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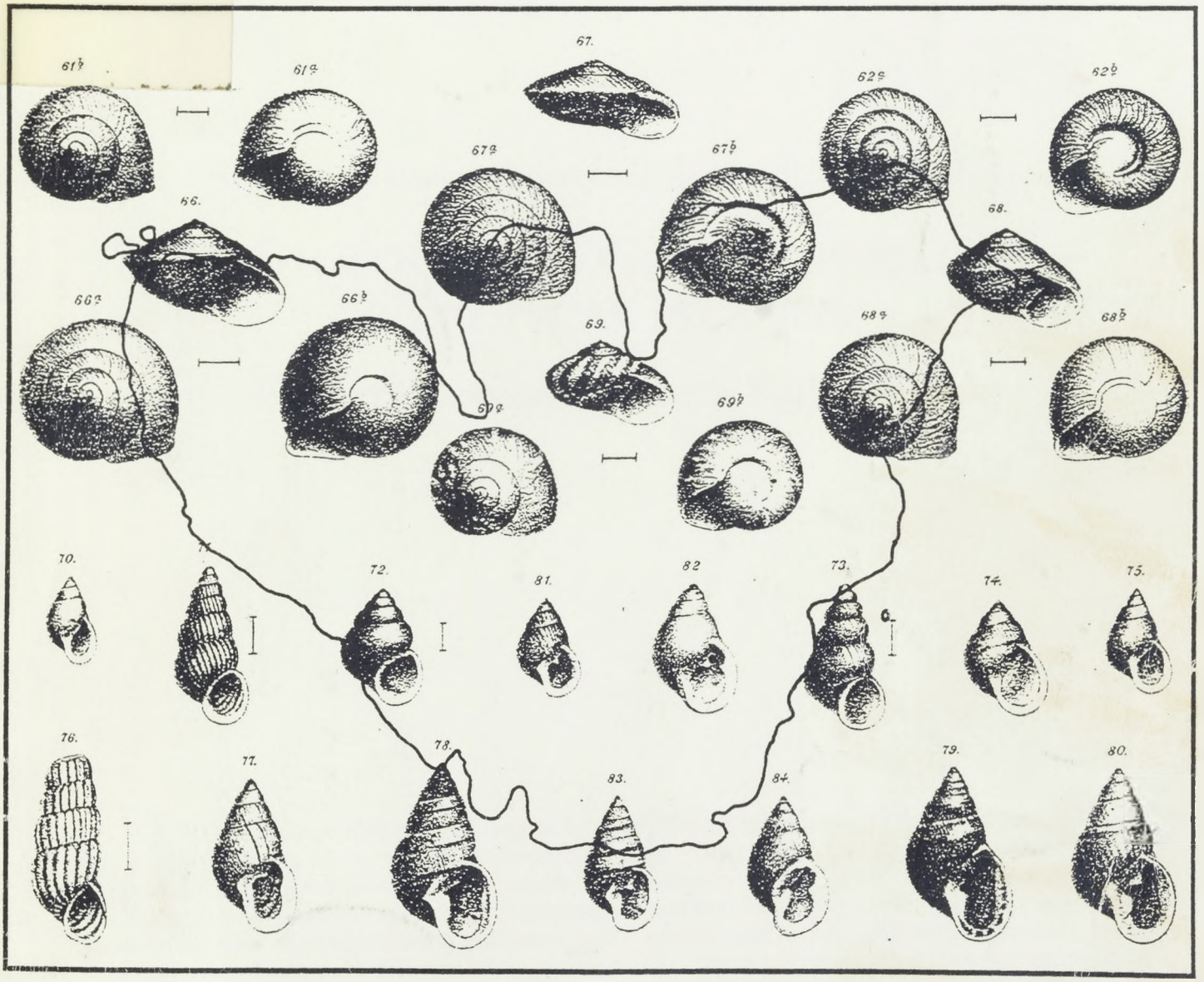
The Biology and Geomorphology of Tropical Islands

Student Research Papers, Fall 1997



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

University of California, Berkeley

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Cover: Endemic French Polynesian land snails, from Andrew Garrett's 1884 monograph of "The Terrestrial Mollusca inhabiting the Society Islands." Polymorphic species of the genus *Partula* on Moorea serve as a text-book example of adaptive radiation and study of genetic variation and the mechanisms of evolutionary change. Although all of the endemic Moorean species suffered a mass extinction following the unfortunate introduction of an alien predatory snail, breeding populations have been maintained in laboratories and zoos throughout the world. U.C. Berkeley maintains a "*Partula* reserve" on Moorea, where an international experiment is currently underway to reintroduce populations in a protected site to determine if captive-bred snails are still capable of readapting to their natural habitat and diet.

