form the basis of the adaptability of
different species to varying conditions of light and shade (Saenger 1982). The observations from this study therefore suggest that seedlings of *R. stylosa* in establishing stands have xeromorphic adaptations.

Field observations of the variation in morphology lead to experimental tests on the effect of light on seedling morphology.

**Effect of light on propagule morphology:** No significant effect of light was shown on the morphology of propagules (Table 2). Initial roots and root biomass of the propagules placed under experimental light conditions (sun, of and shade) were not significantly different. The root to shoot ratio was not shown to be significantly different in this study. This may be as a result of the short time for the experiment. In my experiment, after four weeks there was no change in the cotyledonary stage (plumule remained closed). This suggested that there was a period of rest or diversion of energy to ensure successful root establishment before the expansion of leaves.

**Effect of light on newly established seedlings:** Seedlings which were taken from the field, with only the first set of leaves, appeared to be already adapted to the environmental conditions, particularly the light intensity, at the location in which the propagule had dispersed. When these seedlings were removed and placed under different light conditions they were on average affected negatively, indicating a less successful ability to adapt to sudden changes in the light conditions (Figure 12 & 13).

Seedlings from the shade, when placed under different light intensities showed comparatively the most loss in total biomass (Figure 12). This suggested that these seedlings were highly sensitive to changes in light intensity. Seedlings from the establishing stand, in comparison, survived better on average and were able to withstand the changes in light conditions. Seedlings from the established stand, when placed in the sun, were the only set to significantly increase in leaf area (Figure 13). This indicated that they are best suited to those same light conditions.

My results suggested that light was a factor affecting the survival of *R. stylosa* from seedling to juvenile stage of development, primarily in the mature stands. In the establishing and newly establishing stands, light was not clearly shown to be a limiting factor to seedling establishment, yet it certainly influences their morphology. These observations support the original hypothesis that *R. stylosa*, during the seedling stage of development is phenotypically plastic. My observations on the response of seedlings from different environmental conditions in the field, to transplantation into new conditions, further suggests that in addition to being phenotypically plastic during initial stages of development, that *R. stylosa* seedlings canalize. In other words, as they grow, they lose their plasticity and are less successful in adapting to changes in the environment.

Demographic studies of plants reveal variation at many levels, both within and among species (Schaal 1984). *Rhizophora*, as a genus is considered shade intolerant (Saenger 1982). My observations, however indicate that *R. stylosa* is both shade and light tolerant, suggesting therefore demographic variability within this species. *R. stylosa* seems to have a discrete phenotypic plasticity between the stages of propagule establishment and juvenile development. This phenotypic plasticity is expressed in very different seedling morphologies, which according to my observations correspond to the environmental light conditions available at different mangrove stands. Determining the basis of demographic variability is central to an understanding of the evolutionary genetics of plant populations (Schaal 1984). Wright (1931) indicated that a single genotype may produce an array of environmentally dependent phenotypes (phenotypically plastic). The mechanism of a genotype to produce different phenotypes however, is still debated. Is the variation we see in plants within populations such as *R. stylosa* environmentally induced or is there an underlying genetic base? Perhaps the variation seen is a combination of environmentally induced phenotypic
plasticity and genotypic variation. Attempts to sort out variation in the field into genetic or environmental components will be necessary in the future in order to answer these questions. On the whole however, it is evident from this study that the greater flexibility of the *R. stylosa* phenotype, during seedling establishment, enables it to better cope with environmental uncertainty such as light and shade conditions.

**Conclusion**

Mangroves were not found to be spreading exponentially and on average a decreasing trend was observed. The distribution of *R. stylosa* was found to occupy less than 3 km of the coastline and only an additional 3 km of the coastline was identified as favorable for potential establishment. The primary explanations for this were natural distribution, as it is limited to few favorable habitats and human impacts due to increasing housing and shoreline development.

Several patterns of establishment were observed and light as a potential factor affecting these patterns was examined. Seedling densities patterns at each age category mangrove stand were found to be significantly different from each other, increasing in density with increasing age. A pattern of survival from seeding to juvenile stage was observed to be greater in establishing stands, however was not shown to be statistically significant due to limited sample size. The affect of light was shown to have significant influence on the variation in seedling morphology (leaf area, stem length) observed at different aged stands. These results suggest that following propagule establishment, the seedling stage of development is phenotypically plastic. Phenotypic plasticity enables the seedling to adapt to the particular habitat in which the propagule happens to be dispersed and there by increases its chance of survival in an already harsh environment. Results of experimental planting of already established seedlings seems to indicate that in addition to being phenotypically plastic, that *R. stylosa* seedlings canalize as they age. The question as to whether the phenotypic plasticity observed is environmental or genetically determined still remains to be answered.

The results of this study on may be influenced by the limit of time for experimental treatments. A longer experimental period would be necessary to indicate more clearly if seedlings maintain their plasticity or canalized as well as resolve if success of *R. stylosa* to juvenile stage is exclusively by light conditions or if there are other factors affecting the success of seedlings to adult trees. In addition, a field experiment of the response of *R. stylosa* seedlings to light gaps in the mature canopy, could potentially indicate if phenotypic plasticity is indeed limited to early seedling establishment or if *R. stylosa* in fact has an environmentally determined trait for phenotypic plasticity.

In conclusion, an understanding of establishment patterns of *R. stylosa* is important as it increases our knowledge of the biological dynamics of a relatively new plant to Moorea and French Polynesia.

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Behavior of the male short-tailed cricket, *Anurogryllus muticus* de Geer, affecting reproductive success in Moorea, French Polynesia

Betty Y. Lin
Department of Environmental Science Policy and Management
University of California, Berkeley 94720

ABSTRACT. Behavior of the male short-tailed crickets, *Anurogryllus muticus* (de Geer), was studied at Moorea, French Polynesia. The vegetative preference of *A. muticus* and the nightly activities of males were studied. To test whether *A. muticus* have a food preference, a laboratory feeding experiment was conducted. In the field, the number of burrows were counted and plant species around the burrows were recorded to test whether more burrows were found around *A. muticus*’s preferred food plant. To study the activities of the males, individual males were followed for approximately one hour. Two types of calling behavior, burrow-calling and wandering, were observed. The number of male and female encounters and mating occurrences were counted and compared between burrow-calling males and wandering males. The distance traveled by the wandering males was measured. The result of the vegetative preference study showed that the crickets did have a food preference, and more burrows were found around their preferred plant species. The result of study on males’ nocturnal activities showed that wandering males encountered more females than burrow-calling males. However, when comparing data on the number of successful mating encounters using Fisher’s Exact Test, burrow-calling males have greater chance of mating than wandering males. There was no correlation between distance traveled by a wandering male and the number of crickets it encountered.

Introduction

The burrowing cricket, *Anurogryllus muticus* (de Geer), is an introduced species in Moorea, French Polynesia. Its geographical distribution includes Mexico, Antilles, Florida, Louisiana, Texas, Jamaica, Puerto Rico, St. Croix, Trinidad, and Argentina (Chopard 1967; Walker 1973; Weaver and Sommers 1969). The genus *Anurogryllus*, also known as short-tailed crickets because of their vestigial ovipositors, is the only subsocial genus in the order Orthoptera in which the females practice brood care. Lee and Loher (1995) have studied *A. muticus* females’ behavior following mating and the mating strategy of the male (Lee and Loher 1993). According to Walker (1973), *A. muticus* male callings are recorded within a temperature range of 18 to 20°C. Campbell (1971) and Weaver and Sommers (1969) have studied the important economic influence of *A. muticus* on the regeneration of pines in Louisiana. Walker and Whitesell (1982) have studied the singing schedules and sites of males in Panama. Two types of calling behavior were described by Walker and Whitesell. They distinguished the male crickets as burrow-calling males or wandering males. Burrow-calling males stridulate near burrows in which they can retreat, whereas the wandering males are burrowless calling males that move from place to place. Which behavior has a greater chance of encounter with female crickets is unknown, although males with greater chance of female encounter may have greater chance of mating. Furthermore, if wandering males have greater chance of encountering females and their chance increases with increasing distance they travel, then mating chance also increases with increasing distance traveled.

Although many studies have been done on *A. muticus*, little is known about male’s activity in the field. To begin to study *A. muticus*’s activity, one must find out where these crickets live. One of the important factors determining where they live is the availability of food. Therefore, gaining an understanding to *A. muticus*’s food preference is an essential part of the study of *A. muticus*’s behaviors affecting their reproductive success.

In this study, I examine whether *A. muticus* show preference toward a particular plant species and make their burrows around it. Through field observation, I analyze and compare the
potential mating success between burrow-calling males and wandering males. I also test whether wandering males' encounter rate with females is correlated with distance traveled.

Site, Materials and Methods

Study Site

At Moorea, French Polynesia, Anurogryllus muticus are commonly found in cow pastures, gardens, road sides, and grass fields. These areas are disturbed areas where early successional R-species (Campbell 1993), or weedy species, dominate. These R-species have high reproductive rate, thus provide a constant food source for the crickets.

The study site is a grass field approximately 1125 m² located at The Gump Biological Station, Moorea at sea level (Figure 1). The field is situated between the student dormitory and the Moorea Field Laboratory (Figure 2). To the east of the grass field is Cook's Bay, and to the west is an asphalt road. Two 60 watt light bulbs in the plant drier in the lab, and one 60 watt porch light at the dormitory constantly illuminate parts of the field. The grass is kept short by mowing once a month on average.

Vegetative Preference Study

A. muticus' vegetative preference has been explored by Lee (1996 submitted). To study vegetative preference, a feeding preference test was set up in the lab, and in the field the cricket burrows were counted and the type of plant at the burrow's were recorded.

On the night of 11 October, ten crickets were collected to conduct feeding preference test. Each cricket was housed in a 100 ml glass vial with screened snap lid, and the vial was half filled with moist sand.

From 13-16 October, the crickets were fed with plants gathered from the field. Seven plant species were collected and fed to the crickets. The plants were also collected for identification. Each plant's blade or leaf was cut into 1 cm sections. A random assemblage of different plant species was fed to each of the 10 crickets once in the morning and once in the evening. Each time before a new assemblage of plants was given, the previous one was taken out and the amount of plant eaten was measured.

In the field experiment, the grass field was divided into forty-five 25 m² quadrats (Figure 3). Twenty quadrats were chosen at random and the number of cricket burrows were counted in each quadrat on 9 November 1995. A. muticus burrows typically have two openings at the ground level, or they were often covered in mounds of small soil pellets resulted from newly constructed burrow or recently enlarged burrow (Weaver and Sommer 1969; Campbell 1971). The cricket burrows in the quadrats were counted and marked with flaggings. On 10 November, different plant species in the quadrats were recorded. Data on the burrow counts and the type of plant species in the quadrats were compared to see if more burrows were found in quadrats where a particular plant species grew.

Male's Nocturnal Activity

To study where and when the male crickets sing at night and their attractiveness to the female and other male crickets, individual crickets were followed for approximately one hour each night, or until they were lost. A red headlight was used to observe the crickets. For identification, crickets were marked with correction fluid (whiteout) and numbered with a permanent marker on the pronotum.

Males were divided into two categories, burrow-calling males or wandering males based on the behavior it was practicing during the time of observation. Since the amount of time spent following a wandering male was highly variable, only males observed longer than 0.15 hour were included in the analysis. Crickets were observed between 23 October - 13 November on nineteen non-consecutive nights.

The observations were made in pairs in an effort to control variables such as weather, temperature, amount of cricket activity, etc. Twelve pairs of burrow-calling males and wandering males were
Figure 1. The Gump Biological Station, where the study takes place, is situated at the northern part of Moorea, French Polynesia.

Figure 2: Gump Station Study Site

Figure 3: Study Site
observed in nineteen non-consecutive nights. The total number of male/male encounters and the total number of male/female encounters made by the observed crickets were counted and compared by behavior type.

The burrows of the burrow-calling males and the trails of the wandering males were marked with flagging tape. The length of each trail was measured the next morning using a meter tape.

The data from twenty wandering males were analyzed. Each wandering male’s encounter with other males and females were divided by time and plotted on graphs against the distance traveled per hour.

Results

Vegetative Preference Study

The result of burrow counts showed that most burrows tend to concentrate in one area of the grass field. Data on plant species in the field showed that *Cyperus rotundus* grew in abundance in that area. No attempt was made to distinguish the male burrows from the female burrows and from the nymphal burrows, and empty burrows were not distinguished from occupied burrows.

The plant species collected at Moorea were compared with the voucher specimens at the University Herbarium, Berkeley, and identified. The seven plant species used in the feeding preference experiment were *Mimosa pudica*, *Oxalis corniculata*, *Alysicarpus vaginalis*, *Paspalum conjugatum*, *Cyperus rotundus*, and *Cynodon dactylon* (Figure 4). The crickets showed a preference among the seven experimental plants (*n*=10; ANOVA *p*≤0.0001). *Cyperus rotundus* was preferred over *Mimosa pudica* and a *Paspalum* species. No other significant preference was found between the other plant species.

Male’s Nocturnal Activity

A total of fifty-four male crickets were marked. Seventeen were resighted. Predation on crickets was observed in the field. These predators included rats, geckos, centipedes, earwigs, and ants.

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Figure 4. The result of the feeding preference test showed that *Cyperus rotundus* was preferred over *Mimosa pudica* and a *Paspalum* species. No preference was found between *C. rotundus* and other species.
No significant difference in male/male encounters per hour was found between the burrow-calling males and the wandering males (Mann-Whitney U Test p=0.21) (Figure 5).

![Figure 5. No significant difference in male/male encounters per hour was found between the burrow-calling males and the wandering males (Mann-Whitney U Test p=0.21).](image)

However, a significant difference was found in the number of male/female encounters per hour (Mann-Whitney U Test p=0.02) between the burrow-calling males and the wandering males (Figure 6).

![Figure 6. A significant difference was found in the number of male/female encounters per hour between the burrow-calling males and the wandering males (Mann-Whitney U Test p=0.02).](image)

Wandering males encountered over ten times more females than burrow-calling males.

The burrow-calling males called from thumb-print like depressions near burrows, or they called from the burrow entrance. A burrow-calling male attracted both wandering males and females. The wandering males moved from place to place, singing from different sites. A wandering male may encounter a burrow-calling male or another wandering male, as well as females that were attracted to its calling or females that it sought out. Observation in the field was made that a wandering male may wander from burrow to burrow, digging in the burrows, finding females and trying to force its way into the burrow.

Two out of two female encounters with burrow-calling males led to mating. Of the twelve observed wandering males’ encounter with females, only one out of twelve resulted in successful mating. Using Fisher’s Exact Test, the result showed that when burrow-calling males encountered females, they were more likely to have successful mating than the wandering males (p=0.038) (Statxact 3 for Windows 1995).

Observation in the field showed that a cricket practicing one calling behavior sometimes switched to the other calling behavior during another night. Sometimes crickets switched behaviors during the same night. Of the seventeen crickets resighted, four crickets switched their behavior and thirteen crickets remained faithful to their first observed calling behavior. In four other cases, burrow-calling males switched to wandering during the same night.

No correlation for the wandering males was found between the number of male/male encounters and the distance traveled (Regression p=0.9311), or between the male/female encounters and the distance traveled (Regression p=0.2650).

**Discussion**

*Vegetative Preference Study*

The result of this study suggested a wide range of food preference for *A.*
only on preferred *Cyperus rotundus* compared to *Mimosa pudica* and *Paspalum* species. The structure of these plants could have contributed to this preference because they possessed traits that may have made them an undesirable food source. *Mimosa pudica* is a sensitive and spiny plant that closes its leaves at night. *Paspalum* appeared to be a plant hard to eat because it had a tough collenchyma and white hair covering the surface of the blades. In a similar study conducted by Lee at Moorea (1996 submitted), *Alysicarpus vaginalis* was preferred as a food source. In this study, few *A. vaginalis* were found on the grass field. However, analysis showed that no preference could be determined between *Cyperus rotundus* and *Alysicarpus vaginalis*, or among *Cynodon dactylon*, *Oxalis corniculata*, and *Paspalum conjugatum*.

The results indicated that distributions of the preferred plant species and burrow abundance were correlated. Crickets apparently constructed burrows where their preferred food is readily available. Shorter distances to obtain food could reduce the chance of predation and the possibility of not finding the way back to the burrow.

**Male's Nocturnal Activity**

Male/male encounter rates between burrow-calling males and wandering males were not significantly different (Mann-Whitney U Test p=0.21), but wandering males have a significantly higher chance of encountering females than the burrow-calling males (Mann-Whitney U Test p=0.02) (Figure 5 & 6). Encounter rates were affected by the cricket behaviors. A burrow-calling male’s attractiveness is restricted to those crickets within the vicinity of its call. A wandering male broadened its range for encountering other crickets by singing from different sites and digging into female burrows. It was not clear how the wandering males found these burrows. They may come across these burrows by chance, or perhaps chemical signals were used. This wandering behavior increased the males' chance in encountering females.

On the other hand, wandering males seemed to be wasting energy digging into burrows and finding females that have already mated. Burrow-calling seemed like a more efficient behavior because females that want to mate would seek out the males. According to data analysis, burrow-calling males have a higher chance of mating when they encountered females than the wandering males (Fisher’s Exact Test p=0.038).

Despite the advantages and disadvantages of both behaviors, the males showed no preference toward one behavior over another. Based on observation, both behaviors were practiced by some individual males. This switching of behavior could be a male's response to the females' activity. At times when the females were not active, there could be more wandering males than burrow-calling males because wandering behavior could increase a male's chance of encountering females. At times when females were active, there could be more burrow-calling males because there would be no need to search for females. The amount of female activity over one night could also explain the fluctuation in male's singing activity. According to this theory, all male crickets would adopt one behavior at a given time depending on females' activity. In practice, that was neither true nor ideal. For example, when females became active, it would be theoretical for all males to adopt burrow-calling behavior. However, if all the burrows were densely concentrated in one area, it might be advantageous for a male to adopt wandering behavior and move to a less crowded area with fewer competitions. This practice would be more agreeable to the field observation, according to which both behaviors were found at any given time.

An increase in the distance traveled by the wandering males was expected to increase their chance of encountering other crickets. However, no correlation was found between the distance traveled and the number of cricket encounters. Observations seemed to indicate that the number of female encounters really depend on how active the females were at any particular night. At
times when females were not active, a wandering male may travel a long way to find one female; whereas, when the females were active, he may encounter many females while traveling the same distance.

Cricket behavior varied over the sampling period. It was observed that after a heavy rain, cricket activity would tend to increase. During the period of study from October to November, season changed from dry to wet. This could have affected the cricket activity. It was also observed that full moon seemed to have a dampening effect on cricket activity. During those few days when the moon was full and bright, crickets were very sensitive to movement on the grass field. Cricket following became a difficult task. The singing activity during that time was generally low. One possible way to overcome these over-riding factors would be to follow cricket activities over few seasons or lunar cycles. A different result might be observed under these conditions.