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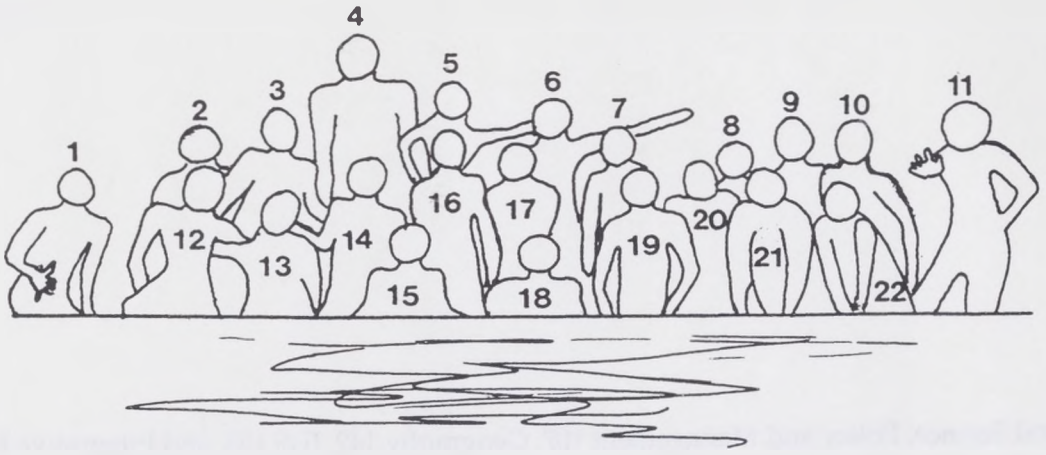
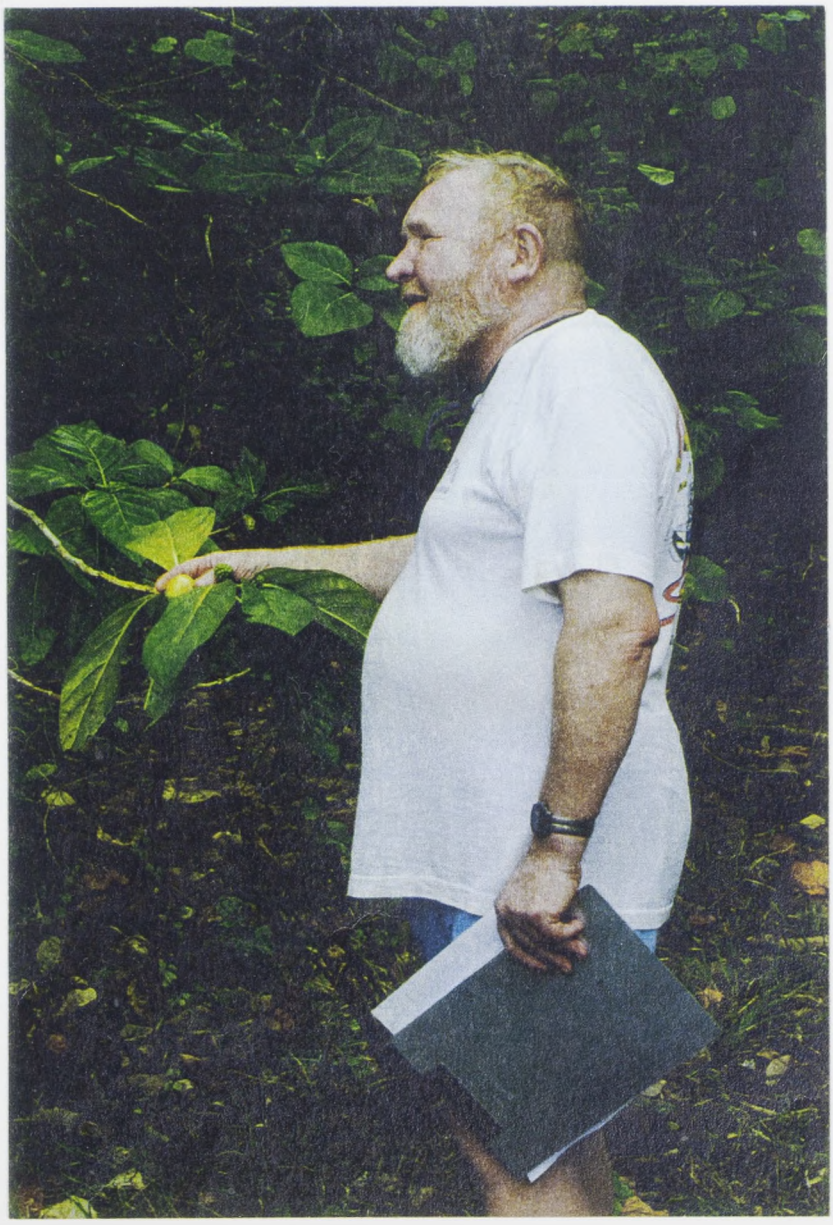


The 1991 Moorea Class, at the base of Putoa Falls. 1. John Herr (Graduate Student Instructor), 2. Lauren Gershman, 3. David Borslien, 4. Ryan Petterson, 5. Jung Lee, 6. Kelly Boyle, 7. Erica Garcia, 8. Heather Cooley, 9. Kate Shafer (Graduate Student Instructor), 10. Sarah Boyer (Graduate Student Instructor), 11. Carole Hickman (Professor, IB), 12. Jon Lee, 13. Emily Hatley, 14. Sarah Bickel, 15. Helene Tolliver, 16. Patrick Bock, 17. Minh Le, 18. Jessica Sisco, 19. Devon Muto, 20. Celina Salizar, 21. Jere Lipps (Professor, Integrative Biology), 22. Rachel Shapland.

Professor David Stoddart
(Geography)



1997 Student Research Paper

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1997 Student Research Papers

Biology and Geomorphology of Tropical Islands

INTRODUCTION

The papers in this volume are the final research product of sixteen Berkeley undergraduates chosen to participate in an intense, 15-week interdisciplinary field research course. Spanning zoology, botany, ecology, geology, geography, and conservation biology, this course offers a rare opportunity to generalize as well as specialize. Students learn about and experience the meaning of tropical oceanic islands. It is a learning and growing experience for faculty and graduate student instructors as well; a joyful (and occasionally painful) experience in living together and sharing it all.

For first month of the course students spent five days a week attending lectures and workshops, reading, assembling literature, participating in logistic preparations, talking with faculty, and thinking about the kind of research they might want to undertake. Moving from the academic setting to the Richard B. Gump South Biological Research Station, they had two weeks of intensive introduction to the natural history of French Polynesia and the range of habitats and research possibilities on Moorea. In consultation with faculty and Graduate Student Instructors, they formulated their research questions and design, in many cases around problems that became obvious and interesting only after first-hand observation and discovery in the field. They spent the next nine weeks completing their projects. They returned to Berkeley at the end for two weeks to finish data analysis and prepare their camera-ready final papers and their formal symposium presentations with professional quality slides and visual aides. Although students had an opportunity to make revisions based on our comments, the papers in this volume are unedited and appear exactly as they were turned in for reproduction.

The remarkable mix of backgrounds and interests in this year's class is reflected in their choice of habitats (marine, brackish, fresh water, and terrestrial) and taxa (e.g. vascular plants, algae, invertebrates, reef fish, freshwater eels, skinks). Two of the projects this year had no organismal component: one examining the physical and chemical features of soils as a function of practices of pineapple cultivation and the other investigating the peculiar formation of a barrier reef within a barrier reef. There was a strong component of interest in this year's class in environmental problems and research with an applied message. Seven of the research projects in this volume have an environmental component. Two deal with alien or invasive species, and five deal with the effects of land use practices or the health of natural systems. Two of the papers in the volume have been through peer review and have been accepted for publication.

The most important function of these introductory remarks is not to explain the course or this volume, but to thank the many people who have made it possible.

As organizer and coordinator for the 1997 course, I had the pleasure of working with Tracy Benning, Jere Lipps, David Stoddart, and Steve Strand as primary faculty. Other faculty who contributed guest lectures included Carla D'Antonio, Roy Caldwell, Brent Mishler, Cherie Northon, Deborah Penry, and Vince Resh. We are grateful to Beth Weil for providing orientation to library resources, Jim Hayward for working with students on water-safety skills, Karen Wetmore and Brent Mishler for orientation sessions in the Museum of Paleontology and the University Herbarium, to Cherie Northon and Don Bain for assistance with cartography, surveying, and computer resources, and to the staff of the Valley Life Sciences Building Visualization Center for assistance with graphics. Dale DeNardo was extremely helpful in help with writing the Animal Use Protocol that enabled several students to do research projects on

vertebrate subjects. Peter Connors of the Bodega Marine Laboratory contributed to a session early in the course, designed to introduce students to field research problems and techniques.

This course would not function without mature, dedicated, and talented graduate student instructors. Sarah Boyer, John Herr, and Kate Shafer were the people who really made the course work, and they are the people the students and faculty are likely to remember first as they look back on the experience.

Support for this course came from many sources. The departments of Environmental Science, Policy, and Management; Geography; and Integrative Biology all contributed personnel, equipment, and facilities. The University of California is extremely fortunate to have the Richard B. Gump South Pacific Biological Research Station as a facility for instruction as well as research, and Vince Resh as its director and also long-time faculty participant in the course. We thank Steve Strand, Executive Director of the station, and his wife Pat, for all of their help and support of the Course. We are grateful to Dr. Rene´ Galzin, Director of the Centre de Rescherches Insulaires et Observatoire de l'Environment for opening the doors of the French Station on Moorea to assist students with library and collection resources. We also thank Marimari Kellum for the tour of her garden and for sharing her knowledge of the history of Moorea.

Finally, two people who deserve extraordinary thanks for their logistical assistance are Dorothy Tabron of Integrative Biology, for her help assembling supplies and equipment, and Julie Myers of Integrative Biology for dealing cheerfully and skillfully with the nightmares of accounting and finances for the course.

Moorea is a small and geologically young island, a paradise partially spoiled and seriously endangered. For more than a century, it has provided scientists with an outdoor laboratory for research on some of the most important problems in the historical sciences. The body of research on the partulid land snails, now extinct in the wild on Moorea, is one of the monumental achievements of evolutionary biology and provides a context of importance and urgency. The Moorea course gives undergraduates a chance not only to learn science by doing science, it also puts them into a truly extraordinary island laboratory setting, where the ticking clock constantly reminds us all that, in the exciting problems that still abound here, there is research that can make a very big difference to both science and to humanity.

Carole S. Hickman

Carole S. Hickman
Department of Integrative Biology

Soil characteristics of varying aged pineapple plantations in Pao Pao Valley, Moorea, French Polynesia

Helene Tolliver
Department of Geology and Geophysics
University of California, Berkeley 94720
tigger1@uclink2.berkeley.edu

ABSTRACT. This study examines the soils of 7 pineapple plantations of varying ages on Moorea, and 2 native soil sites, to look at changes in physical and chemical characteristics in the soils. All sites have similar physical characteristics of clay quantity, texture, color, horizonation, consistency, stickiness, and plasticity. Native soil physical characteristics differ from pineapple plantation soils in structure, root and pore quantity and in pH. There are no noticeable differences in physical characteristics between pineapple plantations of varying ages. Pineapple soils usually have lower organic matter, ranging from 18.3 to 25.6 percent, than native soils, ranging from 27.3 to 29.7 percent. Pineapple soils usually have a lower water content percent than native soils. Native soils tend to have higher NH_4 concentrations and lower NO_3+NO_2 concentrations than pineapple soils. There are few differences in chemical characteristics between varying aged pineapple soils.

Keywords: tropical soils, pineapple, cultivation, Moorea, French Polynesia

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Introduction

The island of Moorea in the Society Islands of French Polynesia is a major producer of pineapples, although it was once an important vanilla bean production center during the 1950's and 1960's. The vanilla industry was abandoned due to an infestation of a destructive pest in the mid 1960's and the production of artificial vanilla flavoring. With the decline of vanilla, farmers turned to the production of pineapple, approximately 30 years ago.

Pineapple is a fruit native to the tropics, growing well in warm tropical regions with a high annual temperature and rainfall (Collins 1960). Temperature plays a significant role in the formation and maturation of the fruit, with temperatures ranging between 20-27°C for optimal growth conditions, while the maximum annual rainfall for pineapple growing regions is ~2,000mm (Ramlie 1972). The climate of Moorea is nearly optimal for growing pineapples with an average annual temperature of +22.7°C and an average annual rainfall of 2.00m (Orston 1993).

Pineapple production is centered in Pao Pao Valley with many small plots scattered throughout it. New plots for pineapples are being cleared regularly on more steep slopes of Pao Pao Valley due to the now limited space on the valley floor. The principle use of Moorean pineapples is in the production of juices and alcoholic beverages at the Jus de Fruits de Moorea factory on Pao Pao Bay. Pineapples are also sold in markets and fruit stands on Moorea and distributed throughout French Polynesia.

The pineapple farming techniques on Moorea require little use of large machinery, with the exception of the need of bulldozers every 6-7 years when fields are cleared for replanting. Farmers plant by hand, pick by hand and fertilize when needed. Pesticides are not used on Moorean pineapples due to the tough skin of the fruit and low susceptibility of the fruit to pest attacks. Even though the farming techniques on Moorea have a moderately low impact on the soils and on erosion, the pineapple plants require large amounts of nutrients from the soils to grow (Ramlie 1972). Plants are repeatedly grown on the same soils in Moorea for years without the use of cover crops or other nitrogen fixing plants to replenish soil nitrogen. Fertilizers are used when plants are first sown and a few times each year depending on the individual plot necessities.

The concepts of soil conservation are important to Moorea, 132 km^2, due to the limited availability of land for agriculture and the lack of renewable soil on the island. The combination of intense pineapple farming and increased farming on steep slopes could lead to the depletion of usable soils on Moorea due to nutrient uptake and erosion. El-Swaify (1997) states that erosion is a primary problem in agriculture expansion of tropical regions and that nutrient loss is accelerated when areas are cleared for agriculture. This could potentially be dangerous to the economy of

Moorea and the well being of the Moorean community, if current pineapple plantations are not well cared for.