Results from the field experiments done on male crickets’ nocturnal activities also raised new question. It was observed that both males and females were attracted to singing males. Why were the males attracted to the singing male? Theoretically, other males may take advantage of the singing male by staying around it and mate with the females that come by. By relying on the singing male, other males could avoid attracting predators to themselves and save the costly energy of stridulation. However, field observation could not support this theory. Males that visited the singing male were often warned and chased away by the singing male. If the singing male was the weaker one of the two, it quickly moved away.

Conclusion

This study showed that crickets did have a food preference, and they constructed burrows around their preferred plant species. To further prove this, more plots of land with various plant species need to be sampled.

The study on male’s nocturnal activity showed that wandering males have greater chance of encountering females than burrow-calling males. It also showed that wandering males’ chance of encountering females did not increase with increasing distance traveled. However, data analysis indicated that when burrow-calling males encountered females, they have a higher chance of successful mating than wandering males. These results suggested that males change their behavior in response to female crickets’ activities. Future study should focus on how male crickets’ activity corresponds to female crickets’ activity.

More researches are still needed to examine male *A. muticus*’s activity in the field. More importantly, a study on female *Anurogryllus muticus*’s activity should be conducted to gain a better understanding of both male’s and female’s behaviors that may affect their reproductive success.

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LITERATURE CITED


Factors affecting the distribution of freshwater gastropods on Moorea, French Polynesia

Tina Liu
Department of Environmental Sciences, Policy and Management
University of California, Berkeley, CA 94720

ABSTRACT. The microdistribution and abundance of freshwater gastropods in relation to substrate composition, flow, and depth were investigated in three lower reach stream sites on Moorea, French Polynesia. The Neritidae and Thiaridae, consisting of 7 different species, were two important gastropod families found within these streams. Field experiments indicate species richness was higher in riffles than in runs. A stepwise multiple regression analysis demonstrated that flow was the most significant variable associated with species richness in more riffles. Flow, depth and substratum roughness were the three most significant variables associated with the number of species found in riffles. Snails were also found on small cobbles than to any other substrate type. Laboratory experiments were also conducted to examine the different microhabitat preferences among these species. The habitat preference study suggest that certain species were more commonly found utilizing certain microhabitats than others. A greater percentage of Neritina canalis and Clithon spinosa were found on the bottoms of rocks than any other microhabitat. A hydraulic stress test indicated the ability of some species to adhere to a uniform bottom under high flow conditions. Results indicate that Septaria porcellana had the tightest hold, followed by Clithon spinosa, Neritina canalis and Neritina turrita. Results from this test give indication to why certain microhabitats are utilized more than others. Factors influencing the limited geographic range of Neritina auriculata within streams were also examined. Results from the salinity bioassay suggest that once N. auriculata migrate out of saltwater influence, their tolerance of salinity decreases. Flow, depth, substrate composition and salinity are important determinants of gastropod abundance and distribution within streams. These factors give indication to how similar species coexist within similar environments.

Introduction
Environmental factors are important in determining the distribution and abundance of organisms in natural communities. Abiotic factors, such as water speed and type of substrate, are dominant factors influencing microhabitat use of some freshwater gastropods (Haynes 1988).

Neritidae and the Thiaridae are two important gastropod families found in streams and rivers of Pacific Islands (Haynes 1988). The Neritid snails possess unique life history traits characteristic of island stream fauna. These snails possess a diadromous life cycle, where they are confined to freshwater as adults, but have marine larval stages (Resh et al. 1992). The freshwater gastropod family Neritidae is thought to have evolved from the marine genus Nerita (Govindan and Natarajan 1972). They are descendants of marine forms that have colonized stream habitats (Ford and Kinzie 1982). Previous studies suggest that adaptation to freshwater has occurred several times indicating that each freshwater genus represents a separate line of evolution (Haynes 1988 and references within). Interestingly, Neritidae marine ancestors actively select microhabitats based on physical factors of light, water depth and slope (Bovbjerg 1984). The second gastropod family found within the streams is the Thiaridae (=Melaniidae), represented by two species. Members of this family are parthenogenic and viviparous.

Haynes (1988) reported a general habitat preference of these freshwater species within the Pacific Islands. Haynes (1988) noted that water speed and type of substrate were the dominant factors affecting the distribution of gastropods upstream from tidal influences. Other abiotic elements have also been identified as dominant factors affecting distribution and abundance of different animal species. Økland (1983) noted that total hardness, pH, macrovegetation in the water, and substrate were the primary factors influencing freshwater snail distribution between lakes. Rabeni and Minshail (1977) noted that substratum-detritus interaction were factors influencing insect microdistribution within streams.
Habitat selection has been described for some intertidal Neritids (Bovbjerg 1984), as well as the land snail *Theba pisana* (Hazel and Johnson 1990). However, microhabitat preference of these freshwater snails has not been studied.

The goal of this study has been to establish the most important factors influencing distribution and microhabitat use among different freshwater gastropod species by examining substrate composition, flow, depth and salinity in some species. Vermeij (1971) concluded that within a similar group of animals relevant dimensions of niche separation depend on the structure of the environment, as well as the structure of the animals themselves. It is important to examine the factors affecting the distribution of these species in order to understand how similar species coexist within related environments.

Methods and Materials

**Study Site**

Field data was collected from three lower reach stream sites during the months of October and November 1995 (Figure 1). The first study site was conducted 0.4 km upstream from the Opunohu Bay at the first road bridge located in the Opunohu Valley. Cattle grazing occurs in adjacent pastures. The canopy is dominated by Tahitian chestnut and hibiscus; taro plants are found surrounding the stream bed. The second study site was conducted in the Uufau River near Haapiti, 75 m upstream from the mouth of the river. This site was sampled at the road bridge. It is tidally influenced by saltwater intrusion. The third study site located in Afareaitu was sampled downstream from the road bridge or 0.6 km upstream from Afareaitu Bay. This stream is one of two streams that flow into the Afareaitu Bay. Study sites were selected for their high species richness as judged by preliminary visual surveys. All study sites measured less than 60 m in total length.

**Substrate Preference**

Ten quadrats were sampled within each of the riffles and runs. Within each quadrat (0.25 m²), 5 rocks were randomly chosen and the number of all attached gastropods were counted. The intermediate axis and the longest perimeter of each rock was measured (Figure 2), then it was classified as one of the following substrate types: pebble, small cobble, large cobble and boulder. Classification of substrate type based on the intermediate axis is as follows: <3 cm=granules, 3.1-6 cm=pebble, 6.1-15 cm=small cobble and 15.1-26 cm=large cobble and 26.1 and up=boulder. Surface area of rocks was calculated using the formula \( S.A. = 2.22(x)(+/-.26) \) with \( x \) being the longest perimeter of the stone (Southwood 1978).

![Figure 1. Stream sites where environmental factors and snail abundance were sampled.](image)

![Figure 2. Axes of substrate that were measured. (Figure adapted from the California Salmonid Stream Habitat Restoration Manual.)](image)
A second measure of substrate composition was conducted, using the method of Winget (1985) for calculating substratum roughness. The formula was: 

\[ KV = \left( 5C_1 + 3C_2 + C_3 \right) / 9 \]

with \( C_1 = \) most dominant substratum type, \( C_2 = \) second most dominant substratum type and \( C_3 = \) third most dominant substratum type (Statzner et al. 1988). A high substratum roughness value (\( k_v \)) indicates coarser substrate composition within streams.

**Density Counts**

Density of the different gastropod species were sampled with a surber sampler. Ten quadrat samples (0.01 m² area) were collected within each of the 7 selected habitats. Within each quadrat, all large stones were overturned, surfaces scraped and substrate bottom agitated, allowing all the snails to be washed into a collection net to be counted.

Measurements of average depth and flow were taken within each quadrat. Three flow measurements were taken by releasing a neutrally buoyant glass vial at the surface of the water and noting the time it takes to travel a distance of 1 meter. The average flow rate (m/s) was then calculated from these three measurements. A visual estimate of the substrate within each quadrat was also recorded based on the classification of substrate types: granule, pebble, small cobble, large cobble and boulder. Estimates of substrate types were used to obtain a degree of substratum roughness as described above.

Average depth, width, flow of the stream channel and salinity measurements were taken at set intervals downstream and upstream from the road bridge in the Uufau River near Haapiti.

**Laboratory Habitat Preference**

Two species were examined for microhabitat preferences in laboratory settings. Groups of 10-15 snails of *Clithon spinosa* and *Neritina canalis*, collected from the Opunohu River, were placed in freshwater aquariums. The locality and activity patterns of each snail was recorded in the morning (between 7:00-9:00 AM) and in the evening (between 5:00-8:00 PM) over a period of three days. Number of snails were counted in six different habitats: tops of tank, bottom of tanks, sides of tank, tops of rock, bottom of rock and sides of rock. Six replicate groups of *C. spinosa* and *N. canalis* were observed in the laboratory.

**Hydraulic Stress**

Experiments were conducted to test the ability of each species to adhere to a uniform bottom under high flow conditions. The amount of water flowing from a hose through a flume for two minutes was recorded. Four species were tested by placing a snail into the center of a flume and measuring the time needed for each snail to detach from the bottom surface under these high flow conditions. Each trial was terminated after two minutes; six snails of each species were tested.

**Salinity Bioassay**

To test how salinity influences the distribution and abundance of *N. auriculata*, these snails were collected from the Uufau River near Haapiti. Seventy *N. auriculata* were collected upstream, 110 m from the mouth of the river, and placed into rearing tanks. 35 were placed into tanks with freshwater; 35 were placed into tanks with seawater. Percent surviving were recorded on a daily basis for the two tanks. In the second part of the experiment, the same procedure was conducted with downstream-collected *N. auriculata*, 40 m from the river mouth. Snails were allowed to acclimate in both habitats for 48 hours before observations were made. Salinity measurements were also taken, both upstream and downstream from the road bridge.

**Statistical Analysis**

A stepwise multiple regression analysis was conducted to determine the most important independent variables associated with snail abundance and distribution. Variables included in the model were: flow, depth and substratum roughness. A one-way ANOVA followed by a Tukey's multiple comparison test, was conducted to test differences between the different microhabitats under laboratory
observations and differences between riffles and runs within each study site. A paired sample T-test was also conducted to test differences in densities among the different gastropod species between riffles and runs.

Results


Field Substrate Preference

The densities of different gastropod species were not significantly different in riffles and runs. General patterns among these species were observed, however these patterns suggest that densities of most gastropod species were higher in riffles than in runs. *N. canalis, C. spinosa, M. tuberculata* and *T. granifera* were most common in riffles, whereas *S. porcellana* was prevalent in both types of habitats (Figure 3). *N. auriculata* and *N. turrita* were not considered in this analysis due to limited sampled areas and small sample sizes, respectively.

No longitudinal pattern of snail abundance from most downstream habitat to most upstream habitat within each study site was observed in riffles. An increase in abundance upstream was observed among *N. canalis, C. spinosa* and *T. granifera* in run habitats (Figures 4 and 5), but these differences were not significantly different (p>.05).

![Figure 4](image)

![Figure 5](image)

Figure 4. Density of species in riffle habitats. Riffle #1; #2; #3 are at Opunohu, and Riffle #4; #5 are at Afareaitu. Habitats are arranged from downstream to upstream within each study reach.

Figure 5. Density of species in run habitats. Run #1; #2; #3 are at Opunohu, and Run #4; #5 are at Afareaitu. Habitats are arranged from downstream to upstream within each study reach.

Results from a step-wise multiple regression analysis suggest that certain
variables are important in determining snail abundance. Flow rate was the dominant variable influencing snail abundance in run habitats, while flow, depth and substratum roughness were all important variables associated with snail densities in riffle habitats (Table 1, attached at end of text).

The results show that depth was a significant variable associated with densities of *N. canalis* in riffle habitats (p<.05), but no variables significantly influenced densities in run habitats. Flow and depth showed negative correlations with respect to *N. canalis* densities in riffles. Depth was an important variable associated with densities of *C. spinosa* in riffles (p<.05) and no variables were significant to influence densities in runs. Depth and substratum roughness showed positive correlations to *C. spinosa* densities in riffles. No variables significantly affected *S. porcellana* densities in riffle habitats, however flow was an important variable associated with densities in run habitats (p<.05), showing a positive correlation. Flow was the most important predictor of densities in both habitats showing negative correlations with respect to densities of *M. tuberculata* and *T. granifera* (p<.05).

Results from the substrate preference study indicate that the most dominant substrate found within these habitats provided the most common substrate choice among several gastropod species. *N. canalis* and *C. spinosa* were found most frequently attached to small cobbles (Tables 2 and 3; attached at end of text). Results of the other species can also be seen in tables 2 and 3. Due to small sample sizes, a clear pattern in substrate preference among the other species was not observed. However, a general habitat preference in relation to substrate composition and locality within the stream has been observed (Figure 6).

**FIGURE 6**. Distribution of gastropods across a stream showing the different habitats of each species. 1. *Thiara granifera*; 2. *M. tuberculata*; 3. *N. canalis*; 4. *S. porcellana*; 5. *C. spinosa*; 6. *N. turrita*; 7. *N. auriculata*. Figure was adapted from (Haynes, 1988).
Laboratory Habitat Preference

C. spinosa and N. canalis demonstrated significant microhabitat differences during the day and night. C. spinosa differed significantly in its utilization of all six microhabitats during the day (p<0.05) and during the night (p<0.05) using a one-way ANOVA followed by a Tukey’s Test. A higher percentage of C. spinosa were located on the bottoms of the rock during both observed times and greater movement was detected during the night (Figure 7).

N. canalis also differed significantly in its utilization of all six microhabitats during the day (p<0.05) and during the night (p<0.05) using a one-way ANOVA followed by a Tukey’s Test. They were more frequently found on the bottoms of rocks during the day, though more activity was observed during the night as other microhabitats were also being utilized (Figure 8).
Hydraulic Stress

There was no statistical difference among the four species (p > .05), although strong patterns were observed (p = 0.06). S. porcellana had the tightest hold with an average time of 120 seconds. C. spinosa, N. canalis and N. turrita adhered to the bottom surface with times averaging from 94 seconds, 59 seconds and 61 seconds, respectively (Figure 9).

Salinity Bioassay

100% of upstream collected N. auriculata survived freshwater rearings and upstream N. auriculata resulted in a 97% survival rate in seawater rearings after 144 hours (Table 4, attached at end of text). The experiment was replicated a second time with a 100% freshwater survivorship and a 77% survivorship in saltwater (Table 5, attached at end of text). This experiment was conducted with downstream collected N. auriculata as well. The survival rate for seawater rearings and freshwater rearings resulted in similar survivorship after 144 hours: 86% and 89%, respectively (Table 6, attached at end of text).

Discussion

Patterns of microhabitat use

Neritina canalis is found in the lower and upper reaches of the stream. Haynes (1988) found these species on the sides or on the under sides of rocks. Resh et al. (1990) found this species on boulders in fast moving waters. In this study, I found them occurring in faster flowing waters (riffles) on the sides or under the sides of small cobbles. Laboratory experiments suggest that during the day, a higher percentage of this species is found attached to the bottoms of rocks. These results correlate with my field observations. The utilization of other microhabitats suggest that more activity is occurring during the night. Schneider and Frost (1986) observed that under low flow conditions, tropical freshwater neritid snails were capable of being dislodged. Finding refuge against the strong downstream current can further explain their occurrence on the bottoms of rocks. The hydraulic stress test also indicated that N. canalis does not have a great ability to hold on to an even surface under high flow conditions (t = 69 seconds). To avoid being dislodged and swept downstream, this species may find refuge under rocks as it migrates upstream.

Neritina turrita is confined to the lower reaches of the stream. Haynes (1985) found this species occurring in mud substrates in slower moving currents. Resh et al. (1990) found it attached to boulders and smaller rocks. Although this species was rarely sampled with the methods used, some habitat preferences were noticed in the field. They were found attached to the tops of boulders in the side regions of the stream. The side regions of the stream can be characterized by slower moving waters, even in faster moving habitats. Laboratory experiments showed that a high percentage of N. turrita were found at the tops of the tanks. Despite its motility in laboratory rearings, it has a restricted distribution within stream reaches as observed in the field as well (Resh 1990). The hydraulic stress test indicated a weak ability to hold on to an even bottom surface (t = 41 seconds). Therefore, this weak holding ability may explain their restriction to slower moving waters.
Clithon spinosa is found throughout the lower reaches of the stream. Haynes (1985) reported this species on rocks in faster moving currents. In this study, I found this species on the bottoms of rocks in faster moving waters (riffles). Laboratory experiments suggest that they occur most frequently under or on the sides of rocks. A high percentage of C. spinosa were found at the bottoms of the tank as well. They appear to be more active during the night than the day. This nocturnal activity explains why a greater percentage are located on the bottoms of the tank and the sides of the tank when compared to the microhabitats being utilized during the day. Results from the hydraulic stress test indicate that they attach tightly to a uniform surface \((t=94\) seconds). However, they would usually fall off rocks as they were being lifted out of the water (personal observations). Density counts suggest that a greater number of C. spinosa were found within riffle habitats. Despite this weaker ability to hold on to even surfaces under high flow conditions, they have adapted to living in this type of habitat with the use of the bottoms of rocks as a refuge from accidentally being swept downstream. They have adapted to these high flow conditions, by actively selecting their microhabitats.

Septaria porcellana is found in all reaches of the stream. Haynes (1988) reported an ability to live on the upper surfaces, as well as the sides of rocks. Resh et al. (1990) found it attached to boulders in faster flowing waters. I found them occurring in faster moving waters (riffles) on the upper surfaces, as well as the sides of rocks. Results from the habitat preference study indicate that they are found in both types of habitats. They possess a structural adaptive strategy that permits them to hold on to surfaces very tightly (Vermeij 1971). They have an adaptive advantage over other species that permits them to live in faster flowing waters. Hydraulic stress experiments indicate the effectiveness of their ability to hold on tightly \((t=120\) seconds) because they were never dislodged. This species was the least motile one in the laboratory rearings.

Melanoides tuberculata and Thiarara granifera were most common where granules or finer substrate composition made up the dominant substrate type. A few were found attached to the sides of small cobbles as well (personal observation). They are found in both faster and slower moving waters and higher densities were found in faster flowing waters (riffles). However, Dudgeon (1989) found this species occurring most frequently in slower moving or standing waters. The hydraulic stress test was not conducted on these two species due to their substrate preference within streams (=granules).

Neritina auriculata was only sampled at the Uufau River near Haapiti and found most abundantly in the downstream-most riffle and run habitats. This species was only found in the lower reaches of the stream where salt water influences freshwater habitats. They were located on all substrate types within the stream (personal observation). Higher numbers of N. auriculata were found where few other species were observed. Animals and plants vary in their ability to tolerate salinity (Ford and Kinzie 1982). Perhaps this tolerance will explain the limited range of N. auriculata and the disappearance of other gastropod species. Short-term survivorship experiments have been conducted with N. canalis, N. turrita, C. spinosa and S. porcellana, indicating lower tolerances to seawater rearings (Resh, unpublished data).