The purpose of this project is to examine the physical and chemical characteristics of soils from different aged pineapple plantations, along with soils of native vegetation. Differences in pineapple plantation soils may be due to the loss of nutrients from pineapple uptake and erosion, along with changes in physical characteristics due to water infiltration, soil tillage and organic matter inputs. This study will look at changes in the pineapple fields through time and the potential long term effects of pineapple farming on the soil quality. It is important to look at the current conditions of the pineapple soils to determine the future of the pineapple fields, their potential decline, and the consequent environmental and economic effects on the people of Moorea.

Methods and Materials

Study Sites

The volcanic island of Moorea, 1.8 million years old, is located in the South Pacific Ocean (17° 30'S and 149° 50' W) (Figure 1). This island was chosen as a study site because the University of California, Berkeley, Gump Biological Research Station is located there, on Pao Pao Bay. Nine study sites were selected in Pao Pao Valley, seven of which were pineapple plantations of varying ages and two were uncultivated native vegetation areas (Figure 2). During efforts to gain permission to dig soil pits in the pineapple fields, farmers were also questioned about the history of their fields and their farming practices.

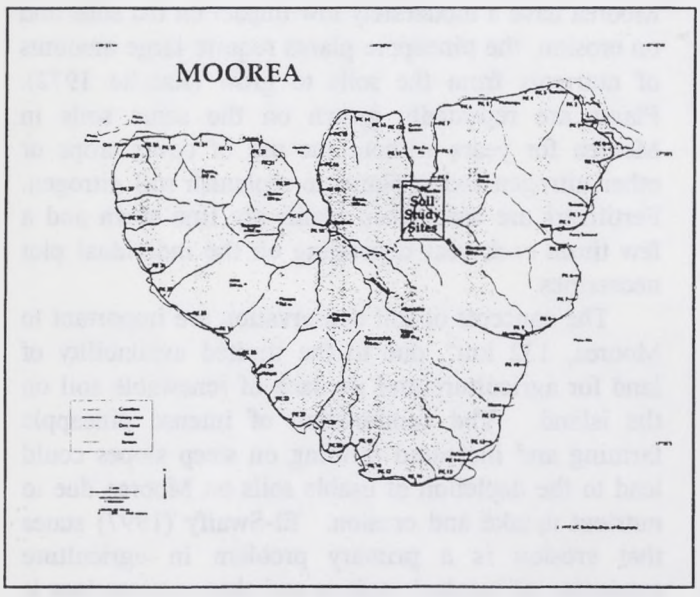

Figure 1. Location of soil study sites on the island of Moorea, French Polynesia

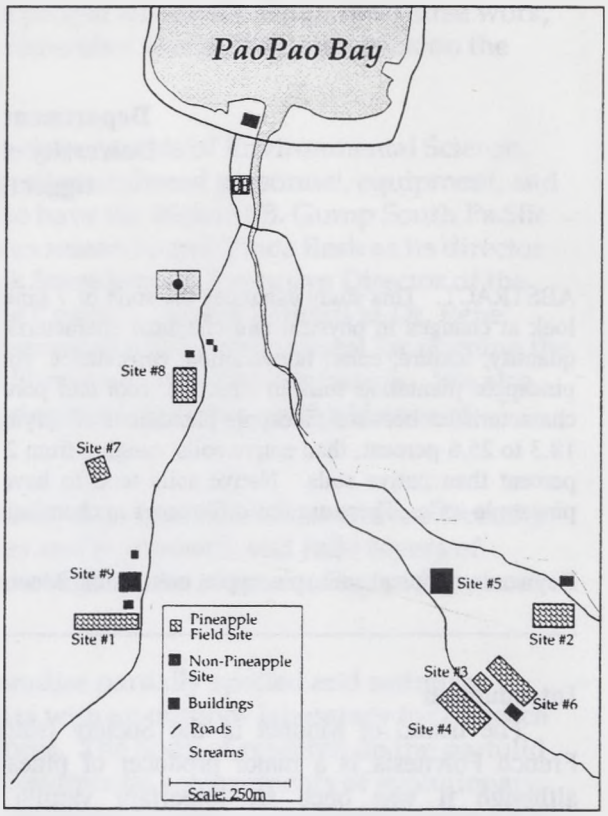

Figure 2. Location of the nine soil study sites within Pao Pao Valley, Moorea

Pineapple plantations were selected based on Hans Jenny's (1994) principles of the factors of soil formation. This includes keeping all soil forming variables including topography, climate, vegetation and parent material the same for each pineapple field, except the age of the field which varied (Table 1). Native vegetation sites were chosen based on the principles of the factors of soil formation which includes keeping topography, climate, age and parent material consistent and varying the vegetation from pineapples to native vegetation. All sites are on shallow slopes of less than 10° to reduce natural erosion as a factor in the soil forming processes. Each soil site is in the same climate regime which has the same annual rainfall and temperature, along with the same parent material. Pao Pao Valley is in an ustic moisture regime and has an isothermic temperature regime.

Soil Formation Factor	Native Vegetation Soil Sites	Pineapple Plantation Soil Sites
Topography	>10 degrees	>10 degrees
Climate	Precipitation, 2.00m/year Temperature, +22.7°C	Precipitation, 2.00m/year Temperature, +22.7°C
Vegetation	Trees and vines	Pineapples
Parent Material	Basalt and volcanic ash (1.7 million years)	Basalt and volcanic ash (1.7 million years)
Soil Age	years cultivated (0)	years cultivated (1-30)

Table 1. Factors controlling soil formation

Physical Characteristics

One soil pit was dug in each pineapple field between the rows of pineapples. Native vegetation soil pits were dug in a random location within the selected area. The soil pits were dug as deep as possible depending on the conditions of the soil, using a shovel and rock pick to dig through thick clay horizons. On average soil pits were ½ meter deep. After the soil pit was dug, horizon boundaries were selected in the field based on variations in color, structure and root depth. The thickness of each horizon was measured with a tape measure and the horizon boundary appearance was recorded in the field. The size and location of roots and pores were recorded in the field along with the structure for each horizon. The horizon boundary, root, pore and structure descriptions were made using the USDA-SCS 1994 Soil Description Guide notation methods. A sample from each horizon was collected and taken to the Gump Research Station for further analyses.

At the research station, each horizon sample was dried in the sun and both dry and moist colors were recorded using a Munsell Soil Color Chart. Soil texture was determined using the Texture-by-feel method and the corresponding flow chart. Clay percentage was estimated using the textural classification triangle. Consistence, stickiness, and plasticity were all determined by hand and the descriptions were made using the USDA-SCS 1994 Soil Description Guide notation methods. The solutions used to measure pH were made with a 2:1 distilled water to soil ratio. These solutions were stirred in small jars and then allowed to settle for one hour before measuring the supernatant with an Orion 290A pH meter.

Chemical Characteristics

Additional soil samples were collected in a single morning from each field for transport back to the United States for chemical analyses. Three samples were randomly taken at each field site from the top 10cm of the soil. The samples were brought back to the Gump Research Station and all three samples from each site were homogenized and then sieved using a 1mm sieve to remove roots. Five grams of sieved soil from each site was placed in a small cup and 50ml of 2.00M KCl solution was added to make an extraction to test for inorganic nitrogen compounds. The process was repeated for each site, shown as replicates a and b in Figures 3-6. Cups containing silt and solution were vigorously shaken for several minutes to ensure through mixing, and then allowed to settle for the next 24 hours. One cup with only 50ml of 2.00M KCl was also made as a blank and allowed to settle for 24 hours. After 24 hours, the soil solutions were poured into small vials, labeled and frozen. These were later brought back to the United States for nitrogen analyses.

To test for water content, 10g of sieved soil was put in a paper bag and then into a plant drier, along with a blank bag to determine the water content of the bags before drying. The bags were weighed before and after drying in the plant dryer for 72 hours. The remaining soil was sieved and two soil samples from each site, sieved and unsieved, were brought back to the United States for further analyses. The KCl extracts were analyzed in the ESPM Department on a Lachett Auto-Analyzer to report NH_4 and NO_3+NO_2 concentrations. Soil organic matter was determined by the combustion of 500mg of sieved soil in an oven at 845°C for approximately 1 hour. Soil samples were weighed before and after heating to determine the percentage of organic matter in the soil.

Results

Physical Characteristics

Appendices 1 and 2 list the Pedon Descriptions for each soil study site. All soil sites have high quantities of clay (with several Bt horizons) along with similar texture, dry and moist colors, boundaries, moist consistency, stickiness, and plasticity. There are differences between the native vegetation and pineapple soils in terms of structure, root and pore density, and pH. Native soils had a densely packed structure, more roots and pores throughout the horizons and a higher pH than plantain soils.

Pineapple plantation soils of different ages all have similar structure, root and pore density and pH.

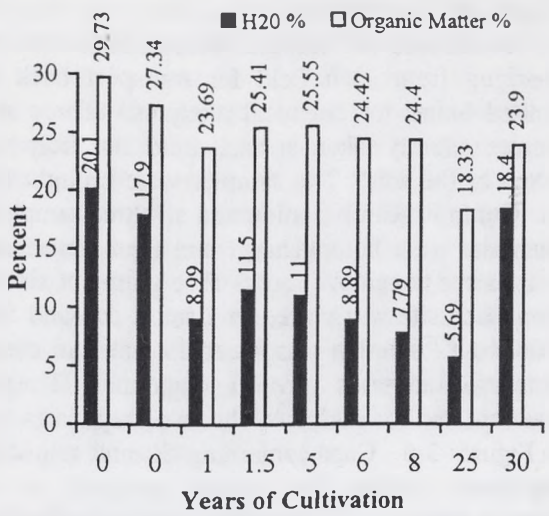

Figure 3. Years of Cultivation vs. H_2O and Organic matter percentages. Values of zero for years of cultivation represent uncultivated/native vegetation sites.

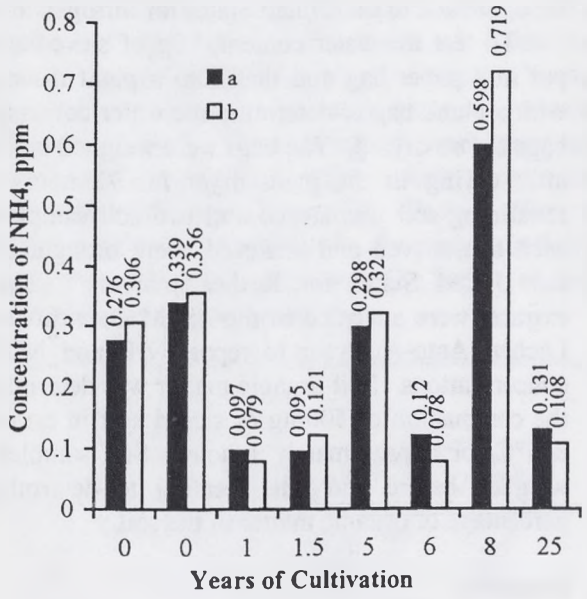

Figure 4. Years of Cultivation vs. NH_4 concentration

Chemical Characteristics

The variation in water content and organic matter in relation to time of cultivation is displayed in Figure 3. The results show a higher soil H_2O percent in the native soil sites (age 0) (17.9% to 20.1%) compared to the pineapple soils (5.69% to 18.4%). Organic matter percentages are also higher in native soils with values from 27.3% to 29.7%, while the pineapple soil values range from 18.3% to 25.6%. There is a trend between time of cultivation and water content percentages. Older pineapple soils tend to have lower water content percentages than native soils and young pineapple soils.

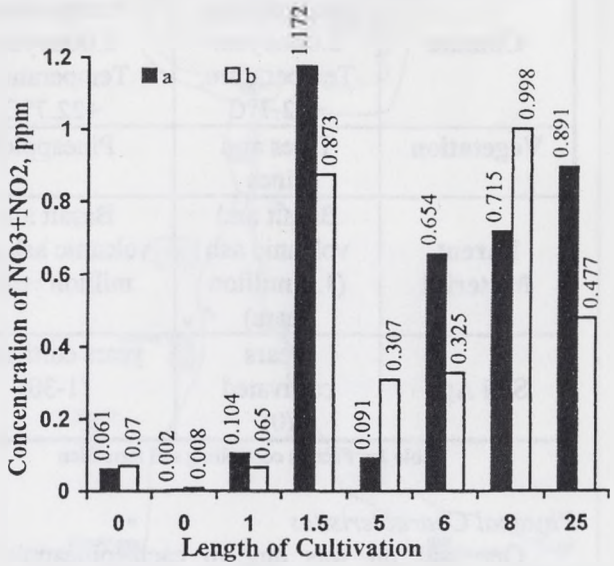

Figure 5. Length of Cultivation vs. NO_3+NO_2 concentrations

Figures 4 and 5 show the NH_4 and NO_3+NO_2 concentrations in the KCl extractions. Native soils have higher NH_4 concentrations than pineapple soils, with the exception of the 8 year plantation which had the highest NH_4 concentrations. In contrast, native soils have lower concentrations of NO_3+NO_2 ranging from 0.002ppm to 0.07ppm, compared to 0.065ppm to 1.172ppm in the cultivated soils. There were variations between the replicate tests for both NH_4 and NO_3+NO_2 which is shown in both figures. The relationship between length of cultivation and the ratio of $NH_4/(NO_3+NO_2)$ shows that native soils have high $NH_4/(NO_3+NO_2)$ ratios compared to the values for the soils under pineapple plantations (Figure 6).