Under high-base flow conditions, salinity levels start to decrease as one approaches the end of run #1 or 35 m upstream from the bridge. This boundary also defines the uppermost limit of N. auriculata. Beyond this boundary, numbers of N. auriculata start to drop immediately. It is interesting to note how this change in water composition corresponds to this sudden drop in numbers of N. auriculata and the appearance of other species as well (Table 7). Under low-base flow conditions, salinity levels start to decrease as we approach the end of run #1 or 35 m upstream from the bridge as well (Table 8).

The survivorship of upstream-collected N. auriculata under saltwater and freshwater conditions should be taken into
consideration when analyzing distribution of this species. These snails were collected in habitats with low conductivity measurements. The results indicating high survivorship in saltwater habitats are truly remarkable. Lower survivorship percentages were observed for those *N. auriculata* collected downstream from the bridge. The snails in this reach of the stream are subject to constant changes in water composition, with saltwater and freshwater influencing tolerance levels. Under high-base flow conditions, saline waters reach further upstream, thus snails found in less saline waters (just above the road bridge) are subject to changes in water composition as well. The snails in this reach display an adaptation to living in both freshwater and saltwater habitats. The snails further upstream are not subject to this constant influx of saline waters during high tide conditions, thus their ability to survive in saline waters decreases.

*Future Study*

The present study did not differentiate between instream and surface flow/substratum roughness estimates because I assumed that these measurements would be similar. However, taking instream flow rates versus surface flow rates may in effect have provided different results and deserve further study.

We know little about the life history of the larval stage of these snails. It would be very interesting to study the migration and settling patterns during the time they develop into small snails and migrate upstream. It is not known whether they stay within that same reach of the mouth of the river or travel with the wind to other streams. This may explain differences in shell coloration found within the same species.

Another interesting study would be to examine upstream migration patterns of *C. spinosa*. Unique behaviors in which *C. spinosa* were seen travelling unidirectionally, in a straight line, along the sides of the tank, were observed. This behavior has also been noted in relation to spiny lobsters migrating in single file between their summer homes in shallow waters and their winter homes in deeper waters (Herrnkind and Kanciruk 1978).

Other important considerations when conducting a microhabitat study are factors governing species abundance/composition across spatial scales; within streams, among streams and between habitats (Crowl and Schnell 1990). Results from this study may be affected by the spatial scales that were used.

It would also be interesting to conduct a hydraulic stress test on *N. auriculata* in order to determine if their ability to hold on to a substrate is an important factor limiting the distribution of this species.

**Conclusion**

The results from this study suggest that the distribution and abundance of freshwater snails are influenced by flow, depth and substrate composition. Salinity is also an important factor influencing distribution and abundance of some species. The utilization of certain microhabitats within the stream influence this distribution as well. These factors not only govern behavioral patterns observed among these snails, but furthers our understanding of how similar species can coexist within similar environments.

**Acknowledgments**

I would like to extend thanks to Dr. Jere Lipps, Dr. Brent Mishler, Dr. Roy Caldwell, Dr. William Alevizon, Dr. Cherie Semans, Pam Jutte and Ferenc de Szalay for their help and guidance throughout this project. My warmest and sincerest gratitude goes out to Dr. Vincent H. Resh for his overwhelming enthusiasm, advice, encouragement and most importantly his belief in me throughout this whole process! Thanks to you all and to the class of 1995.

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**TABLE 1-8** are attached on the following pages.
TABLE 1. Results of stepwise multiple regression analysis on flow, depth and substratum roughness (independent variables) and abundance of snails (dependent variables). Coefficient values indicate the relationship between each variable with respect to density. Blanks (-) in table suggest that no variables were statistically significant. Variables with * are statistically significant. However, flow and roughness variables were not statistically significant because p > 0.05 for N. canalis and C. spinosa in riffles.
TABLE 2. Results indicate the numbers of each species found attached to different substrate types in riffles.

<table>
<thead>
<tr>
<th>RIFFLES</th>
<th>N. canalis</th>
<th>N. turrita</th>
<th>C. spinosa</th>
<th>S. porcellana</th>
<th>M. tuberculata</th>
<th>T. granifera</th>
<th>N. auriculata</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pebble</td>
<td>8</td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>79</td>
</tr>
<tr>
<td>Small Cobble</td>
<td>68</td>
<td>1</td>
<td>26</td>
<td>2</td>
<td>4</td>
<td>0</td>
<td>262</td>
</tr>
<tr>
<td>Large Cobble</td>
<td>22</td>
<td>0</td>
<td>4</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>30</td>
</tr>
<tr>
<td>Boulder</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

TABLE 3. Results indicate the numbers of each species found attached to different substrate types in runs.

<table>
<thead>
<tr>
<th>RUNS</th>
<th>N. canalis</th>
<th>N. turrita</th>
<th>C. spinosa</th>
<th>S. porcellana</th>
<th>M. tuberculata</th>
<th>T. granifera</th>
<th>N. auriculata</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pebble</td>
<td>5</td>
<td>0</td>
<td>3</td>
<td>9</td>
<td>0</td>
<td>0</td>
<td>79</td>
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<tr>
<td>Small Cobble</td>
<td>41</td>
<td>0</td>
<td>36</td>
<td>11</td>
<td>0</td>
<td>0</td>
<td>147</td>
</tr>
<tr>
<td>Large Cobble</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>6</td>
<td>0</td>
<td>0</td>
<td>37</td>
</tr>
<tr>
<td>Boulder</td>
<td>2</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
TABLE 4. Short term % survivorship of upstream *N. auriculata* in freshwater and seawater rearings. *N. auriculata* were collected in the Uufau River near Haapiti. (Replicate #1)

<table>
<thead>
<tr>
<th>Species</th>
<th><em>N. auriculata</em></th>
<th><em>N. auriculata</em></th>
</tr>
</thead>
<tbody>
<tr>
<td># Individuals</td>
<td>36</td>
<td>35</td>
</tr>
<tr>
<td>Habitat</td>
<td>Freshwater</td>
<td>Saltwater</td>
</tr>
<tr>
<td>48 hrs</td>
<td>100%</td>
<td>100%</td>
</tr>
<tr>
<td>56 hrs</td>
<td>100%</td>
<td>97%</td>
</tr>
<tr>
<td>73 hrs</td>
<td>100%</td>
<td>97%</td>
</tr>
<tr>
<td>96 hrs</td>
<td>100%</td>
<td>97%</td>
</tr>
<tr>
<td>125 hrs</td>
<td>100%</td>
<td>97%</td>
</tr>
<tr>
<td>144 hrs</td>
<td>100%</td>
<td>97%</td>
</tr>
</tbody>
</table>

TABLE 5. Short term % survivorship of upstream *N. auriculata* in freshwater and seawater rearings. *N. auriculata* were collected in the Uufau River near Haapiti. (Replicate #2)

<table>
<thead>
<tr>
<th>Species</th>
<th><em>N. auriculata</em></th>
<th><em>N. auriculata</em></th>
</tr>
</thead>
<tbody>
<tr>
<td># Individuals</td>
<td>25</td>
<td>25</td>
</tr>
<tr>
<td>Habitat</td>
<td>Freshwater</td>
<td>Saltwater</td>
</tr>
<tr>
<td>48 hrs</td>
<td>100%</td>
<td>100%</td>
</tr>
<tr>
<td>56 hrs</td>
<td>100%</td>
<td>88%</td>
</tr>
<tr>
<td>73 hrs</td>
<td>100%</td>
<td>88%</td>
</tr>
<tr>
<td>96 hrs</td>
<td>100%</td>
<td>88%</td>
</tr>
<tr>
<td>125 hrs</td>
<td>100%</td>
<td>77%</td>
</tr>
<tr>
<td>144 hrs</td>
<td>100%</td>
<td>77%</td>
</tr>
</tbody>
</table>

TABLE 6. Short term % survivorship of downstream *N. auriculata* in freshwater and seawater rearings. *N. auriculata* were collected in the Uufau River near Haapiti. (Replicate #1)

<table>
<thead>
<tr>
<th>Species</th>
<th><em>N. auriculata</em></th>
<th><em>N. auriculata</em></th>
</tr>
</thead>
<tbody>
<tr>
<td># Individuals</td>
<td>25</td>
<td>25</td>
</tr>
<tr>
<td>Habitat</td>
<td>Freshwater</td>
<td>Saltwater</td>
</tr>
<tr>
<td>48 hrs</td>
<td>97%</td>
<td>100%</td>
</tr>
<tr>
<td>56 hrs</td>
<td>97%</td>
<td>94%</td>
</tr>
<tr>
<td>73 hrs</td>
<td>94%</td>
<td>91%</td>
</tr>
<tr>
<td>96 hrs</td>
<td>91%</td>
<td>91%</td>
</tr>
<tr>
<td>125 hrs</td>
<td>89%</td>
<td>89%</td>
</tr>
<tr>
<td>144 hrs</td>
<td>86%</td>
<td>89%</td>
</tr>
<tr>
<td>Distance (m)</td>
<td>Location from bridge (upstream/downstream)</td>
<td>High Tide Salinity (microsiemens)</td>
</tr>
<tr>
<td>-------------</td>
<td>------------------------------------------</td>
<td>----------------------------------</td>
</tr>
<tr>
<td>35</td>
<td>downstream</td>
<td>10000</td>
</tr>
<tr>
<td>25</td>
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<td>10000</td>
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<tr>
<td>5</td>
<td>downstream</td>
<td>1400</td>
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<tr>
<td>5</td>
<td>upstream</td>
<td>1100</td>
</tr>
<tr>
<td>15</td>
<td>upstream</td>
<td>200</td>
</tr>
<tr>
<td>25</td>
<td>upstream</td>
<td>200</td>
</tr>
<tr>
<td>35</td>
<td>upstream</td>
<td>200</td>
</tr>
<tr>
<td>45</td>
<td>upstream</td>
<td>200</td>
</tr>
<tr>
<td>55</td>
<td>upstream</td>
<td>100</td>
</tr>
</tbody>
</table>

**TABLE 7.** High tide base flow characteristics of the Uufau River near Haapiti, Moorea, French Polynesia (October 28, 1995). The length of the bridge = 10.5 m.

<table>
<thead>
<tr>
<th>Distance (m)</th>
<th>Location from bridge (upstream/downstream)</th>
<th>Low Tide Salinity (microsiemens)</th>
<th>Depth (m)</th>
<th>Width (m)</th>
<th>Flow (m/s)</th>
<th>Discharge (m³/s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>35</td>
<td>downstream</td>
<td>10000</td>
<td>0.32</td>
<td>8.97</td>
<td>0.15</td>
<td>0.315744</td>
</tr>
<tr>
<td>25</td>
<td>downstream</td>
<td>10000</td>
<td>0.22</td>
<td>8.97</td>
<td>0.05</td>
<td>0.09867</td>
</tr>
<tr>
<td>15</td>
<td>downstream</td>
<td>10000</td>
<td>0.2</td>
<td>8.97</td>
<td>0.15(--)</td>
<td>0.2691(--)</td>
</tr>
<tr>
<td>5</td>
<td>downstream</td>
<td>800</td>
<td>0.18</td>
<td>8.11(--)</td>
<td>0.15(--)</td>
<td>0.17424(--)</td>
</tr>
<tr>
<td>5</td>
<td>upstream</td>
<td>1300</td>
<td>0.09</td>
<td>2.7</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>15</td>
<td>upstream</td>
<td>200</td>
<td>0.25</td>
<td>3.27</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>25</td>
<td>upstream</td>
<td>200</td>
<td>0.34</td>
<td>2.6</td>
<td>0</td>
<td>0.1309</td>
</tr>
<tr>
<td>35</td>
<td>upstream</td>
<td>100</td>
<td>0.08</td>
<td>3.5</td>
<td>0.11</td>
<td>0.0308</td>
</tr>
<tr>
<td>45</td>
<td>upstream</td>
<td>200</td>
<td>0.28</td>
<td>2.4</td>
<td>0.09</td>
<td>0.06048</td>
</tr>
<tr>
<td>55</td>
<td>upstream</td>
<td>100</td>
<td>0.08</td>
<td>2.2</td>
<td>0.21</td>
<td>0.03696</td>
</tr>
</tbody>
</table>

**TABLE 8.** Low tide base flow characteristics of the Uufau River near Haapiti, Moorea, French Polynesia (October 28, 1995). The length of the bridge = 10.5 m.
LITERATURE CITED


Succession of epiphyllous liverworts and lichens in the Opunohu Valley of Moorea, French Polynesia

Peter A. Elston
Department of Integrative Biology
University of California, Berkeley CA 94720

ABSTRACT. Epiphyllous communities occur in tropical rain forest environments worldwide. The mesocosm of the epiphyll community is ephemeral — the life cycles and growth of epiphyll species are limited by the age of the host plant leaves. The colonization, development and competitive interaction patterns of epiphyllous communities on the new habitats of young leaves has previously been shown to conform to successional models. A study was made of epiphyll growth on Inocarpus fagiferus leaves in the Opunohu Valley of Moorea, French Polynesia. Percent cover of epiphyll species was estimated, species richness assessed, species diversity calculated and reproductive status determined. Statistical analyses of the data were performed and the significance of correlations between leaf age and various characteristics of the epiphyllous community are discussed in the context of successional patterns. Suggestions for possible future studies of this microecology are made.

Introduction

Bryophytes, lichens, algae and other organisms that grow on the upper surface of living leaves are known as epiphyllae. Epiphyllous communities are found almost exclusively in tropical environments, occurring worldwide in lowland and montane rain forests with high atmospheric humidity (Richards 1984; Olarinmoye 1974). The requirement of a highly humid environment tends to restrict epiphyllous communities to the shady understory layer of the forest, up to three meters from the ground, often in proximity to streams. (Pocs 1982). For some taxa (liverworts), cover has been shown to increase with increased rainfall (Coley et al. 1993) whereas other taxa (lichens) appear to be more successful in drier areas (Pocs 1982). In addition to micro-climatic conditions, the nature of the leaf substrate also affects the distribution of epiphyllous communities. A stable surface and long life-span are essential characteristics of host leaves, because epiphylls occur primarily on evergreen host species with hard, smooth leaves (Pocs 1982; Richards 1984).

Foliose liverworts, primarily of the family Lejeuneaceae, lichens, macroscopic algae and mosses are the most common species found in the epiphyllous mesocosm. The “phyllosphere” (Ruinen 1961) is a complex and complete ecosystem, containing, in addition to plant species, populations of microorganisms (including nitrogen-fixing cyanobacteria) and small invertebrates, such as mites, nematode worms, spiders and insect larvae (Richards 1984; Ruinen 1961; Pocs 1982). Comparative biogeographical data of epiphyllous taxa are sparse. Pocs (1978, in Richards 1984) places the epiphyllous liverwort species richness of Africa at 164, and comparisons of representative epiphyllous taxa suggest that tropical America is about 1.5 times as rich, and Asia twice as rich, as Africa.

The effect of epiphyllous communities on the host plant has been discussed, though not extensively tested, as an important component of the ecology of tropical rainforests. Epiphyllous lichens and algae can damage the cuticle of host leaves and the rhizoids of at least one liverwort species penetrate the leaf cuticle and may function hemi-parasitically (Berrie 1975). However, the amount of water and nutrients that could be obtained by a hemi-parasitic epiphyll from the host leaf is probably negligible (Pocs 1982). Water retention by epiphyll cover may increase the chance of infection of the host leaf by pathogens (Gregory 1971). The negative effect of epiphyll growth on the photosynthetic capacity of the host leaf has also been considered, though no clear determination has been made. Epiphyllous
cover can significantly reduce the photosynthesis of some plant species (Sand-Jensen 1977; Coley et al. 1993), but have little effect on others (Roskoski 1981). In contrast, epiphyll communities may play an important beneficial role in rainforest ecology as "nutrient scavengers" and nitrogen contributors (Ruinen 1961; Olarinmoye 1974; Roskoski 1981; Richards 1984). Epiphyllous liverworts may also provide a defense against leaf herbivory, as demonstrated in Mueller and Wolf-Mueller's (1991) study of leaf-cutter ants.

Successional patterns of colonization and competition in the phyllosphere have also been discussed. Richards (1932) reported successional changes in the growth of epiphyllous liverworts in Guyana and observed an eventual climax state dominated by one species. Other investigators have found a "settling rhythm" in the relative abundance of liverwort species during colonization of leaves, while others observed no such pattern (Olarinmoye 1975).

Both interspecific and intraspecific competition have been reported in epiphyll communities (Olarinmoye 1975). Among liverwort species, competition may be allelopathic (Winkler 1967, in Richards 1984) and often involves the overgrowth of one species by another. Liverworts and lichens are frequent competitors (Olarinmoye 1975). A clear negative correlation between liverwort cover and lichen cover has been demonstrated in one case where liverwort species commonly overgrow lichens (Coley, et al., 1993). Liverworts are always at a competitive advantage over lichens because of overgrowth (Coley et al. 1993), but apparent allelopathic exclusion of liverworts by lichens has been observed (personal observation).

The number of epiphyllous species present on a single leaf can vary considerably, but has been found to increase with leaf age (Richards 1984; Pocs 1977, in Richards 1984). Further, epiphyll cover also increases with time (Richards 1932; Roskoski 1981; Coley, et al. 1993). Different epiphyll species were seen to have different frequencies on successive leaves in Winkler's study (1967, in Richards 1984). The epiphyllous species involved in the initial colonization of new leaves may be solely dependent on which species' propagules reach the new habitat first, as in some cases where no particular colonizing species could be identified (Olarinmoye 1975). Winkler's study (1967, in Richards 1984) in El Salvador did identify particular species as consistent primary colonizers (obligate epiphylls) and others as secondary colonizers (facultative epiphylls).

Succession is a well-documented, but highly complex, ecological process and has been elucidated in a variety of ecosystems with vastly different taxonomic compositions and spatio-temporal scales, from the successional changes of tree species in forests, measured in centuries, to those of algal and mollusc species in intertidal zones, measured in decades, to those of bacteria on agar plates, measured in days. Some salient patterns in succession include increasing cover, biomass and abundance of individual species over time and increasing species richness and diversity over time. These factors are commonly observed to reach an equilibrium state and often decrease in the terminal stage of the succession process. Changes in species composition (via the mechanisms of competition, facilitation, inhibition, replacement, etc.) over time are also important aspects of succession (Smith 1980; Farrell 1991).

Epiphyllous communities, because of their small size and the presence of different-aged substrates in proximity, provide a good opportunity for investigation of successional processes. The present study is one of only a handful of quantitative studies of epiphyllae undertaken, despite their potentially important role in the tropical rainforest ecosystem (Roskoski 1981), their poorly understood microecological dynamics and their uniquely ephemeral nature.

On the island of Moorea, French Polynesia, epiphyllae were observed in both lowland and montane rainforest habitats, most commonly and abundantly in the former. In some areas, and on at least one host species, variations in the cover and
species composition of epiphyllous communities among successive leaves on a branch was noted. The discontinuous temporal sequence represented by a series of leaves on a branch will hereafter be referred to as "relative time."

This study addressed the question: Do variations in the growth of epiphyllous communities on Moorea demonstrate successional patterns over relative time? In particular, the working hypotheses were that total epiphyllous cover, species richness and species diversity all increase linearly in relation to relative leaf age, as understood in larger scale systems, such as forests. Furthermore, I hypothesized that the cover of individual epiphyllous species varies according to a pattern of competitive exclusion. The null hypothesis in this case was that no patterns of variation in relation to leaf age are present. Alternatively, distinct patterns of variation might indeed be present but affected by a combination of factors, including leaf age, or a single factor other than the leaf age.

Materials and Methods

Study site

The study site was located on the Three Cocos Trail in the Opunohu Valley of Moorea, approximately 1 km from the trailhead, at the second stream crossing (Figure 1). This site was chosen because there I found the largest assemblage of epiphyll species of various sites surveyed around the island. The site is located in a deep ravine along the Riviere Opunohu, at approximately 100 meters of elevation. The ravine is approximately 70 to 80 meters deep, with sides of angle 60 to 70 degrees. At the bottom of the ravine is a flat floor, 50 to 70 meters wide, flanking the stream. The vegetation is lowland tropical rainforest, with dense canopy cover, dominated by the Tahitian Chestnut tree, Inocarpus fagiferus. Hibiscus tilaceus is a minor tree species at the site. The vegetation of the understory is sparse, consisting primarily of the large fern, Angiopteris erecta, I. fagiferus seedlings, and the shrub Syzygium malaccense.

Sample collection

Differences in epiphyllous cover and species richness were observed among the leaves of I. fagiferus branches. Although periodicity of leaf production was not studied, it was determined that leaves at the apical end of branches (or sub-branches) are younger than leaves located nearer the base of branches because the growth of I. fagiferus leaves occurs from a terminal bud (Mishler, personal communication). Thus, only relative time can be inferred from a series of leaves on a branch or sub-branch. In order to test the hypothesis of successional change over time in the epiphyllous communities present at this site, a series of leaves on a branch, representing a temporal scale, was identified as an appropriate sample unit.

For the purposes of this study, a sample series consisted of the first nine leaves (at least 75% intact) from a single branch or sub-branch of I. fagiferus. Sample series were collected at the study site within a roughly 30 meter X 50 meter area. This area was located along the flat floor of the ravine, downstream of the intersection of trail and stream. Ten sample series were collected randomly from the study site: Ten coordinate pairs were selected from a random number table, each coordinate pair was paced out in the collection area and the nearest suitable
branch from the coordinate point was collected. I collected sample series from branches that were located one to three meters above the ground. Series were collected between 28 October and 16 November 1995.

Data collection

I. fagiferus leaf samples were surveyed using a dissecting microscope and a wire grid (grid square = 6 mm X 6 mm). Surveys consisted of four 10-grid samples (one randomly selected in each quarter of the leaf).

Percent cover of each species was visually estimated to the nearest 5%. The three most common liverwort species were identified to genus, as follows: Leptolejeunea sp., Drepanolejeunea sp., and Diplasiolejeunea sp. Taxonomic identification of the lichen species proved to be difficult, so species were instead designated by abbreviations, as follows: La through Ld (four lichen species). For small cover estimates (<25%), a smaller grid was used (grid square = 1 mm X 2 mm).

Reproductive status of the species on each leaf was ascertained by visual identification of reproductive structures, i.e., isidia and/or apothecia for lichen species and gynoecia and/or androecia for liverwort species.

Species richness was determined by counting the total number of species present on each leaf.

Species diversity was calculated using Simpson's Diversity Index \(1/p^2_1+p^2_2 + \ldots + p^2_n\), where \(p\) = proportion of species.

Four I. fagiferus branches with unfolding apical leaves (and with no visible epiphylls present) were marked with colored tape on 3 October 1995. The new leaves were surveyed by hand lens periodically (on the dates of leaf series collection above and then on 18 November 1995) for appearance of epiphyll species.

Voucher Specimens

Voucher specimens of I. fagiferus, and specimens of leaves with epiphyll growth were dried and deposited, along with voucher specimens of associated species, in the University Herbarium at U.C. Berkeley. Specimens of each epiphyll species were collected from leaves, stored in paper packets and deposited in the Herbarium for archive and identification purposes.

Statistical Analysis

Cover percentages and reproductive status percentages were given arcsine transformations so that the values would be more normal and homoscedastic (Sokal 1981). Species diversity and species richness values were given log+1 transformations, as recommended by Carla d’Antonio (personal communication), for the same purpose. Several linear regression analyses were performed on the data, as follows: Relative leaf age was compared to total epiphyllous cover, cover of each of the five most abundant epiphyllous species (Leptolejeunea sp., Drepanolejeunea sp., Diplasiolejeunea sp., La and Lc), reproductive status, species richness, and species diversity. The cover of Leptolejeunea sp. was compared to that of Drepanolejeunea sp. and the cover of Leptolejeunea sp. was compared to that of Lc.

All analyses were performed using the Excel® computer program.

Results

An overall pattern of increasing epiphyllous cover, species richness, species diversity and appearance of reproductive structures on leaves along branches, from branch apex to branch base, was found to be present. In other words, leaves located at the apical end of branches had less of each of the characteristics described above than leaves located towards the base of the branch. In addition, a gradation pattern in these epiphyll community characteristics, progressing by leaf from apex to base, also appeared to be present.

Mean values of total cover, species diversity and species richness data are displayed in Figures 2, 3 and 4 respectively. Mean cover values of three common liverwort (liverwort) species are displayed in Figure 5. Mean cover values of three common lichen species are displayed in Figure 6.
Figure 2. Mean total percent cover (Bars are +/- 1 Std. Err.) of epiphyllous species on Inocarpus leaves.

Figure 3. Mean species richness changes over relative time. Bars are +/- 1 Std. Err. Leaf 1 is the youngest and apical leaf; Leaf 9 the oldest and basal leaf.

The results of the linear regression analyses demonstrate that increasing leaf age and increasing total cover are significantly positively correlated (p < 0.0005, $r^2 = 0.132$). Increasing leaf age and increasing cover of Leptolejeunea sp., Drepanolejeunea sp. and Lc also show a significant positive correlation ($p = 0.08$, $r^2 = 0.034$; $p < 0.04$, $r^2 = 0.052$; and $p < 0.1$, $r^2 = 0.032$, respectively), whereas increasing leaf age and increasing cover of Diplasiolejeunea sp. and cover of species Lc were not significantly correlated ($p > 0.3$, $r^2 = 0.01$ and $p > 0.1$, $r^2 = 0.029$, respectively). Increasing leaf age and increasing appearance of reproductive structures show a significant positive correlation ($p < 0.0003$, $r^2 > 0.15$), as do increasing leaf age and increasing species richness ($p < 0.0001$, $r^2 = 0.172$) and increasing species diversity ($p < 0.0001$, $r^2 = 0.164$). Cover of Leptolejeunea sp. and cover of Drepanolejeunea sp. were found not to be significantly correlated ($p > 0.55$, $r^2 < 0.004$), nor were the cover of Leptolejeunea sp. and cover of species Lc ($p > 0.47$, $r^2 < 0.006$).

Results were considered significant if the p-value was less than or equal to 0.1 (d’Antonio, personal communication).

Figure 4. Mean Simpson’s diversity value changes over relative time. Bars are +/- 1 Std. Err. Leaf 1 is the youngest and apical leaf; Leaf 9 the oldest and basal leaf.

These analyses indicate that there are significant positive correlations between leaf age (relative time) and increasing total epiphyllous cover, increasing reproductivity, increasing species richness and increasing species diversity.

Two of the four marked I. fagiferus branches showed colonization by lichen and
liverwort species after approximately five weeks.

Figure 5. Mean percent cover of three common epiphyllous liverwort species (LWA; LWB; LWE) in relation to leaf position. Leaf 1 is the youngest and apical leaf; Leaf 9 the oldest and basal leaf.

Figure 6. Mean percent cover of three common epiphyllous lichen species (LA; LB; LC) in relation to leaf position. Leaf 1 is the youngest and apical leaf; Leaf 9 the oldest and basal leaf.

Discussion

The results described above are consistent with previously described characteristics of succession patterns in other communities. Plots of the mean data for these factors (Figures 2-4) suggest that total cover and species diversity increase in the early seral stages of the system (younger leaves), level off in later stages (older leaves) and finally decrease at the terminal stage (oldest leaves). However, only a relatively small portion of the variation observed in these factors can be directly correlated to leaf age.

Variations in the cover of individual species over relative time were found to be significant in some cases. A plot of the mean data for one species (Figure 5) suggests a general trend of increase, and eventual terminal decrease, as a function of relative time. Plots of the mean data for five other epiphyllous species suggest that, among some of the species, patterns related to interspecific competition and replacement may be present. Specifically, the pattern of fluctuation of the liverwort species Leptolejeunea sp. and Drepanolejeunea sp. (Figure 5) could be explained by competition. The cover values of the third liverwort species and the three lichen species appear to fluctuate randomly and do not significantly increase with leaf age.

My use of the arrangement of leaves on branches (relative leaf age) as a time scale in this study makes it difficult to determine rates of change. The relative age order of leaves is always correct, but differences in age of successive leaves undoubtedly vary and comparisons of community dynamics made in such disjunct time increments can be difficult to interpret. Future studies would benefit from observations of community changes made in real time.

Causal factors other than leaf age are clearly important in the successional processes of this ecosystem. A variety of abiotic factors, e.g., humidity, precipitation, exposure and host plant characteristics, may affect species composition, competitive interactions and rates of colonization and succession. The present study did not consider a myriad of
such variables that could be important in phyllosphere succession.

As noted by Olarinmoye (1975), initial colonization of new leaves, and the subsequent dominance of particular species, may simply be a function of propagule dispersal, especially if there are only weak competitive interactions among species (Farrell 1991). Studies could be designed to test this hypothesis, including comparisons of species composition and relative abundance on newly colonized leaves with that of nearby leaves with reproductively active epiphylls.

Farrell (1991) notes that, while many studies of succession have demonstrated that community development is a "deterministic and repeatable process," newer conceptions of succession attempt to consider the "complexity and contingency" of ecological processes. Among the implications of this new view of succession is the idea that no single model may be efficacious in describing succession occurring at different stages and that a given ecosystem is likely to consist of a mosaic of successional patterns occurring simultaneously. In this study, leaf series were collected over a large area and cover data from all series were pooled for analysis. It may be the case that each leaf series (indeed, each leaf) undergoes a different succession process depending upon the nature of initial conditions and other factors. An assumption of this study was that epiphyllous succession at the study site would be uniform for leaf series; the lack of clear patterns in the results may be due to a mosaic effect. Studies that consider epiphyll communities branch by branch, or leaf by leaf, may have more unequivocal success.

In addition, oceanic island ecosystems tend to be more species depauperate than continental ecosystems. Moorcan epiphyllae are no exception, with far fewer species than reported for continental epiphyllae (five liverwort species compared to more than 100 for each continental tropical area). The importance of competitive interactions in succession has been related to species richness (Olarinmoye 1975) and the low richness of Moorcan epiphyllae may reduce the contribution of competition to succession here.

In sum, succession is occurring in the epiphyllous communities examined in this study, but the models and mechanisms giving rise to the patterns observed cannot be more than roughly sketched from the data collected. Future studies that more extensively test the inter-and intra-specific interactions of epiphyllous organisms in the context of particular successional models, with consideration of other biotic and abiotic variables, are required to shed more light on the community development of the phyllosphere. Consideration of the mechanisms of succession is also crucial in any study of succession (Farrell 1991). Of particular interest for future discussions would be comparisons of epiphyllous succession to succession in ecosystems of different spatial and temporal scales.

Conclusion

The development of epiphyllous communities in the rainforest of Moorcan is successional. Determination of the precise nature of that succession awaits further research. An understanding of successional patterns in this microecology would contribute significantly to the larger view of succession.

Acknowledgements

I would like to thank Dr. Brent Mishler and Dr. Carla d’Antonio for their invaluable assistance in every aspect of this project.

LITERATURE CITED


An ethnopharmacological study of possible anticancer and antimicrobial plants on Moorea, French Polynesia

Abinash P. Achrekar
Department of Integrative Biology
University of California, Berkeley, CA 94720

ABSTRACT. This study presents the first phytochemical screening of Tahitian medicinal plants. Traditional Tahitian healers were consulted in selecting 12 plants of anticancer and 14 plants of antimicrobial use. A total of 27 crude extracts corresponding to 26 different plant species from 18 families were investigated. Anticancer compounds are cytotoxic. A brine shrimp cytotoxicity screen was employed on possible anticancer plant extracts. Possible antimicrobial plant extracts were screened by their activity against yeast and E. coli cultures. 9 of 15 possible anticancer extracts were found to be cytotoxic. 13 of 14 possible antimicrobial extracts were found to inhibit microbial growth. This initial screening will aid future studies of local pharmacopia, which nevertheless, may be in jeopardy due to deforestation and loss of traditional medicinal knowledge.

Introduction

The importance of plant-derived compounds in modern medicine is often underestimated. One in four Western medicines was either originally discovered in plants then synthesized, or is still extracted from their plant sources (Bird 1991). 25% of Western pharmaceuticals are derived from medicinal plants (Myers 1992). 80% of people in developing nations rely on medicinal plants for primary health care (Farnsworth 1991). The importance of medicinal plants and traditional medicinal knowledge cannot be overstated. Many pharmaceutical companies conduct random searches in tropical areas for medicinal compounds within plants (Martin 1995). This process is costly and time consuming, with only a small percentage of screened plants containing useful medicinal compounds (Schultes 1991). Ethnopharmacology, the use of local medicinal plant knowledge to seek out new medicinal compounds, is a more efficient screening method (Waller 1993).

The most recent major study of Tahitian medicine (Petard 1972) is a collection of remedy recipes; no phytochemical tests were conducted to justify the value of local pharmacopia. Therefore, a broad preliminary phytochemical screening was conducted on medicinal plants used by local Tahitian healers on Moorea; the objective being to chemically evaluate the medicinal value of local pharmacopia. Traditional Tahitian healers were consulted in selecting plants of anticancer and antimicrobial use. Anticancer compounds can be screened by their cytotoxicity (Farnsworth 1968). Compounds extracted from possible anticancer plants were subjected to a brine shrimp cytotoxicity test (Beloz 1992). Because many of the medicinal plants reported in the traditional medicine of Tahiti are used against microbial infections (Petard 1972), antimicrobial screening of plant extracts was performed. The possible antimicrobial compounds were tested by the activity of the plant extract against cultured microbes (Brain and Turner 1975). Because alkaloids often exert some type of pharmacological activity and a large majority of natural products used today are alkaloid in nature (Martin 1995), an alkaloid screen was employed.

Materials and Methods

Plant Material

All plant material was collected by the author after referring to a traditional Tahitian medicine recipe book (Grepin 1980), a paper on traditional aspects of Tahitian medicine (Gaertner 1994), and interviewing Leontine Naore and M.
Louisa, two local healers. Most plants were found in littoral, rain forest, and riparian habitats; some plants were found in cultivation, namely *Premna tahitensis*, *Ocimum basilicum*, *Pandanus odoratissimus*, *Morinda citrifolia*, *Ficus prolixa*, *Citrus aurantiifolia*, *Gardenia tahitensis*, *Psidium guajava*, and *Atrocarpus incisa*. Only the reputed medicinal parts of the plant were collected for testing (Hedberg 1993). Voucher specimens were deposited at the University Herbarium in Berkeley, CA, and the Richard P. Gump Biological Research station.

**Preparation of Extracts**

The air-dried plant material was weighed, ground and extracted with 70% ethanol to attain a 1g/ml concentration of plant extract (Vlietinck 1995). The macerated plant suspension was stored at 4°C. Filter paper disks (7 mm in diameter) were impregnated with ethanol extract and dried for the antimicrobial screen (Dimayuga 1991).

**Cytotoxicity Screen**

Brine shrimp (*Artemia salina*) were hatched in aerated sea water under a 40 Watt light source. After 48 hours, brine shrimp were separated from the shells and unhatched eggs; 20 brine shrimp were placed in each test vial. 10 ml of sea water was added to each vial to dilute the plant extract. A syringe was used to deposit .2 ml of each possible anticancer plant extract into different test vials. 70% ethanol was run as a control and a nonmedicinal plant, a mature red *Cordyline frutcosa*, was used as a negative control. *Catharanthus roseus*, a known cytotoxic plant (Farnsworth 1991), was incorporated to validate the cytotoxic screen. The number of brine shrimp killed was counted after 24 hours. Six equivalent replicates were conducted.

**Antimicrobial Screen**

**Growth medium**

Screening was performed on plates of sterilized peptone agar (15-20% agar, pH 7.0-7.4). Approximately 20 ml of sterilized liquid agar was added to each 100 mm sterile petri dish and stored at 4°C to control sterility.

**Antimicrobial test**

All tests were done by placing the disks with the ethanolic crude extracts of possible antimicrobial plants on an agar surface (Dimayuga 1991) previously inoculated with a sterile hyssop containing a suspension of either *E.coli* (Gram-negative) or yeast. The suspension was inoculated in 10 ml of nutrient agar liquid and incubated for 24 hours at 37°C. A disk of amoxycilin, extracted in the same manner as the test plants, was used as a positive control. A disk with evaporated ethanol, which was used for the preparation of plant extracts, served as a negative control. Plates were incubated at 37°C for 24 hours and zones of inhibition around the disk were measured at the end of the period.

**Alkaloid Screen**

Each plant extract was impregnated on 7 mm filter paper disks. The disks were allowed to dry before dipping into Dragendorff’s reagent which gives a chromogenic response with alkaloids (Rios 1988). The filter paper was allowed to dry again before a drop of water was placed onto the disk to aid the chromogenic response (Farnsworth 1968). If alkaloids were present the disk turned a characteristic orange, indicative of a positive test.

**Statistical Analysis**

The data from the cytotoxicity screen was analyzed with the use of Microsoft Excel. A one-way randomized block ANOVA test and Tukey's test were conducted on the data, determining the statistical significance of extract cytotoxicity.

**Results**

A total of 27 crude extracts corresponding to 26 different plant species of 18 families were investigated. Table 1 shows the botanical and vernacular names, habitat, reputed medicinal activity, the plant parts used, and voucher/identification information for
each species screened. Figure 1 shows the results of the cytotoxicity screen. The statistical relationship among plant extracts can be seen in Table 2.

The most cytotoxic activity was found in *Ramalina* spp., *Hibiscus rosa-sinensis* leaves, and *Ficus prolixa*. While not statistically different from each other, all three were statistically different from the control, the nonmedicinal plant, and *Freycinetia demissa*. *Ramalina* spp., being the most cytotoxic extract, was statistically different than the control, nonmedicinal plant, and five other plant extracts. Raau cancer, a traditional cancer remedy prepared by Leontine Naore, showed cytotoxic effects but was not statistically significant. 9 out of 15 extracts showed statistically significant cytotoxic effects compared to the control and nonmedicinal plant.