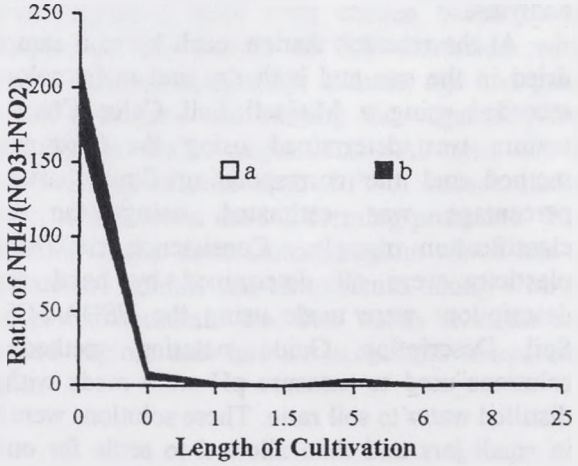

Figure 6. Length of Cultivation vs. $NH_4/(NO_3+NO_2)$

Discussion

Clay Content and Texture

All soil study sites on Moorea have several clay horizons, each with high clay percentages and fine textures. This is a result of the parent material and the climate conditions of the island. Moorea was formed from the eruption of basalt and volcanic ash which has weathered into the soils that are on the island. In tropical regions with high annual rainfall and temperature, chemical weathering of the parent material is generally accelerated by available water and the increased biological activity due to high temperatures (Shoji et al. 1993). Basalt and volcanic ash weather into several types of clay minerals which are very fine particles that are able to hold nutrients and water for plants within the charged layers of the clays (Brady 1990; Foth 1984). This is important to the soils on Moorea, which are all high in clay and therefore should be able to hold water and nutrients for plants. Pineapple plantation soils generally have lower water content percentages than native soils. This is most likely from the loss of water through evaporation from rows as a result of decreased soil cover and more direct exposure to sunlight and the aeration of the pineapple soils from bulldozing.

Color

Soil color is a factor of organic matter content and the weathering products of the parent material (Brady 1990; Foth 1984; Shoji et al. 1993). The study site soils all have similar colors indicating similar organic matter content and weathering products. The study soils are all in yellow-red Munsell Color Chart pages from the oxidation of iron within the soil, which gives the soils a red color. Low value and chroma for each soil indicates a darkening of the soil from the accumulation of organic matter. Organic matter content differs between study sites (Figure 3), but it is not as apparent through simple color analysis.

Horizon Boundaries, Moist Consistency, Stickiness, and Plasticity

Horizon boundaries of all study sites are not very distinct and therefore the given categories are gradual or diffuse. This is a result of the large amount of clay within the soils and the depth of the soil clay horizons. All soils have similar moist consistency, stickiness, and plasticity due to the similar clay contents of the soils. These features of the soil are important in planning the tilling of the soil. Since the soils are highly plastic and sticky, disturbance of the soils when wet will effect the structure of the soils and cause the clay to stick in large aggregates.

Structure

The significant difference in structure between native soils and the pineapple plantation soils is that all native soil horizons had wedge shaped aggregates which were densely packed throughout the soil profile. Pineapple plantation soils have subangular blocky structures in the top horizons with some wedge shaped aggregates in soil horizons of the bottom part of the profile. The appearance of the subangular blocky structures is a result of the tilling and bulldozing of the field for pineapple planting and due to increased soil movement in the top horizons by erosion. Soil structure is important in the movement of water within the soil profile. Loosely structured soils tend to dry out quickly and do not hold water as well as densely structured soils, similar to the native soils.

Root and Pore Density

The study sites of the native soils have high root and pore densities throughout the profiles. while pineapple plantation soil profiles have dense roots only in the top horizons. The high root density of the native soils is from the vegetation of the area and the higher number of trees on the sites. Roots tend to be large and abundant throughout the entire profile and include many small roots throughout the profile. Pineapple roots are very shallow and only extend approximately 10cm in the soil profiles of the plantations. Pores in native soils are made by organisms such as worms. which are not abundant in pineapple plantations. Pores in the upper horizons of the pineapple plantations are due to organisms and the plowing of the fields, which changes the structure of the soil and increases porosity.

Soil pH

Pineapple plantation soils tend to be lower in pH than the native soils, which are more buffered. In some agriculture situations, acidic soils would inhibit plant growth, but in the case of pineapples, they grow well in slightly acidic soil conditions (Collins 1960; Foth 1984; Ramlie 1972). Pineapples grown in less acidic soils develop calcium chlorosis, in which the pineapple is not able to absorb iron from the soil (Collins 1960; Ramlie 1972). The addition of fertilizers to the plantation soils may also reduce the pH of the soils.

Organic Matter and Water

The lower percentages of organic matter in the pineapple plantation soils is due to the decomposition of the native organic matter by microbes, stimulated by tillage, and due to the lower organic matter input from

pineapple plants. When soils are tilled, there is a general decrease in organic matter due to the breakdown in the structure of the soil and increased microbial activity, which decomposes organic matter (Brady 1990). Although there is a difference between native soils and pineapple plantation soils, the organic matter percent at each site is relatively high compared to soils of other regions of the world (Shoji et al. 1993). These relatively high organic matter values are due to the high clay content of the volcanic soils and the ability of the clay to hold organic matter physically and chemically within layers (Shoji et al. 1993). The water percent is related to organic matter percent because of the ability of organic matter to hold water within layers.

The organic matter and water content percentages of the pineapple plantations show a decreasing trend from younger pineapple plantations to older plantations (Figure 3). This trend is due to the continual growth of pineapple on the same plots with no cover cropping or rotation, and therefore the only organic matter input is from the pineapple leaves and roots. Pineapple leaves are very tough and have a waxy coating which would not allow quick decomposition and renewal of organic matter into the soils.