![Figure 1. Results of cytotoxicity screen.](image)

Error bars represent +/- 1 standard error. Bars represent average brine shrimp killed after six replicates.

Table 1. Information of medicinal plants in the study. * signifies already documented anticancer activity. U.C Herb. = University Herbarium at U.C. Berkeley. Gump st. = Gump Biological Research Station, Mo'orea F.P. + ID means that species has previously been cataloged by University Herbarium.

<table>
<thead>
<tr>
<th>FAMILY/species</th>
<th>Vernacular Name</th>
<th>Habitat Found In</th>
<th>Reputed Activity</th>
<th>Plant Part Tested</th>
<th>Voucher &amp; ID Info.</th>
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<td>Riparian</td>
<td>Antimicrobial</td>
<td>Leaf, sori</td>
<td>U.C Herb.: +</td>
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<td>Leaf, stem</td>
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<td><strong>COMBRETACEAE</strong></td>
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<td><em>Terminalia catappa</em></td>
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<td><em>Cordylina fruticosa</em></td>
<td>Auti</td>
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<td>Young leaf</td>
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<td><em>Cenchrus echinatus</em></td>
<td>Pinipiti</td>
<td>Cultivation</td>
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<td><strong>LABIATAE</strong></td>
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<td><em>Ocimum basilicum</em></td>
<td>Miti</td>
<td>Rainforest</td>
<td>Anticancer</td>
<td>Fruit and leaf</td>
<td>Gump st.: +</td>
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<td><strong>LYCOPDIACEAE</strong></td>
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<td>Antimicrobial</td>
<td>Fruit</td>
<td>U.C Herb.: +</td>
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### Table 2. Statistical comparison between cytotoxicity extracts. Analysis done with a Tukey’s Test. X indicates extracts are statistically different from each other. 

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Time and equipment limitations allowed only a qualitative study of the antimicrobial activity of the plant extracts. One trial was conducted and the results are presented in Table 3. The control showed no bacterial inhibition in either culture; while the positive control, amoxycillin, inhibited both cultures. *Casuarina equisetifolia* showed no antimicrobial activity against yeast or *E. coli*.

Table 3 Qualitative results of antimicrobial screen. 0=no inhibition, + = relative inhibition.

<table>
<thead>
<tr>
<th>Extract</th>
<th>Yeast</th>
<th>E. coli</th>
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<tr>
<td>control</td>
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<tr>
<td>Amoxycillin</td>
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<tr>
<td>Premna obtusifolia</td>
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<td>+</td>
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<tr>
<td>Ocimum basilicum</td>
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<td>Thespesia populnea</td>
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<td>Terminalia catappa</td>
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<tr>
<td>Citrus aurantifolia</td>
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<td>Anigopteris erecta</td>
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<td>Hibiscus taintensis</td>
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<tr>
<td>Pandanus odoratissimus</td>
<td>+++</td>
<td>+++</td>
</tr>
<tr>
<td>Psidium guajava</td>
<td>+++</td>
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<tr>
<td>Cordylene fruticosa</td>
<td>+++</td>
<td>+++</td>
</tr>
<tr>
<td>Artocarpus altillus</td>
<td>0</td>
<td>+</td>
</tr>
<tr>
<td>Oxalis corniculata</td>
<td>+</td>
<td>+++</td>
</tr>
</tbody>
</table>

No results were obtained from the alkaloid screen. Numerous manipulations of the experiment protocol were attempted, all resulting in negative tests. Caffeine and Quinine, both alkaloids, tested negative with the Dragendorff’s reagent.

**Discussion**

The brine shrimp (*Artemia salina*) screen provided cytotoxic information of the plant extracts (Beloz 1992). Anticancer compounds are cytotoxic (Martin 1995). The brine shrimp screen determined that *Ramalina* spp., *Hibiscus rosa-sinensis* leaves, *Ficus prolixa*, *Cenchrus echinatus*, *Capsicum frutescens* fruit, *Hibiscus rosa-sinensis* flower, *Morinda citrifolia*, *Usnea spp.*, and *Capsicum frutescens* leaves were cytotoxic compared to the control. These nine extracts passed the initial anticancer compound screen. While six replicates were enough to determine the statistical difference between *Ramalina* spp. and seven other categories, *Hibiscus rosa-sinensis* leaves, *Ficus prolixa*, and *Cenchrus echinatus* were statistically different from only three categories (Table 2). The last five cytotoxic extracts were statistically different from only the control and nonmedicinal extract (Table 2). The *Catharanthus roseus* extract, a known cancer therapy, and the Raau cancer were statistically determined not cytotoxic (Table 2). More replicates would probably show increased variation and a provide greater chance to see differences in the cytotoxicity of the extracts. Thus, extracts found to be non cytotoxic cannot be disregarded as possible anticancer compounds.

Antimicrobial evaluations are carried out by means of standard *in vitro* assays (Farnsworth 1968). The qualitative nature of the antimicrobial screen determined the activity or lack of activity of the plant extracts. Table 3 shows that extracts with highest antimicrobial activity inhibited both cultures, while extracts that inhibited only one culture were comparatively less active. *Casuarina equisetifolia* showed no antimicrobial activity in either culture. A nonmedicinal plant could not be incorporated into this screen because of limited laboratory equipment, but the *Casuarina equisetifolia* extract revealed that not all plants have cytotoxic effects. 13 out of 14 plant extracts exhibited antimicrobial activity and therefore passed the initial antimicrobial screen. Though the number of extracts that passed the screen was high, it is not unusual considering the ethnopharmacological collection technique employed. In a past study, 29.5% of randomly selected plants exhibited antimicrobial activity, while 65% of plants selected because of reputed use against infection were found to be active (Farnsworth 1968). A more extensive study, including more replicates and more microbial culture screens, should be conducted in order to clearly observe antimicrobial activity.
Though many of the plant extracts exhibited either cytotoxic or antimicrobial activity, further study may reveal that neither occurs. Nevertheless, the healing value of the traditional Tahitian therapies has been documented (Gaertner 1994). This may be attributed to other plants or combinations of plants in the remedy, special dietary restrictions imposed during treatment, and/or the placebo effect. To further the understanding of traditional medicine, screening should incorporate anthropology, nutritional science, and psychology, in addition to botany and chemistry.

35-70,000 of the 250,000 higher plant species have been used at some point in time by some culture for medicinal purposes (Farnsworth 1991). 80% of people in developing nations rely on medicinal plants for primary health care needs (Farnsworth 1991). The importance of medicinal plants is evident, and the first step in obtaining pharmaceutical products from plants is screening. It is important to have a well conceived sampling methodology, preferably one relying on folk, or traditional, medicine indigenous to the region where the samples are to be obtained (Principe 1991). This consideration has been taken into account in this study, providing a broad initial screening of the local pharmacopia.

Ethnopharmacology may eventually become futile; its cornerstones: species diversity and traditional knowledge are rapidly disappearing (Martin 1995). 8-11 million hectares of tropical rain forest is deforested annually (Farnsworth 1991). The erosion of traditional knowledge is nowhere more rapid than in the realm of medicinal, narcotic, and toxic plant species (Schultes 1991).

"Indigenous knowledge is essential for the use, identification, and cataloguing of the tropical biota. As tribal groups disappear their knowledge vanishes with them. The preservation of these groups is a significant economic opportunity for the developing nation, not a luxury." (Goodman 1981)

Conclusion

The commercial value of plant-derived pharmaceuticals is in excess of $20 billion per year (Myers 1992). The indigenous people of Polynesia use medicinal plants for their primary health care needs. Though Tahitian remedy recipes have been recorded, no phytochemical tests have been conducted on the local pharmacopia. This study represents the first antimicrobial and anticancer screening of local medicinal plants. 9 of the 15 possible anticancer plant extracts exhibited cytotoxic activity, a requirement for an anticancer therapy (Martin 1995). A qualitative study revealed that 13 of the 14 possible antimicrobial extracts were active. The extracts which have passed the initial screen are not necessarily useful medicinal compounds, but have exhibited a desirable activity which requires more study. There are many plants of reputed medicinal value used on Moorea; though, they are slowly disappearing along with the medicinal knowledge of the local healers. More documentation and phytochemical tests need to be conducted before Tahitian medicine is lost.

Acknowledgments

This research could not be conducted without the help, interest, and patience of Hinano Murphy. The guidance of Dr. Brent Mishler, Dr. Jere Lipps, Dr. Vince Resh, Dr. Bill Alevizon, Dr. Cherie Semans, Dr. Roy Caldwell, Pam Jutte, and Ferenc de Szalay was greatly appreciated. Finally, thank you to Dr. Werner Loher, director of the Richard P. Gump Biological Field Station, and Frank Murphy, station manager.
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Endnote: A medicinal plant garden was started at the Gump Field Station. Only rare plants were planted; including Tiapito (Ophioglossum reticulatum) an extremely rare and reputed powerful antibiotic. Tiapito could not be screened because of insufficient plant material.
Species concepts in the 
*Echinometra mathaei* complex

Eric A. Collisson
Department of Molecular and Cell Biology
University of California at Berkeley
colliman@mendel.berkeley.edu

ABSTRACT. Species complexes can pose a challenging obstacle to taxonomists. It is often fruitful to investigate the taxonomic status of the respective morphotypes of such complexes in a variety of ways. The taxonomic status of *Echinometra mathaei*, a species complex consisting of distinguishable morphotypes, was examined on Moorea, French Polynesia using three different species concepts. The reproductive, ecological, and phylogenetic characteristics of the complex were considered. Reproductive barriers were found to be strong and the basis of their origin was discussed. Ecological habitat partitioning was found to be definite in physically distinct areas but overlapping in others. Parsimony analysis showed two possible phylogenetic reconstructions, and conditions for each were explained. Species status was assigned to the individual morphotypes of the complex after an integrative consideration of all examined factors.

**Introduction**

There is little agreement between biologists as to what criteria should be used in defining a species. Darwin (1859) attempted to differentiate between separate species and morphotypes of the same species. He used the fact that some populations intergraded with respect to morphology as evidence for his theory of natural selection but offered little guidance in classification. However, biologists have yet failed to agree on a single definition of their most basic taxonomic unit. Numerous species concepts have been proposed, each having its own advocates and critics. Three concepts dominate contemporary discussions of species today.

The **biological species concept** interprets a species as an interbreeding community of populations that is reproductively isolated from other such communities (Mayr 1942). Under this definition, two populations that are distinct morphologically, ecologically, and typologically still share the most fundamental taxonomic grouping provided they reproduce or potentially could do so. This concept stresses the biological factors that keep populations distinct from one another in nature. Populations remain isolated in two separate gene pools via reproductive barriers. Several mechanisms have been shown to achieve this separation including geographical separation, temporal breeding differences, gamete incompatibility, zygote mortality and hybrid sterility.

The **ecological species concept** sees a species as "a lineage (or a closely related set of lineages) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range" (Van Valen 1976). This definition considers an "adaptive zone" (the temporal and geographical components of ecological niche) as the forum in which natural selection works. The ecological species concept considers descent and explicit use of adaptation(s) as the integral factors in evolution, finding ecological difference more important than the occurrence of reproductive isolation in defining species. Through invasion of and adaptation to a new zone, organisms are separated from one another. The characters that allow them to flourish in this new zone also serve as segregating factors, with the adaptive population eventually speciating. Two distinct ecological species cannot occupy the same adaptive zone as one would eventually be displaced the other, or else they were not two species to begin with (Van Valen 1976).

The **phylogenetic species concept** consists of ancestor-descendant related
groups of organisms that are spatiotemporally restricted, and that exhibit cohesion and integration with respect to the process of evolution (Mishler and Brandon 1987). In this view species are monophyletic groups, consisting of all and only the biological entities that share derived characters (synapomorphies) and a single ancestral origin and common end. The phylogenetic species concept (as all concepts) includes two criteria, grouping (to assess the phylogenetic relatedness of organisms) and ranking (to determine the level of relatedness at which species status can be assigned). Monophyly serves as an evolutionarily justifiable grouping mechanism (Avise 1994) but a pluralistic approach should be taken to ranking (Mishler and Donoghue 1982). The rank must reflect the processes crucial in originating and maintaining the examined lineage (possibly, but not necessarily reproductive isolation or ecology).

Each of these concepts utilizes unique criteria to resolve the taxonomic status of closely related races within populations. However, all use the word "species" to express a population's relationship to other populations and not to convey intrinsic characteristics of that population. To make an analogy, a species is neither a male nor a female, but instead an aunt or cousin, defined not by personal characteristics but rather relationship to another such population.

Another similarity between the abovestated concepts is that all three attempt to identify the level at which forces (reproductive isolation, ecological adaptation, developmental canalization) uniting a lineage into a single evolutionary line dominate over the forces attempting to bifurcate the lineage into daughter lines. In other words, all three seek to group the population that is actively merging as opposed to splitting (Horvath 1992). It is at this level, the species level, that evolution is thought to occur, as the species responds to natural selection as an individual unit (Hull 1988; also see Mishler and Brandon 1987 for description of "cohesiveness").

The tropical urchin *Echinometra mathaei* expresses a number of unique morphotypes, collectively known as a species complex or group of sibling species. These morphotypes occur across the Pacific basin and the species status of the individual morphotypes within the complex is controversial. Historically, two distinct species were described in the 19th century (de Blainville 1825). De Blainville's conclusion was later refuted by Mortensen (1925), who concluded that only one species existed. This species, *E. mathaei*, is one of the world's most abundant urchins and dominates shallow, tropical reef ecosystems. There are four discrete morphotypes of this urchin known to exist (Tsuchiya 1984). *E. mathaei* has been best studied in Hawaii and Okinawa.

There is considerable reproductive, ecological and morphological variation in this species complex (Uehara 1985; Tsuchiya 1984; Palumbi 1991), making it an ideal paradigm by which to study species concepts. In addition, there has been extensive research done in the area of echinoderm evolution. Comparative phylogenies of extant urchins, complete with estimated speciation dates and discussions of morphological and molecular character differences abound (Littlewood and Smith 1995; Smith 1988). Mayr (1954) postulated that long evolutionary divergences were needed to precipitate reproductive isolation in urchins, because of their potentially long-range broadcast spawning planktonic gamete dispersal.

On Moorea two morphotypes of *E. mathaei* are present: Type A, (white tipped lagoon inhabitant), and Type B, (solid colored fore reef inhabitant). These two morphotypes also appear in Hawaii, where the Hawaiian language recognizes Type A as 'ina ia and Type B as 'ina ula (Michael Poole, personal communication).

The geomorphology of Moorea offers an opportunity to study the ecology of *E. mathaei* in a barrier reef ecosystem not present in either of the previously studied populations in Japan or Hawaii. Additionally, the Society Archipelago's geographical location represents an important facet of the distribution of this echinoderm in the Pacific Basin. The location, in the South Pacific, offers biogeographers a third point from which to
assess the historical, distributional aspects of this species complex.

The purpose of the present study is to test the applicability of the three above mentioned species concepts to the case of the *E. m athaei* complex. I addressed this project in three ways: (1) The degree of gamete incompatibility present was examined as it invariably leads to reproductive isolation and is rarely completely established between closely related urchin congeners. (2) Ecological distribution was described in representative zones of the barrier-reef ecosystem to assess ecological separation. Water flow, shown to affect urchin zonation (Vogel 1984) was experimentally examined. (3) Additionally, the historical aspects of speciation were investigated. In order to establish the phylogenetic relationship of the two types, molecular data from Hawaiian urchins was examined and a phylogeny reconstructed.

Materials and Methods

**Ecological Studies**

**Site Descriptions**

Morphotype distribution was examined across two ecological zones at three different site types on Moorea, French Polynesia. Lagoons and fore reef zones near the towns of Temae, Vaipahu and Tiahura were sampled. While fore reefs were topographically similar, lagoons were distinct. The lagoon at the Sofitel hotel at Temae is an area of low water flow. Sandy substrate and *Acropora formosa* corals, both indicative of slow moving water, dominate the lagoon. Sand is deposited in areas of low water movement and *A. formosa* is a fragile, branching stag coral that cannot tolerate high water flow. The lagoon is between one and three meters deep and has eastern exposure.

Inner Vaipahu is not a true lagoon (Galzin and Pointier 1985). It is an area contiguous to two large bays, Cook’s and Opunohu. These bays fill during high tide and drain during low, causing high water flow at and around their mouths, four times a day (Renee Galzin, personal communication). The fragile *A. formosa*, abundant in the calm Temae lagoon, is not present here. Instead, resilient head corals such as *Porites* and *Pocillapora* punctuate the large rubble substrate in Inner Vaipahu.

Three fore reef areas were examined: Vaipahu, Temae and Tiahura. These three sites share similar environmental characteristics. A sloping calcium carbonate platform, free of sediment and punctuated by spurs and grooves and small *Pocillapora* corals characterized all three fore reef sites. A fore reef area receives intense wave impact and is the first structure encountered by open ocean storm energy (Stoddart 1969).

**Morphotype Distribution**

Transects were taken at the aforementioned sites to assess distribution patterns between the two morphotypes of *E. m athaei*. Because each site differed physically, alternate methodologies were adopted at each. In Temae lagoon, five 50 meter transects were taken in *A. formosa* patches. All *E. m athaei* along the transect line were counted and their morphotypes recorded.

In Vaipahu lagoon five 100 meter transects were taken oriented perpendicular to the algal ridge and extending towards shore. Random coral heads were sampled along the transect line. Five additional point assessments were done at 200 meters from the algal ridge. Distance from the algal ridge, depth and coral type were noted. Each morphotype of *E. m athaei* was counted and the morphotype recorded. A x2 test (df=3) was performed on a contingency table of morphotype distribution in Vaipahu lagoon and distance from the algal ridge.

To examine fore reef urchin distribution, 6 fifty meter transects on the fore reef (2 on Vaipahu fore reef, 2 on Temae fore reef, 2 on Tiahura motu fore reef) were taken, oriented parallel to and 15 meters from the algal ridge. Each morphotype of *E. m athaei* was counted and recorded.

**Water Flow Assessment**

In order to compare water flow between the fore reef at Vaipahu and the lagoons of Vaipahu and Sofitel, the clod card technique was used (Doty 1971). In this method, plaster of paris “cloths” of a known mass are placed in water for a known
amount of time. The clods are then reweighed. The mass difference is the dissolved plaster, which dissolves in a linearly proportional manner to water flow around it. Presoaked 60 g plaster clods were elevated ten centimeters above the fore reef platform at Vaipahu, above Porites heads 0 meters and 100 meters from the algal ridge in Vaipahu lagoon, and in an A. formosa patch in Sofitel lagoon. A control 60 g clod was placed in 30 liters of sea water at ambient temperature in the laboratory (see Jokiel and Morrissey 1993 for discussion of effect of calibration container volume). All clods were submerged in sea water for exactly 24 hours, blotted dry, weighed, exposed at their respective site for eight hours (with the exception of the fore reef clod) and then reweighed. Because of rapid decomposition, the fore reef clod was exposed for one hour and its dilution percentage multiplied by eight to make results among sites comparable. A diffusion factor (DF) was calculated for each block, and relative water movements extrapolated.

Reproductive Studies
Gamete Compatibility

Urchins were induced to spawn by injection of .1mls of .5M KCl (Wilt 1985). Eggs were collected directly from the gonadopore, while sperm was allowed to drain onto a petri-dish and diluted 500X. Equal volumes of egg and sperm solution were mixed, in order to bring the final sperm concentration to about 1/1,000 original (Uehara 1986). Gametes were mixed by manual agitation and incubated at room temperature for 2 hours. Fertilization was assigned by presence of first cell division (Uehara 1986). Each of five replicate cross-fertilizations involved four individuals, each involved in two fertilizations: a Type A male was crossed with a Type A female and a Type B female and a Type B male was crossed with the same Type A and Type B female individuals. A light microscope was used to count 50 eggs in each fertilization of each cross, the highest consistently countable number of eggs in a fertilization.

Phylogenetic Studies:

Sequences of the mitochondrial Cytochrome Oxidase I (COI) gene (450 base pairs) were compared using the Phylogenetic Analysis Using Parsimony (PAUP) computer program for Macintosh, Version 1.1. Echinometra lunter was used as an outgroup. The sequences were obtained from three Hawaiian Type A urchins, two Hawaiian Type B urchins and one Guam Type B, graciously provided by Dr. Steve Palumbi (Department of Zoology, University of Hawaii).

Results

Ecological Studies

Transects on the fore reef contained 193 Type B urchins and no Type A urchins. Transects at the Sofitel lagoon at Temae contained 292 Type A urchins and no Type B urchins. The lagoon in Vaipahu contained 125 Type A urchins and 119 Type B urchins. Both morphotypes display different zonations with respect to the algal ridge in Vaipahu lagoon. Type B is more common closer to the algal ridge, with its occurrence waning further back in the lagoon. Type A displays the opposite pattern, with greater abundance observed further away from the algal ridge (Figure 1). The x2 test performed on the contingency table from Vaipahu transect data confirmed these patterns(p<.001). Water flow was lowest in the Sofitel lagoon. In Vaipahu lagoon, 100 meters from the algal ridge, water flow measured 4.16 times higher than in Sofitel lagoon. Water flow at the algal ridge in Vaipahu was 6.16 times higher than in Sofitel lagoon. The fore reef at Vaipahu had the most intense water flow, 20 times that of the Sofitel lagoon (Figure 2).

Reproductive Studies

Of the eggs scored in intramorphotype crosses (e.g. Type A with Type A), 98% were fertilized after two hours. In intermorphotype crosses (e.g. Type A with Type B), 4% of the eggs scored were fertilized after two hours, irrespective of sperm or egg donor (Figure 3).

Phylogenetic Species Concept

Two equally parsimonious phylogenetic trees were reconstructed in the
PAUP analysis. The first tree groups the three Type A individuals and the three Type B individuals into two separate, monophyletic groups. In the second tree, Type B is paraphyletic, with Type A monophyletic and sister to the Guam Type B individual (Figure 4 a,b).
Discussion

Ecological Species Concept

The physical differences of fore reef and lagoon habitats have been suggested to dictate urchin distribution (Vogel 1984; Lissner 1983). *E. mathaei* appears to be no different in this respect. Tsuchiya and Nishihira (1984) name microhabitat differences, namely crevice
type, to be the major habitat difference between these two morphotypes. Type B demands sturdy, burrowed out crevices while Type A will settle in sand, rubble or branching coral if no better burrows are available. On Moorea, this behavior may be an artifact of a factor zoning Type B to faster moving water and Type A to slower moving water. Sturdy burrows are essential in the areas of intense water movement (where Type B dominates) if the urchin is to stay attached to its food source, the algae bearing coral heads. In calm water (Sofitel) however there is no risk of being swept away and Type A thrives in A. formosa patches, rich in algae and unexploited by Type B. Alternatively, because no head corals (the substrate into which the sturdy burrows are scoured) were found in slow moving water, it is also possible that burrow substrate availability creates the two morphotype zones. In Sofitel, there are no suitable substrates for Type B, and thus it does not occur there. Type A, under this scenario, has transcended this burrow preference, and can invade the branching A. formosa.

Of particular interest in the ecology of these echinoderms on Moorea was the cohabitation of the two morphotypes in the lagoon at Vaipahu. One of two scenarios are most likely the case here: first, the two morphotypes inhabit two distinct niches, with regions of overlap; or second, the population has not yet reached equilibrium on Moorea, with one morphotype currently in the process of displacing the other out of the same niche.

The water flow tests and algal ridge distance distribution data support the first scenario. Intermediate values of water movement correspond to the cohabitation of the two types. Additionally, there is a positive correlation between morphotype distribution from the algal ridge and water flow in Vaipahu lagoon. But water flow also has repercussions on the substrate and food resources available in the lagoon. It is likely that subtle differences in the niches of each morphotype in Vaipahu exist, possibly caused by water flow rate and reflected by their differential affinity for the high water flow areas. However, when considering species status in an ecological context this study did not find the adaptive zones of the two morphotypes to be even minimally different from one another in Vaipahu. Even though the drastic habitat separation on the fore reefs and at Sofitel suggested quite different adaptive zones, and thus different ecological species, cohabitation in Vaipahu disallows this conclusion at the present time.

Biological Species Concept
The two morphotypes display a high degree of gamete incompatibility (Figure 3). This leads to strong reproductive isolation between the two types and effectively eliminates the possibility of gene flow between these two populations on Moorea. These results (Figure 3) classify the morphotypes of E. mathaei on Moorea as different species according to the biological species concept. Especially relevant in this classification is that the types retain their separate identities in sympathy, the "acid test" for biological species status (Avise 1994). The gametes of these two morphotypes are freely dispersed into the water column and thus are in contact with one another. However, when the gametes do meet, fertilization does not occur. The reproductive isolating barriers are intrinsic biological factors rather than extrinsic limits to reproduction caused solely by geographical separation. Gamete incompatibility is a divergent force in the continuing evolution of these urchins, suppressing the genetic bridge of reproduction and thus maintaining each morphotype as separate gene pool.

A substantive issue in the reproductive isolation of this group is the historical basis of its origin. One allowable possibility would be that reproductive barriers, and thus speciation, occurred allopatrically, as a result of extensive genetic drift, with a more recent range overlap. Such a scenario seems unlikely when considered in light of both the broadcast spawning mechanism of urchins and the low genetic divergence (difference at the genomic level) between the two types (Palumbi and Metz 1991). A more probable history is a sympatric
speciation event occurring between closely related individuals in reproductive contact with one another. The establishment of reproductive isolation was the result of a small, but important genetic distance between two interbreeding groups. This lies in direct conflict of Mayr's theory of large evolutionary distance necessary to precipitate reproductive isolation in broadcast spawning organisms. Instead, there seems to be reproductive divergence without stabilizing selection, possibly caused by small genetic drift in sperm-egg recognition coat proteins (O'Rand 1988).

Phylogenetic Species Concept

As two equally parsimonious phylogenies were obtained through the phylogenetic analysis (Figure 4 a, b), consideration must be given to each. In the first tree, two monophyletic groups are formed, one containing all the Type As and another containing all the Type Bs. Under Mishler and Brandon's (1987) phylogenetic species concept, this forms (groups) two populations as candidates for consideration of species status. However, monophyletic groups exist at many levels in all taxa. For example, *E. lucunter*, all three Type As and all three Type Bs collectively form a single monophyletic group at a more inclusive level on the tree. It is therefore necessary to adopt a methodology to recognize (rank) the least extensive monophyletic group in which a salient biologically isolating mechanism can be observed. In this species complex, reproductive barriers may have caused the two types to splinter from a parent lineage in recent evolutionary history (Palumbi and Metz 1991), so reproductive isolation is a good candidate ranking criterion. Assuming that the Hawaiian urchins examined phylogenetically in this study mirror the Moorean urchins with respect to reproductive barriers, both the monophyletic groups in the first tree (Figure 4a) represent distinct phylogenetic species using a reproductive ranking component. That is, each morphotype groups together genealogically and ranks as a species that is reproductively separate from all others.

If ecology is used as the ranking component, a more ambiguous phylogenetic taxonomy results. As the two morphotypes intergrade in some areas (Figure 1), they probably do not justify separate rankings with respect to ecology. If, however, a definite boundary between the adaptive zones of the two morphotypes was found to exist in nature then an ecological ranking would yield the same results as the reproductive ranking in consideration to phylogenetic species status. Type A and B would be distinct phylogenetic species.

Figure 4.b shows Type B separating into two distinct lineages and Type A arising from one of these (Guam) lineages. The pleiomorphic Type B lineage was certainly a diverse taxa and from a portion of this diverse group came Type A. Therefore, the Type As in figure 4b are still more related to the Guam Type B from which they came than the other Type Bs.

In the second tree (Figure 4b) the morphotypes do not group together genealogically and thus fail the first criterion (grouping) of the phylogenetic species concept. Therefore, the morphotypes A and B are not candidates for species status under the phylogenetic species concept, regardless of their reproductive or ecological characteristics. Instead three taxa; Type B (Hawaii) Type B (Guam) and Type A, must all be considered as species candidates, using comparative studies on the biology of the three groups to rank them. Assuming Type B's to be infertile (Figure 3) this ranking study would reveal that Type B Guam and the other Type B's cross-fertilizing. The biological species concept accepts those candidates (Type B Guam and the other Type B's) as the same species that the phylogenetic species concept rejects for lack of genealogical relatedness.

If the reproductive barriers in the phylogenetically examined urchins are similar to their Moorean counterparts (Type A fertilizing Type A and not Type B and vice versa) then time may build up the number of synapomorphies shared between the currently paraphyletic (in Figure 4b) Type B grouping. Then, if a similar study were done later in the evolutionary timeline (or currently, using more or different characters than COI), Type B
would be reclassified as monophyletic (as in Figure 4 a) and ranked a species by reproductive criteria. This potentially perplexing condition demonstrates an interesting aspect of the phylogenetic species concept. A conclusion stating that Type B has changed its historical status from paraphyletic to monophyly sounds disturbingly like rewriting history, when it is actually simply correcting a false assumption made by parsimony using insufficient data sets in the first studies. Although phylogenetics offers possibly the most intellectually satisfying concept of what is a species, incorporating genealogical history with current observable separating mechanisms, it depends on large data sets (ideally all the characters of a population) in order to accurately and unambiguously group populations in the first place.

Conclusion

The present study examined the species complex *Echinometra mathaei* for species status using ecological, reproductive and phylogenetic criteria. Habitat studies found strong examples of differential inhabitation of unique adaptive zones but morphotype inhabitation overlap prevents defining the two as separate ecological species as of yet. Studies of reproductive isolation, namely gamete incompatibility demonstrated that the two morphotypes are strongly reproductively isolated. Phylogenetic analysis resulted in contradictory, but equally parsimonious phylogenies, with Type B as the plesiomorphic state in each.

For now data warrants that Type A and Type B deserve recognition as separate species. Regardless of which formal definition of species is used, the biology of these two urchins is substantially different to a degree warranting species status. Reproductive isolation has etched out two independent gene pools, ecology has dictated two independent habitats (with zones of overlap between them) and phylogenetics has shown at least the possibility of two unique and separate genealogies. In nature the two morphotypes are separate species by a number of yardsticks.

Avenues for future research abound in this complex. Transplantation experiments between the calm water lagoon and fast water fore reef and more exhaustive examination of areas of cohabitation would lend greater insight into the ecology of this urchin. Additional characters, molecular or morphological, would resolve a more definite phylogeny for the complex. Crosses between individuals from different parts of the Pacific Basin would resolve whether reproductive barriers are common to morphotypes in different areas or locality specific, providing a broader geographical picture of this species complex. Additionally sequence data from throughout the Pacific would both resolve the phylogeny of the two types as well as locate the source of the original diversity prior to speciation (presumably the Indonesian archipelago). Also of interest is the relative chronology of speciation and distribution in this complex. Did *E. mathaei* splinter into separate species before it radiated throughout the Pacific or did the morphotypes originate from a common ancestor on one of the outer island such as Hawaii or Moorea?

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Benthic Foraminifera from mangrove lagoonal environments of Moorea, French Polynesia

Lena Brook
Department of Anthropology
University of California, Berkeley 94720
Email: brook@uclink2.berkeley.edu

ABSTRACT. The introduction of the mangrove Rhizophora stylosa from New Caledonia to Moorea, French Polynesia altered the natural environment of the coastline. A change in microfauna has accompanied this introduction. In order to establish whether a unique foraminiferal assemblage exists in the mangroves the foraminifera of four habitats (mud flat regions, Hibiscus tiliaeus, Paspalum vaginatum and Rhizophora stylosa) with similar substrate composition were compared. Fisher-a indices, triangle plot analysis, and cluster analysis showed mangrove habitats to be unique from other habitats sampled. Four species were limited to the mangrove habitat, and four other species were found in every habitat except mangroves. Independent lines of evidence suggest that an anthropogenic introduction of foraminifera may have occurred with the introduction of mangrove trees, but comparisons with the fauna from New Caledonia must be done to support this hypothesis.

Introduction

The mangrove Rhizophora stylosa was introduced to the island of Moorea (17°30'S, 149°50'W), Society Islands, French Polynesia, from New Caledonia in the mid-1930's, with the intention of cultivating oysters in the extensive prop-roots. Although this project did not succeed, mangroves stands have spread to many new sites in the past 60 years. Such an anthropogenic introduction has the effect of altering original coastline habitats by trapping organic-rich sediments in the dense proproot network of the trees. Mangrove sediments are generally characterized by a muddy clay and silt, rich in organic matter, and have a low oxygen content at depths greater than 0.5 cm below the surface (Boltovskoy 1984). As a result of this alteration in habitat, mangroves begin to support communities of organisms that did not previously exist in these areas such as arboreal arthropods [e.g. insects, spiders, scorpions and isopods, (Begon 1986)], fish larvae (R. Galzin, personal communication) and possibly species of foraminifera. The introduction and subsequent proliferation of Rhizophora stylosa trees on Moorea has been well-documented (Taylor 1979; Cavaloc 1987) which allows the effects of these mangroves on native communities to be monitored.

Foraminifera are abundant in all marine environments, including marginal environments such as marshes and mangroves. Benthic foraminifera that inhabit these marginal ecosystems are well-documented in recent years (Zaninetti 1979; Boltovskoy 1984; Brönnimann et al. 1984; Brönnimann 1986, a,b; Ausseil-Bade 1983; Steinker and Butcher 1981). As mangroves establish themselves in a new habitat, the prop-roots of adult trees trap organic material and fine-grained sediment. Established mangrove colonies create an extremely organic, low oxygen environment that is rich in hydrogen sulfide and is characterized by strong variations in salinity (Boltovskoy 1984, Culver 1990). Foraminifera species that tolerate these extreme environmental conditions have been documented to form unique assemblages, as seen in many mangrove habitats throughout the world (Halicz et al. 1984). Because mangroves were not endemic to Moorea, a question arises about the origins of the foraminiferal assemblages that exist in the mangrove habitats around Moorea. A potential introduction of foraminifera could have occurred when mangroves from New Caledonia were planted in Moorea's Vaianahe Bay (Figure 1). Alternatively, foraminiferal assemblages of modern Moorean mangrove habitats may originate from the nearby mud flats, salt
grass or marine Hibiscus habitats. To assess whether an anthropogenic or natural introduction of foraminiferal assemblages has accompanied the introduction of mangrove tree environments to Moorea, foraminiferal faunal assemblages were analyzed from mangrove, mud flat, hibiscus and salt grass habitats from various sites around Moorea.

Figure 1: Map of sampled sites

Previous studies
Foraminiferal studies have dominated the fields of stratigraphy and micropaleontology, but they have biological and ecological significance as well. The foraminiferal fauna of mangrove swamps have been well-described (Saunders 1958; Zaninetti, et al. 1979; Boltovskoy 1984; Culver 1990 and references therein). These studies, a majority of which were on mangrove environments around the Americas, led to the finding that foraminiferal assemblages of mangroves all over the world have a similar generic composition, although they are not identical (Boltovskoy 1984; Halicz et al 1984). However, most of these studies focus on taxonomy and identification rather than ecological topics. In addition, the study of foraminiferal assemblages from mangrove ecosystems is of great interest, primarily because organic-rich mangrove habitats are significant resource environments of fossil hydrocarbons. Foraminifera are thus a vital link to potential hydrocarbon reservoirs and marker species common to both the fossil record and recent history have been used with great success to identify fossil environments as mangrove habitats. Modern foraminiferal assemblages from the Society Islands have been documented in several papers by Venec-Peyré (1991) but this paper focuses on reef and near-shore lagoonal foraminifera.

The goal of this project was to characterize the foraminiferal assemblages in the mangrove colonies on Moorea and to obtain evidence that allows the origin of these assemblages to be determined. According to Cavalc (1987), 3-10 mangrove propagules were transplanted
from New Caledonian soil onto Moorea. If an anthropogenic introduction of foraminifera occurred with the mangrove, an assemblage unique from other muddy, low oxygen coastline habitats on Moorea should be seen in mangrove sediments. However, if a natural colonization from another environment on Moorea occurred, one would expect to find similar assemblages in other habitats. In order to test these hypotheses, faunal assemblages were described and characterized and effects of mangrove introduction on microfauna and the diversity of foraminifera were also assessed. Additionally, associated changes that occur by replacing fringing reef communities with mangrove habitats were discussed.

Materials and Methods

Site Descriptions

Four primary habitats from various sites around Moorea were sampled: 1) established mangrove *Rhizophora stylosa* stands, 2) *Paspalum vaginatum* marsh, 3) mud flats, and 4) *Hibiscus tiliaceus* groves (Figure 1). Three replicates of each site were sampled. The mangrove sites are characterized by dense stands (20 or more adults) in shallow water (2-5 cm in depth) along lagoon shores, with an organic-rich muddy, siltv substrate. The three *Hibiscus tiliaceus* groves were located along the lagoons (Figure 1) and were rooted in the sandy shore area. The substrate of the *Hibiscus tiliaceus* groves was sandy and characterized by a low organic content. This porous soil becomes aerated and is not as anoxic as the other habitats. However, a low oxygen layer still exists 1 cm beneath the surface of the substrate in two of the three *Hibiscus tiliaceus* sites (*Hibiscus A* and *Hibiscus C*).

The *Paspalum vaginatum* marshes sampled were not always located adjacent to the lagoon. *P. vaginatum* sample A was adjacent to a lagoon, sample B was located in a lagoon/swamp at Temae (about 200 m from shore) and sample C was collected from the edge of an estuary near Teavaro. The sedimentary substrate of this salt grass is also muddy and organic. However, the soil is much denser than both *Hibiscus tiliaceus* and mud flat region to the extensive root network of the plant. This substrate most closely resembles the mangrove soil.