The decrease in the water content is due to the increased tillage in the older fields, which decreases the structure of the fields and increases evaporation. There are high organic matter and water percentages in the thirty year old field which did not follow the trend of the other pineapple fields. This difference may be due to the abandonment of the field, which has not been worked in approximately 8 years. The 30 year field has significant overgrowth of pineapple plants, weeds and grasses. There is little exposed soil to sunlight which would help to remove water from the soil through evaporation. The high amount of organic matter may be due to the input from weed decay and from the input of unpicked pineapples.

The high organic matter content of all of the sites may be due to water in the soil samples which were tested, if the soils were not completely dried before weighing. If there was water in the samples it would have increased the weight percent change of the soil after heating, which would have been accounted as soil organic matter during the measuring process.

NH_4 and NO_3+NO_2

Nitrogen in soil is found in several forms due to the cycling of nitrogen compounds by microorganisms. The relationships between NH_4 and NO_3+NO_2 concentrations within the study sites can partially be explained through the nitrogen cycle within the soil. The concentrations of NH_4 in the pineapple soils show no trend with age, but are generally lower than the concentrations of the native soils (with the exception in the 8 year field) (Figure 4). NH_4 is a product in the process of mineralization of organic matter by organisms in the soil (Brady 1990). Pineapple plantation soils contain less organic matter than the native soils, which may help explain the lower concentrations of NH_4 in the pineapple plantation soils.

NO_3 and NO_2 are produced from NH_4 by the process of nitrification by two groups of organisms, *Nitrosomonas* and *Nitrobacters* (Brady, 1990). Conditions which influence the process of nitrification are the abundance of oxygen and of ammonia (Brady 1990; Amundson and Davidson 1990). Denitrification is a process in which NO_3 and NO_2 are lost to the atmosphere as reduced gases due to processes by anaerobic organisms (Brady, 1990). Denitrification occurs under anaerobic conditions within the soil, often influenced by the presence of excess water (Brady 1990; Amundson and Davidson 1990).

The NO_3+NO_2 concentrations vary randomly within the pineapple soils, but the concentrations of the pineapple soils are all higher than the concentrations of NO_3+NO_2 in the native soils (Figure 5). The low concentrations in the native soils may indicate low oxygen availability, which can be related to the high percentage of H_20 within the sites. The process of nitrification is also known to increase with the cultivation of soils, due to aeration of the soils by tillage (Brady, 1990). This may help to explain the higher values of NO_3+NO_2 within the pineapple plantation soil sites. Low concentrations in the native soils may also be due to the increased number of plants and plant roots which may be taking in more NO_3+NO_2 than the pineapple fields.

The $NH_4/(NO_2+NO_3)$ ratio decreases as the soils are cultivated (Figure 6). It may indicate a trend in nitrogen cycling within the soils of the pineapple plantations. This reduction in nitrogen has led to the need for fertilization of the pineapple plantations on Moorea. There are no set fertilizing plans for the pineapple fields, but it is done at the first planting of the immature pineapple plants and two or three times each year, depending on the requirements of individual pineapple fields.

The effects of fertilization on the NH_4 and NO_3+NO_2 concentrations in the pineapple soils are not completely clear. The process of fertilization with phosphorus or potassium (which are both used on Moorean pineapple fields) can lead to the increase of nitrification in soils (Brady 1990). The increase in nitrification due to fertilization may help to explain the lower NH_4 and higher NO_3+NO_2 concentrations in

pineapple soils than native soils. This may be because of the breakdown of NH_4 by nitrification which would reduce concentrations in pineapple soils, and the subsequent increase in NO_3+NO_2 concentrations as nitrification products.

Conclusions

Pineapple cultivation on Moorea changes the physical soil characteristics very little. Bulldozing of the pineapple fields has led to changes in soil structure, with a change from wedge-shaped aggregates in native vegetation soils, to less dense subangular blocky aggregates in pineapple plantations. Roots and pores are more common in native soils from the increased vegetation. Soil pH tends to be less acidic in native soils than in pineapple plantation soils. The effects of pineapple plantations on the physical aspects of the soils are not significantly damaging to the soils, and are not directly related to the age of the pineapple plantation.

There are differences in chemical soil characteristics between soils of native sites and pineapple plantations. Organic matter and water content percents tend to be higher in native soils. Native soils tend to have higher NH_4 concentrations than pineapple plantations due to the higher percentages of organic matter and water which leads to the production of NH_4 through the process of mineralization. Native soils tend to have low NO_3+NO_2 concentrations due to the higher water content percentages which leads to denitrification, while pineapple plantations have higher NO_3+NO_2 concentrations due to the process of nitrification which is accelerated by agriculture methods. Fertilization may also lead to decreased NH_4 and increased NO_3+NO_2 concentrations in pineapple soils. Further studies of the pineapple soils in Moorea will lead to more conclusive information on the effects of pineapple cultivation on soils. Long term monitoring of nutrients would provide valuable information on nutrient losses from pineapple cultivation practices.

Pineapple farming in Moorea, although low impact, still has an effect on the soils. Nutrient loss can be lessened by the addition of fertilizers, but this does not add organic matter back to the soil. The use of cover crops after plowing or the use of inter-row crops could be an alternative solution to fertilizing and can add organic matter to the soil. The potential erosion problems of the new plantations on steeper slopes in Pao Pao Valley can be reduced through the use of terraces. Terracing would also reduce the runoff of sediment and nutrients from the pineapple plantations into the streams and Pao Pao Bay.

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Appendix 1
Soil Description Terms (from the USDA-SCS Soil Description Guide)

Moist Consitence
NS-Non-smeary
WS-Weakly Smeary
MS-Moderately Smeary
SM-Strongly Smeary

Stickiness
SO-Non-Sticky
SS-Slightly Sticky
MS-Moderately Sticky
VS-Very Sticky

Plasticity
PO-Non-plastic
SP-Slightly Plastic
MP-Moderately Plastic
VP-Very Plastic

Structure
Grade:
1-weak
2-moderate
3-strong
5-weak and moderate
6-moderate and strong
Code Size:
VF-very fine
FF-very fine and fine
F-fine
FM-fine and medium
M-medium
MC-medium and coarse
CO-coarse
CV-coarse and very coarse
VC- very coarse
VN-very thin
TN-thin
TK- thick
VK-very thick
Shape:
ABK-angular blocky
COL-columnar
GR- granular
LP-lenticular platy
MA-massive
SBK-subangular blocky
PR-prismatic
GR-single grain
WEG- wedge shaped aggregates