Mud flat samples A and B were collected close to the *Paspalum A* and B sites, respectively: sample A site was located directly on the lagoon shore near Papetoai, whereas sample B and C sites were located in the Temae lagoon/swamp and near the Mahaerua stream estuary (Figure 1).

Field Methods

Sampling was conducted during October and November, 1995. All samples were collected with a plastic corer (6.5 cm diameter). The corer was pressed into the substrate and the upper 1-2 cm of sample was removed and stored. Two to three samples were collected in a haphazard manner at each site. Samples were collected within the roots of the stands, internal areas, and from the lagoon waters at the edge of the stands. The samples were then washed using two screens (710 μm and 75 μm), dried in an oven, and stored.

Laboratory Methods

Using a dissecting microscope, foraminifera were picked and sorted according to taxa until a total of approximately 250 specimens per site were collected. Reference slides were prepared for each sample, with taxa separated for later identification. The number of species and individuals were counted and plotted into a Fisher-α base graph (Fisher 1943) to analyze diversity patterns within the four habitats. In addition, agglutinated, miliolid, and hyaline specimens were counted separately and plotted into Murray (1973) triangular diagrams. Triangular diagrams have proven to be particularly useful to differentiate shallow-water habitats. This diagram characterizes the composition of faunal assemblages according to the wall structure of foraminiferal tests (hyaline, porcellaneous, and agglutinated). Cluster analyses were performed to determine foraminiferal assemblage patterns among the four different habitats. All statistical analyses was performed using SYSTAT 5.2 computer software.
Results

A total of 2771 foraminifera specimens and 53 taxa from twelve sites were identified. All specimens were generally between 0.1 mm and 1 mm in size. *Ammonia* cf. tepida, *Elphidium simplex*, *Quinqueloculina* sp. and *Trochammina* sp. were the most abundant taxa. The mud flat samples contained the most diverse assemblage (Figure 2) of foraminifera (Fisher’s α value 4.5-7.5) followed by *Hibiscus tiliaeus* (α value 4.5-7.5), and *Paspalum vaginatum* (α value 3-4). The lowest diversity of foraminifera was encountered in the *R. stylosa* mangrove samples (α value 3-4). Four species (*Miliolina* sp.Y, *Haynesina* sp., *Rosalina bradyi*, and *Textularia* sp. B) were found either exclusively or nearly exclusively in the mangroves.

Triangular diagram analysis shows that mangrove assemblages have the highest number of specimens with hyaline tests and salt grass *Paspalum vaginatum* samples show the highest number of agglutinated specimens (Figure 3). *Hibiscus tiliaeus* samples were primarily composed of miliolids, while agglutinated and miliolid species dominated mud flat samples.

Cluster analysis was used to determine foraminiferal assemblage patterns. Q-mode and R-mode analyses were done on the entire data set. A 1-gamma coefficient single linkage method (nearest neighbor) cluster analysis was used to analyze the relationship between the twelve sites sampled (Figure 4).

![Figure 3. Triangular plot diagram depicting percent faunal composition of hyaline, agglutinated, and miliolid species in samples from each habitat.](image)

![Figure 4. Dendrogram of Q-mode cluster analysis showing relationships among sampled sites.](image)
The mangrove *R. stylosa* sample sites A, B, and C were most closely linked to one another. *Hibiscus tiliaceus* sites B and C also showed a high degree of similarity. All *P. vaginatum* sites were very similar to mud flat sites.

R-mode cluster analysis was done on the 53 taxa using the 1-Pearson correlation coefficient average linkage method. *Cornuspira planorbis*, *Wiesnerella auriculata*, and *Triloculina carinata* were found in *Hibiscus* and mud flat samples only. *Triloculina barnardi*, *Elphidium simplex*, *Quinqueloculina* sp. (costate forms) and *Trochammina* sp. were found in every habitat except the mangrove habitats. The remaining 42 species were scattered throughout the four habitats.

**Discussion**

The results of this study yield several independent lines of evidence favoring the hypothesis that an anthropogenic introduction of foraminifera occurred on Moorea. The small size of the specimens collected are an indication that the foraminiferal assemblage living in the mangrove environment has adapted to this habitat because the low oxygen environment found in the substrate favors small-sized specimens. Foraminifera living in this low oxygen environment need to maintain a small size in order to increase their surface area to volume ratio, facilitating respiration (Murray 1991).

The results of the Fisher-α index plot (Figure 2) indicate that the mangrove habitats exhibit the lowest Fisher-α indices among all habitats examined. Comparisons with the standard foraminifera Fisher-α graph show that mud flat and *H. tiliaceus* sites fall into the range of a hypersaline lagoon to normal marine lagoon environment, where lower salinity is expected. However, the *R. stylosa* and *P. vaginatum* habitats have α-values that correspond with the hypersaline lagoon/marsh environment that has a higher salinity. From these results, it may be inferred that the high-saline conditions are a limiting factor for establishing highly diverse assemblages of foraminifera. In addition, low oxygen conditions, as found primarily in the mangrove and salt grass habitats, may also decrease species diversity. Low diversity is common to mangrove environments worldwide (Murray 1991). According to Boltovskoy (1984), samples collected from mangroves throughout the world usually have between two and eight species and only rarely reach 18-20, while "normal " lagoonal or reef habitats are characterized by 100 or more species of foraminifera.

Based on a standard triangular diagram, the species composition of mangrove samples and *Hibiscus tiliaceus* are indicative of a hypersaline lagoonal environment (Murray 1973). However, samples from *Paspalum vaginatum*, and mud flat regions resemble normal marine marshes. This finding follows the general trend that the mangrove environments on Moorea differ from the other sites sampled.

The small size of the fauna and its low diversity is particularly relevant when comparing these assemblages with those found in fringing reefs and lagoonal habitats. Reef foraminifera are larger than 1 mm and can grow up to 1 cm or more in size. Typically, samples from reef environments yield approximately 200 species. This is very different from the mangrove environment, and even the more diverse mud flat and *Hibiscus* habitats. Uncolonized environments become more eutrophic once the mangrove tree colonies are established. About one-fifth of the reef foraminifera can survive in eutrophic condition, with only about ten species becoming truly dominant. The rest are outcompeted by foraminifera that appear to be particularly well adapted to the extreme environmental conditions within the mangrove habitat.

*Quinqueloculina* sp., *Elphidium simplex*, *Trochammina* sp., and *Ammonia* cf. *A. tepida* are the most abundant taxa throughout the twelve sampled sites and therefore cannot be considered endemic to mangroves. Culver (1990) found *Ammonia tepida* to be one of the most abundant species in his samples and transects offshore of a large mangrove island. Although *A. tepida* is not particularly abundant in the Moorean samples (41 specimens in 12 sites), *Ammonia* cf. *A. tepida* is the second most dominant
species (511 specimens) encountered. Although the abundance of *Elphidium simplex* is high in *P. vaginatum*, *H. tiliaceus*, and mud flat regions, it is absent from the mangrove stands on Moorea. However, *E. craticulatum* is the third most abundant species in *R. stylosa*. This finding coincides with Saunders' (1958) results, who found *Elphidium* to be one of the most frequent genera encountered in the seaward end of river estuaries and saline mangrove swamps in Trinidad.

Because all mangrove sites clustered together (Figure 4), it appears that the mangrove environment on Moorea is distinct from other organic, low oxygen habitats on Moorea. There are many common species within *H. tiliaceus*, *P. vaginatum* and mud flats and few common species between *R. stylosa* species and more than one other habitat. Similarly, the clustering of two out of three *H. tiliaceus* habitats is a indication that it is less organic than the other samples. In addition, the four species found to exist only in the mangrove stands could be the beginning of a unique assemblage forming in Moorea. These species may have been introduced with the mangrove propagules from New Caledonia (compare with Debenay 1988), since they are not found in other, similar habitats on Moorea. It is highly unlikely that they were introduced from a reef habitat because no typical reef or lagoonal foraminifera were detected in the mangroves sampled.

Mud flats and *P. vaginatum* sites clustered together. A triangle plot analysis also indicated that they were similar habitats. *Paspalum* site A and mud flat site A were strongly correlated because they were located at the same site. No other patterns were revealed by cluster analysis. It is possible that currents are partially responsible for distributing and introducing new species to these shoreline habitats. Since sampling was not restricted to one portion of the island, each site experiences potentially different current patterns and input, resulting in a variety of assemblages even within similar habitats. However, had a natural colonization from an environment on Moorea occurred, the mangrove assemblages of foraminifera would not differ so drastically from other habitats sampled.

**Conclusion**

The introduction of mangrove trees to Moorea has affected coastal habitats of many sites around the island. Specifically, fringing reefs and other natural environments are replaced by small mangrove colonies. These changes are accompanied by changes in the microfauna, as shown by the foraminiferal faunal analysis. The foraminifera community found in the mangroves represents a separate community, as demonstrated by three independent lines of evidence (cluster analysis, diversity, triangle diagrams). This community is characterized by low diversity and genera that are predominantly adapted to "stress conditions", i.e., low oxygen, high organic content, and variable salinity. The difference in community structure in mangrove stands compared to the other habitats sampled makes natural colonization unlikely. However, to truly accept the hypothesis that an anthropogenic introduction of foraminiferal species occurred with the introduction of mangrove trees to Moorea, the foraminifera in New Caledonian mangroves must be examined.

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Variation in flow and sediment transport across Vaipahu reef-flat, Moorea, French Polynesia: a comparison of back-reef morphology

Ken Greenberg
Department of Geography
and Department of Integrative Biology
University of California, Berkeley, CA 94720

ABSTRACT. The relationship between back-reef geomorphology and water/sediment transport was examined on the reef-flat at Vaipahu, Moorea, French Polynesia, between October 15 and November 15, 1995. Two trends were observed in this study: 1) large sediments moved further than small sediments across the reef-flat and 2) reef-flat sediment transport varied according to two back-reef morphologies. Low tide sediment transport was not found to significantly vary from high tide sediment transport. Flow was significantly greater on a high surf day compared to a low surf day. Both large and small tagged sediments were washed from the fore-reef into the back-reef during two days of particularly high surf. A detailed survey of barrier reef geomorphology, sediment texture and associated flow patterns, before and after a hurricane, would expand the understanding of the functions that major reef morphologies serve.

Introduction

Both fringing and barrier reefs are generally more extensive along coasts of tropical islands that are hit by consistently strong surf and trade winds (Nunn 1994). Previous studies of coral reef hydrodynamics have discussed the cause and effect of the relationship between reef morphology and variation in currents, waves and sediment transport (Roberts et al. 1975, 1982, 1983). An understanding of the hydrodynamics and geomorphology of the reef environment has also been useful to studies of larval dispersal and reef ecology (Andrews et al. 1988; Goldman 1993; Stoddart 1989).

The purpose of this study was to examine whether the daily overflow of water and sediment into Vaipahu channel, Moorea, French Polynesia, varies along the reef-flat in relation to two specific back reef morphologies. Under calm conditions, greater water flow from breaking surf may enter Vaipahu channel at cross sections that empty into washout basins (sections of the back-reef floor covered by coral skeletons aligned perpendicular to the reef-flat) rather than adjacent cross sections that empty into coral-bounded moats (boundary between the reef-flat and the back-reef corals lined with coral skeletons). Higher transport rates of loose coral sediments found on the reef flat may also be associated with this greater water flow. A comparison of water flow and sediment transport across the Vaipahu reef-flat was made between six points aligned with washout basins and six neighboring points with moats. A study of the weather conditions and reef-flat flow energies needed to transport fore-reef sediment into Vaipahu back-reef was also conducted. There has been little if any explicit description of washout basins in the literature. A majority of water entering Cook's and Opunohu bays flows over the reef flat and through these washout basins (Rene Galzin, personal communication 1995, Moorea, French Polynesia).

Materials and Methods

Site

Research began on October 15, 1995 and ended on November 15, 1995. Vaipahu lagoon and reef-flat on the north shore of Moorea, French Polynesia stretches approximately four kilometers between the passes of Cook and Opunohu bays (Figure 1). Measurements were made along the middle one-third length of Vaipahu reef-flat. There are many basins of coral rubble extending from the edge of the reef-flat into the coral community of Vaipahu channel. These ‘washout’ basins are extensions of a moat (Stoddart 1975),
defined as depositional sand flats adjacent to atoll reefs. The term 'moat' has been used in this research to describe the depositional sand flats adjacent to an island's barrier reef. The moat runs parallel and adjacent to the reef-flat on the lagoonal side (Figure 2). Between the washout basins, the coral community is separated from the reef flat by this 0.5-5.0 meter wide moat. The moat slopes from one-half meter below the level of the reef flat down 2.0-2.5 meters to the back reef floor (Figure 3). Along the moat slope there is coral rubble of varying size similar to that found on the floors of adjacent washout basins.

Figure 1. Location of sampled reef.

Measurements of water flow and sediment transport were made on the reef-flat at ten meters from the lagoon. The mid-point of each washout basin was chosen as the reference point for the first set of measurements. From this first measuring point, two additional measuring points were marked at a meter to either side of the first point. These three sets of measurements were averaged for each section of the reef flat at a low tide and the following high tide. Before data was collected, a coin was flipped as to which side of the washout basin the associated moat would be surveyed. The point where Moat A would be surveyed was randomly selected.

Two measures of current speed, one of water depth and one of the distance covered by three different sized coral sediments in five minutes were taken at each of the three points associated with each site.

Current speed
Current speed was measured with a six by eleven centimeter buoy attached by a two meter length of string to a PVC pipe. The buoy was tossed over an oncoming wave and timed from when it passed the stationary PVC pipe until it floated two meters. Six current speeds were averaged for a given site at a given tide on each of six non-consecutive days.

Water depth
The average depth of the ebb of the water and the surge two seconds after a wave passed was measured at each sampling site. Three water depths were averaged for each site at each tide on each of six non-consecutive days.

Rubble races
Rubble races were run from the point of depth and current measurements. This procedure was unique to this research; and performed to imitate periods of increased sediment deposition on the reef-flat. The three classes of labeled rubble used were: small, displacing 1-5 fluid ounces of water; medium, displacing 8-10 fluid ounces of water; and large, displacing 20-24 fluid ounces of water. Different pieces of rubble of the same volume, but different surface area, were used at each pair of sites. For a given washout site and its associated moat site the same pieces of rubble were used at both tides. The distance traveled by each piece of rubble in five minutes was measured and the distances moved were averaged for each site.

The Clod Card method
A modified Clod Card method (Doty 1971) was used to compare reef flat flow differences along the reef-flat. The weight of each 60.5 +/-0.5 gram plaster clod was measured after 7 hours exposure on the reef flat. The clods were pre-soaked in salt water for twelve hours. Two one-gram
Figure 2. Overhead view of the reef at Viapahu showing the moat and a washout.

Figure 3. Side-view of the reef at Viapahu.
wires were set into each clod card mold so that it could be fastened to nails imbedded into the reef flat. Each clod was secured between one and two meters from the lagoon-edge of the reef-flat. A 60.25 gram control clod was placed in a bucket inside a still, salt water tank (>100 liters), at the same salinity and temperature conditions as the experimental clods (Jokiel et al. 1993). Five clods were deployed on a high surf day. Five more clods were then deployed on a following low surf day for a duration of eight hours. Diffusion factors were calculated for each individual clod. A diffusion factor is the ratio of percent weight loss of the experimental clod to the percent weight loss of the control clod (Jokiel 1978). Diffusion factors represent relative water energies.

**Sediment Movement**

Sediment movement from the fore-reef to the lagoon was monitored and compared at a washout and adjacent moat study site. Ten pieces of rubble of the large class (20-24 fl. oz. water) and ten pieces of rubble of the small (1-5 fl. oz. water) class were tagged and placed at each of three locations associated with a moat and a washout: MOAT 1) five meters past the algal ridge into the breaker zone; 2) over the edge of the reef flat in the moat; and 3) five meters into the back-reef past the moat; WASHOUT 1) five meters into the breaker zone; 2) over the edge of the reef flat, and 3) five meters into the washout basin from the edge of the reef flat. Sixty sediments were deployed along two transects of the reef and of those that could be found, their movements were monitored every other day for ten days. Data was collected on fair-weather days with mild trade-winds, predominantly North Easterly with a single day with a South Westerly (5-15 km/hr), and mild waves (1-3 ft).

**Statistical Analyses**

T-tests were calculated for comparisons of two factors, for example, do sediments move further at low tides than high tides? ANOVA tests were calculated for comparisons of three classes, for example, is there a significant difference in the distances traveled by three different sized sediments? Significant differences are indicated when p < 0.05.

**Results**

**Current Speed and Water Depth**

Both current speeds and water depths increased across the reef-flat from low tide to high tide. However, flow (current speed times water depth) was not significantly different (T-test; p > 0.05) in front of washouts than in front of moats, at low tides or at high tides (Figure 4 and Figure 5).

![Figure 4. Mean flow during low tide at Moats and washouts. Flow is a product of speed and depth. Bars are one St. Err.](image)

![Figure 5. Mean flow during high tide at Moats and washouts. Flow is a product of speed and depth. Bars are one St. Err.](image)
Clod Card Method

Water flow, based on the average of the five diffusion factors calculated on two different days, was significantly different (T-test; p < 0.05) across the center of Vaipahu reef-flat, by a diffusion factor of 4.8 +/- 1, on the high surf day as compared to the low surf day (Figure 6).

Figure 6. Relative water energy measures as the diffusion factor using the clod card method. A day with small waves (Sm; waves<1m) was compared with a day with large waves (Lg; waves>2m). Bars are one Std. Err.

Rubble Races

There was no significant difference (ANOVA; p > 0.05) between the distances the three size classes of rubble traveled across the reef-flat in five minute periods (Figure 7).

There was no significant difference (T-test; p > 0.05) in the distance traveled by the three sizes of rubble during high tides and low tides. (Figure 8) There was no significant difference (T-test; p > 0.05) in the distance traveled by the three size classes of rubble in-front of the washouts as compared to in-front of the moats (Figure 9).

Figure 7. Average distance large, medium and small rubble pieces were moved. Bars are one Std. Err.

Figure 8. Average distance rubble pieces were moved at high and low tides at all reef-flat sites. Bars are one Std. Err.
Figure 9. Average distance rubble pieces were moved moats and washouts. Data were collected at high and low tides at each site. Bars are one Std. Err.

Sediment Movement

During the third and fourth days that tagged sediment was monitored for movement, there was a strong surge moving across the reef-flat. The third day that sediments were monitored for movement was the day that the high energy clod card experiment was run. On those two days (third and fourth days of monitoring) large and small sized, tagged and untagged, sediments were observed being transported across the reef-flat from the fore-reef, in front of both the washout and the moat where they were placed originally. That movement was not observed on the other low surge days. On the same two days of high surge, tagged sediments were moved down the moat slope piles of rubble already collected at the base of the moat-bounding coral. Those pieces of rubble were not moved prior to the high surge days. Sediment placed in the back-reef, both behind the moat and on the floor of the washout was not moved during the ten monitoring days. Sediment placed on the upper slope of the washout, adjacent to the reef-flat, was moved down the slope to the floor of the washout during these two days of high surge, and they remained at the base of that slope.

Discussion

Water circulation and sediment distribution in a fringing reef lagoon are determined by lagoon geometry and water overflow (Roberts et al. 1975). When comparing reef-flat sediment transport in front of moats and washouts, a p-value of 0.052, although not statistically significant, strongly suggests that sediments may travel further in front of washouts than in front of moats. In discussing back-reef depositional zones, (moat, rubble flat, rock floor and sand flat) Roberts and Sneider (1982) noted that sediments accumulated in a back-reef adjacent to main channels through a fringing reef. The washout basins of Vaipahu channel may have been deposited during periods of severe weather when the more incised and eroded sections of the reef-flat were channeling water and sediments faster into the back-reef.

Within the group of three rubble sizes a p-value of 0.0765 indicates that there was a strong trend that larger sediments move farther across the reef-flat on calm days. Similar trends in sediment transport were noted by MacIntyre (1987). However, MacIntyre (1987), noted that sediments greater than 25.6 cm were moved only during hurricanes. Although, this would correlate to results of this study if those sediments were in the back-reef or the fore-reef, there were sediments of that dimension used in the rubble races, and they were moved on non-hurricane days.

It is possible that a more extensive study of reef-flat flow would result in a more definitive model linking sediment sources, sediment sinks and the intervening reef morphologies. A greater sample size would allow for data grouping associated with weather conditions, so as to eliminate anomalous weather patterns. A comparison of flow patterns between periods of South Westerly trade-winds and North Easterly trade-winds would also expand on the annual variation in water flow.
The literature supports my finds that sediments placed in the back-reef at Vaipahu remained close to their depositional sites during the periods of calm. In studying sedimentation and hydrology of a barrier-reef off the coast of Belize, MacIntyre (1987) noted that back-reef sand transport occurred only during hurricanes even though sand was continually supplied from the reef-flat, as were other sizes of sediment. Similar sedimentation patterns have been noted in the Pacific, (Stoddart 1975).

The flow conditions during the low wave Clod card day were invariably calm, similar to conditions at low tide. The flow conditions on the high wave Clod card day were similar to conditions at high tide, with fast current and deep water. In light of the results of the Clod card experiment (reef-flat water flow was greater on a day of greater wave energy), it is interesting that there was no statistically significant difference in the distances traveled by the three sediment classes between low and high tides. Since pre-tagged sediments were brought onto and moved across the reef-flat only on the high wave day and the following day of high surge, the lack of a significant variation in measured sediment transport (Rubble Races) was possibly due to a minor variation in wave energies between high and low tides. Similar measures of reef-flat flow have been found in the Caribbean, (Roberts and Suhayda 1982) and Clod card experiments run in Hawaii generated similar high energy, reef-flat diffusion factors (Jokiel 1978). That sediment was washed into the back-reef during only the strongest flows, such as waves 5-6 feet, could imply that storms and hurricanes are responsible for creating the depositional back-reef morphologies examined in this study. Should a hurricane capable of detaching coral colonies from their fore-reef substrate wash these corals into a back-reef coral community, it is possible that the channels in the reef-flat where water flows faster and sediments are transported faster would serve to clear-out the back-reef coral communities aligned with these channels.

Conclusions

The results of this study supported the hypothesis that there was greater sediment transport across sections of Vaipahu barrier reef that flowed into the washout basins. However, there was no such trend related to water flow. This could imply that rubble races were a more accurate measure of calm, reef-flat flow regimes than the hand-held flow meter. The results of the Clod card method indicated that reef-flat flow increases with the magnitude of the breaking surf. The movement and subsequent deposition into the back-reef of loose fore-reef rubble indicates that severe weather could be responsible for the back-reef depositional morphologies described in this study, as suggested in the literature. As two of the basic, integral factors influencing the health of coral reefs, this study of coral reef hydrodynamics and sedimentation should help direct future efforts at assessing and monitoring coral reef health. An in-depth survey of barrier reef geomorphology, sediment texture and associated flow patterns, before and after a hurricane, ought to greatly expand the understanding of the functions that major reef morphologies serve.

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Taphonomy of the coral reef conglomerate platform, Moorea, French Polynesia

Michael Schafler
Department of Geography
University of California at Berkeley
Berkeley, CA 94720

ABSTRACT. The taphonomy of the conglomerate platform on northern Moorea, French Polynesia was studied by comparing the live assemblage of corals and mollusks in the existing reef to the dead, preserved assemblage. Corals and mollusks were identified, counted and measured in quadrats within six zones from the shore to the fore reef. Abundance and diversity in each zone was found to be similar to the corresponding zone at each site but was found to be different from zone to zone. Cluster analysis showed that the conglomerate platform had an assemblage of fauna which is most closely related to zones on the fore reef. Thus the fore reef is probably the primary source of rubble for the conglomerate platform. However, the primary difference between the conglomerate platform and the other zones is the abundance of Pocillopora coral. The disturbance of the present marine environment by tropical cyclones in 1983 may have ‘reset’ the succession patterns. Previous studies have shown that after a major disturbance Pocillopora is the fastest colonizer of all resident corals. Another factor to explain this discrepancy is the reverse sorting in the unconsolidated rubble rampart. It was observed on recently deposited ramparts that small sediment filter to the bottom while the largest sediment remain on the top. Differences in preservation rates were tested to explore a taphonomic explanation. Frailility tests found that Pocillopora is the most fragile and least dense of all corals.

Introduction

How faithful a representation of the live community is present in its death assemblage? The degree of resemblance between the live and the dead assemblages, referred to as fidelity, can only be assessed by a detailed comparison of modern habitats and their accumulating sedimentary records (Parsons and Brett 1991). Examination of bias present in marine fossil assemblages showed that reef systems display a close fidelity in which 70 percent of the life assemblage is preserved (Liddell and Ohlhorst 1988). However, this bias varies greatly according to the organisms’ morphology. Three structurally distinct groups have been identified: 1. Non-skeletonized organisms which comprise from 50 percent to 95 percent of living faunas, leave no record of body fossils; 2. Lightly skeletonized organisms, such as arthropods and echinoderms with non-mineralized chitinous cuticles or thin plates respectively, are preserved but are greatly underrepresented in the fossil records; 3. Well skeletonized organisms, which include mollusks and corals, are best represented in the death assemblage although their abundance and diversity is variable. (Parsons and Brett 1991)

Taphonomy is the study of the laws which govern the transition of organic remains from the biosphere to the lithosphere (Efremov 1940). By this definition, the conglomerate platform is a good system for taphonomic research. These platforms were first described in detail from Funafuti atoll in Tuvalu in 1904 (David and Sweet 1904). They are composed of biogenic detrital material and rise .5 m to 1 m above the high tide level (Newell 1956). The platform originates as a rubble rampart or bank deposited by both wind-driven waves and storm surges of tropical cyclones and is subsequently planed down and cemented (Curry et al 1970; Stoddart 1975; Maclean and Hosking 1991). Thus, rampart rocks are poorly sorted, and benthic organisms are not found in situ. Platforms on Moorea have been dated previously for use as a sea level indicator. However, the platform can be composed of rubble from many different storms. Stoddart (1971) dated the platform from
4500 years B.P. while Montaggioni and Pizzarola (1988) found dates up to 7500 B.P.

The hypothesis tested in this study is that the present marine assemblage has a high degree of fidelity to the conglomerate platform in both abundance and diversity of organisms but that it will vary by genera. By sampling from six zones at two separate sites, this study examines fidelity and faunal changes within and between both life and death assemblages.

Materials and Methods

Study Sites

All field work was conducted on Moorea, French Polynesia (17°30' S, 149°50' W) during the months of October and November, 1995. Data were collected at Aroa Point on the Motu Temae and the north (leeward) side of the Motu Tiahura (Figure 1). These sites were selected because of the presence and accessibility of a well developed cemented conglomerate platform, and they were similar geomorphologically (Figure 2).

At Aroa Point, the platform extends 1000 meters east of the lighthouse and is 10 m to 20 m wide (Figure 2). The coral rubble patch is located landward of and adjacent to the platform on the slight slope of the beach. Rubble patches are 2 m to 8 m wide and are found up to 1000 m eastward along the conglomerate platform. Seaward of the conglomerate platform is the lagoon, which is 3 m to 100 m wide in this area, and extends to the algal ridge. The lagoon depth ranged from .25 m to 1 m. The lagoon channel is the deepest part of the lagoon and it lies 3 m seaward of the conglomerate platform and is 2 m to 3 m wide. The back reef is located about 60 m seaward of the conglomerate platform and is 10 m to 20 m wide. The fore reef lies on the ocean side of the algal ridge. The shallow fore reef was defined as the portion in 3 m to 5 m of water. The deep fore reef was defined as the portion in water 10 m to 20 m deep.

On the north side of the Motu Tiahura site, the conglomerate platform is about 300 m long and 40 m wide. The 15 m nearest to the lagoon are exposed and bare, while the landward 25 m are covered with coral rubble, sand, and Pemphis stands. The coral rubble patch is located behind the highest tide break on the beach slope and is 2 m to 5 m wide and 300 m long. The lagoon at Tiahura is 120 m wide and is 1 m to 2.5 m deep. The channel is 3 m from the conglomerate platform and is 1.75 m to 2.5 m deep. The back reef is 60 m to 120 m from the conglomerate platform. The depth is .25m to 1 m. The shallow fore reef is that portion 3 m to 6 m deep. The deep fore reef was defined as that portion between 8 m and 13 m deep.

Sampling

Ten quadrats were sampled in each of the six distinct zones at both sites. The lighthouse at Aroa Point and the westernmost point at the Motu Tiahura were selected as the starting points of the sampled areas. In both of the conglomerate platforms and the rubble patches, ten randomly selected pairs of coordinates were randomly selected. On the conglomerate platform, 1 m² quadrats were sampled. On the rubble patches, .25 m² quadrats were sampled. At Aroa point, terrestrial quadrats were sampled in three rounds to adjust for increased skill in identifying organisms. The first two rounds consisted of three quadrats observed in both the conglomerate platform and the rubble patch. The third round consisted of four quadrats in each. This factor was also adjusted by examining data collected from round one a second time after round three was completed.

The lagoon environment was sampled in two parts. In the channel, ten .25 m² quadrats were randomly sampled along a 50 m transect line located 3 m seaward from the conglomerate platform. In the back reef, ten randomly selected 1m² quadrats were sampled along a 50 m transect line 70 m seaward of the conglomerate platform.

The fore reef was also divided into two parts. The shallow fore reef (3 - 5m deep) was sampled along a 50 m transect line. Because of increased coral density and time constraints of marine sampling, .25 m quadrats were sampled along the transect. The deep fore reef (between 8 m and 20 m) was sampled with SCUBA. Moving upslope
along the fore reef, divers randomly sampled .5 m² quadrats along a 50 m long transect line.

Fauna within each quadrat were identified, the length of longest axis and its perpendicular axis were measured and their positions noted (Gleason 1994). Corals were identified by comparing those sampled with reference collections at the Centre de Recherches Insulaires et Observatoire de l’Environnement (CRIOBE) located on Moorea and references in Corals of Australia and the Indo-Pacific (Veron 1985). Mollusks and echinoderms were identified by comparing those sampled with references in Coral Reef Indo-Pacific Field Guide (Allen and Steene 1994).

In order to test preservation rates, an assortment of all fauna occurring in the conglomerate platform were collected in rubble patches. In addition to dead skeletons, live fauna was selected from the lagoon at Temae. The mass of all 46 specimens was measured by digital scale and volume by water displacement methods and density was calculated. Afterwards, fauna were individually placed in a 10 liter bucket with five basalt rocks and the bucket was then rolled 50 m. After removal, the largest intact piece of the fauna was measured for mass, volume, and density changes.

**Statistical Analyses**

A cluster analysis was performed on the data to discover similarities between sites and relationships among zones. A Spearman Rank Correlation Coefficient matrix was performed to quantify similarities from zone to zone and site to site.

**Results**

**Abundance and Diversity**

Ten distinguishably different types of fauna were found in the sampling was ten, six corals, three mollusks, and an echinoid. Abundance and diversity of corals varied from zone to zone (Figure 3). Only corals were included in Figure 3 because mollusks and the echinoid were found in low numbers at both sites. Pocillopora is most prevalent at nine of twelve zones. It drops sharply in abundance in the conglomerate platform zones at both sites. In order to examine the fidelity, across zone ranks were assigned based on percentages. Ranks correspond to abundance. In the case of equal abundance, both organisms were assigned one rank lower. Pocillopora showed a very steady rank but it dropped sharply in the conglomerate platform at both sites. Other corals showed sharp changes as well, such as Porites.

**Zone and Site Comparison**

Cluster analyses illustrate the similarity of a zone to the other zones. The tree diagram shows that the top fore reef at both sites are most similar to the deep fore reef. The conglomerate platform at each site was found to be most similar to the other conglomerate platform. However, other zones showed a stronger similarity to zones at the same site, similarity was based on a Spearman Correlation Coefficient. The rubble patch at the Motu Tiahura and the Channel zone at that site were more similar than the corresponding zones at Temae. Both back reef zones were dissimilar to the other zones at either site as seen by the low correlation coefficients.

**Fragility Test**

Fragility of fauna present in any zone at either site was quantified as percent mass change (Figure 4). The fragility test produced significantly different results for live corals and rubbles in three cases: Pocillopora, Acropora, and Fungia genera. For the Fungia, the rubble was more fragile than the live coral. However, the live mass of both Pocillopora and Acropora changed dramatically in the fragility test, with live samples losing approximately 45 percent and 25 percent, respectively, of their original mass. Rubble samples of Pocillopora lost about 10 percent of its mass, as compared with only one percent in the case of Acropora. The most fragile organism was Diadema, which was completely destroyed.
Discussion

There is a strong fidelity of organisms from the life assemblage to the conglomerate platform. However, the *Pocillopora* (Figure 3) distributions were very different between the conglomerate platform and the other zones. There are three possible reasons for this observed anomaly: the first hypothesis is that coral abundances were affected by the succession status of the present assemblage. The last cyclone to disturb Moorea was in 1983 (Gleason 1994), and the effect of storms is removal of corals from the marine assemblage (Maragos 1972). Thus the succession patterns of the marine environment may have been 'reset' twelve years ago. Therefore it may not be valid to compare the conglomerate platform to a reef system in its early stages of colonization. According to Gleason (1994), branching corals rather than boulder corals are the first to colonize a disturbed area, and *Pocillopora* is the fastest and earliest colonizer of the reef at Moorea. This can explain the discrepancies in the ranking of proportions of corals. Because other corals colonize at a slower rate and will eventually change the proportions, the conglomerate may have been formed at a later stage in reef succession. However, this hypothesis fails to address the lack of *Pocillopora* and its occurrence in small fragments.

A second possible explanation for the *Pocillopora* anomaly may be sorting that can take place on the conglomerate platform before it is cemented. Immediately after being deposited, the rubble rampart is a loose pile of rubble which is exposed to both ocean water and rain water erosion. At this stage the rubble rampart is being sorted, or "reverse sorted" (Bathurst 1975). The 'potato chip theory' (Meyer personal communication) describes a phenomenon in which the largest rubble rests on the top of the pile while the smallest sediment filters down towards the bottom. Thus, the conglomerate platform would be composed of the largest pieces towards the top. My field observations confirm this theory. In one quadrat which occurred in depressed areas of the conglomerate platform, organisms were found in smaller fragments and more *Pocillopora* was found. The largest organisms deposited were the *Porites* boulders (>1 m diameter) were always found sitting on top of the platform. Furthermore, *Acropora* was also affected by sorting and was usually found upside down.

A last possible explanation is that different organisms have differential preservation rates. *Pocillopora* may be structurally less capable to withstand the transition from biosphere to lithosphere. This is certainly the case for other organisms such as *Diadema* which is extremely abundant at Point Aroa but is not found in neither the rubble patches nor is it in the conglomerate. *Diadema* are lightly skeletonized organisms, and are too fragile to endure the impact of a hurricane. This is confirmed by the fragility tests which indicated *Diadema* was completely destroyed. *Pocillopora*, which lost 45% of its mass as a live specimen and 10% as rubble, was the most fragile of the corals. *Acropora* showed a high mass change as a live specimen as well but not as rubble. This corresponds with the morphologies of the two genera. Both are branching types and live specimen were highly impacted by the fragility test. However, *Acropora* rubble does not suffer loss because of the thick soldered stem. *Pocillopora* possesses no soldering; Branches extend out of an encrusting structure which affixes itself to the substrate. Thus, it would be appropriate to sub-classify the well skeletonized organisms into further distinctions based on branching or boulder types and the presence of soldering. Furthermore, the densities of the corals correspond with the fragility: The most dense corals are also the least fragile.

Except for *Pocillopora*, most corals displayed high degrees of fidelity from their live assemblages to the death assemblages. *Porites* which ranked last on the fore reef ranked first in the conglomerate. This is not an anomaly because it is important to consider habitat preference. *Porites* is most abundant in the lagoon or back reef area. Other significant findings show that the conglomerate platform derives most of its material from the fore reef. This can be concluded by the similarities of the zones in the cluster analysis and by observation of
biomass. There is not enough material in the lagoon to form a conglomerate platform.

The differences of the rubble assemblages both in the lagoon and landward of the conglomerate platform are due to the statistical test bias towards the relative abundance, in other words the rubble patch and channel had so many more of each organism. The proportions are much more similar if one excludes *Pocillopora*.

**Conclusion**

The conglomerate platform is worthy of much closer examinations especially with taphonomic objectives. The *Pocillopora* anomaly remains relatively unresolved although evidence points to a combination of the 'potato-chip theory' and differential rates in preservation. The *Pocillopora* is broken down by the hurricane forces and subsequently the smaller pieces are deposited lower in the platform. Future studies should include a dissection if the platform and identification a different levels. It is essential to use the fossil record to study coral reef. Its life spans millennia and only few management or conservation efforts can truly judge the health of a coral reef system until the historical record is examined. The conglomerate platform at Moorea may be faithful recorder of the past reef environment if correlated with the 'potato chip theory' and further findings on differential preservasion rates.

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Figure 1. Collecting sites at Motu Tiahura and Point Aroa, Temae, on Moorea, French Polynesia.
Figure 2. Map of the Temae site and diagram of fore reef and lagoon geomorphology.
Figure 3. Proportions and percentage of corals.
Figure 3. Continued from previous page.
RESULTS OF FRAGILITY TEST

Figure 4. Percent mass change as a result of the fragility test on six corals, three mollusks and an echinoid.
The 1995 Mo'orea Class in the Last Week on Mo'orea, November, 1995.

**Left to right, top to bottom:** Dr. Ferenc de Szalay, Nathan Vaziri, Michael Schafler, Nicola Acutt, Peter Elston, Tina Liu, Ryan Houston, Andy Johnson, Ken Greenberg, Maya Skubatch, Eric Collisson, Abinash Achrekar, Lena Brook, Betty Lin, Lindsay Dinn, Camille Nowell.
R. B. Gump South Pacific Biological Research Station
University of California, Berkeley