Roots and Pores
Location:
P-between peds
C-in cracks
T-throughout
Quantity (per area):
F-Few (<1)
VF-Very Few (<0.2)
MF-Moderately Few (0.2-1)
C-Common (1-5)
M-Many (>5)
Size (mm):
V1-Very Fine (<1)
1-Fine (1-2)
2-Medium (2-5)
3-Coarse (5-10)
4-Very Coarse (>10)
11-Very Fine and Fine
V2-Very Fine to Medium
V3-Very Fine to Coarse
12-Fine and Medium
13-Fine to Coarse
23-Medium and Coarse

Boundary
Distinctness:
A-Abrupt
C-Clear
D-Diffuse
G-Gradual
Topography:
S-Smooth
W-Wavy
I-Irregular
B-Broken

Soil #1 (Pineapple plantation, 1year)

Horizon	Depth	Color-Dry	Color-Moist	Texture, % clay	Structure	Clay Films	Roots	Pores	pH	Boundary	Moist Consitence	Stickiness	Plasticity
1-Ap	0-3cm	10YR 3/4	7.5YR 3/4	CLAY LOAM 40%	2-FM-SBK		T-M-12	C-12	5.88	G-W	MS	MS	VP
2-Bt1	3-9cm	10YR 4/3	7.5YR 3/2	CLAY 45%	6-MC-SBK	YES	T-M-2	C-12	5.95	G-W	SM	VS	VP
3-Bt2	9-19cm	7.5YR 3/2	7.5YR 3/4	CLAY 50%	3-VC-WEG	YES	T-C-2	M-13	6.04	C-W	SM	VS	VP
4-Bt3	19-34cm	7.5YR 3/2	7.5YR 3/4	CLAY LOAM 40%	3-VC-WEG	YES	P-C-1	M-13	6.2	C-I	MS	VS	VP
5-BCt1	34-56cm	10YR 4/4	10YR 3/3	LOAM 25%	2-C-WEG		P-VF-11	C-12	6.51	C-I	MS	SS	MP
6-BCt2	56-72+cm	10YR 4/6	10YR 4/4	LOAM 20%	2-MC-SBK		P-VF-1	C-12	6.53		MS	SS	SP

Soil #2 (Pineapple plantation, 6 years)

Horizon	Depth	Color-Dry	Color-Moist	Texture, % clay	Structure	Clay Films	Roots	Pores	pH	Boundary	Moist Consitence	Stickiness	Plasticity
1-Ap	0-2cm	10YR 4/4	7.5YR 3/4	SANDY CLAY LOAM 25%	6-FM-SBK		F-M-12	M-11	5.4	D-S	WS	SS	MP
2-Bt1	2-12cm	7.5YR 3/4	5YR 3/4	CLAY LOAM 35%	6-MC-SBK	YES	P-M-1	M-12	5.12	D-W	MS	MS	VP
3-Bt2	12-24cm	5YR 3/3	5YR 4/6	CLAY LOAM 40%	5-MC-SBK	YES	P-C-1	M-12	4.97	G-I	MS	MS	VP
4-Bt3	24-39cm	5YR 3/4	5YR 4/6	CLAY 50%	5-FM-SBK	YES	P-VF-V1	M-12	4.98	G-I	SM	VS	VP
5-Bt4	39-51+cm	7.5YR 3/4	5YR 3/4	CLAY 50%	6-FM-CDY	YES	P-VF-V1	M-12	5.01		SM	VS	VP

Soil #3 (Pineapple plantation, 8 years)

Horizon	Depth	Color-Dry	Color-Moist	Texture, % clay	Structure	Clay Films	Roots	Pores	pH	Boundary	Moist Consitence	Stickiness	Plasticity
1-Ap	0-3cm	10YR 3/4	5YR 3/3	SILTY CLAY LOAM 30%	6-MC-SBK		T-M-V2	M-23	5.43	G-S	WS	SS	SP
2-Bt1	3-10cm	5YR 3/3	5YR 3/4	SILTY CLAY LOAM 35%	6-MC-SBK	YES	T-M-V2	M-V2	5.12	G-S	MS	SS	VP
3-Bt2	10-17cm	5YR 3/3	5YR 3/4	CLAY LOAM 40%	6-FM-SBK	YES	P-M-V2	M-V2	5.21	C-S	MS	MS	VP
4-Bt3	17-25cm	5YR 3/3	5YR 3/4	SILTY CLAY 45%	6-CO-WEG	YES	C-C-11	C-V2	5.25	D-S	MS	VS	VP
5-Bt4	25-39cm	7.5YR 3/3	5YR 3/4	SILTY CLAY 45%	6-CO-WEG	YES	P-F-11	M-11	5.44	G-S	SM	VS	VP
6-Bt5	39-45+cm	5YR 3/3	5YR 3/4	SLITY CLAY 50%	6-CO-WEG	YES	C-F-V1	M-11	5.29		SM	VS	VP

Soil #4 (Pineapple plantation, 1.5 years)

Horizon	Depth	Color-Dry	Color-Moist	Texture, % clay	Structure	Clay Films	Roots	Pores	pH	Boundary	Moist Consitence	Stickiness	Plasticity
1-Ap	0-4cm	10YR 4/3	10YR 4/3	SANDY CLAY LOAM 25%	6-FM-SBK		T-M-FM	M-V2	5.32	D-W	WS	SS	MP
2-Bt1	4-14cm	7.5YR 3/2	10YR/4/4	SILTY CLAY LOAM 30%	6-FM-SBK	YES	T-M-FM	M-V2	5.13	G-W	MS	MS	VP
3-Bt2	14-21cm	5YR 3/3	10YR 4/4	CLAY LOAM 40%	5-MC-WEG	YES	P-C-V2	C-11	5.41	C-S	SM	MS	VP
4-Bt3	21-34cm	7.5YR 3/4	10YR 4/4	CLAY LOAM 40%	5-MC-WEG	YES	P-C-V2	C-11	5.74	G-S	SM	MS	VP
5-Bt4	34-47+cm	7.5YR 3/4	10YR 4/4	CLAY LOAM 45%	5-MC-WEG	YES	P-C-11	C-11	5.75		SM	MS	VP

Soil #6 (Pineapple plantation, 5 years)

Horizon	Depth	Color-Dry	Color-Moist	Texture, % clay	Structure	Clay Films	Roots	Pores	pH	Boundary	Moist Consitence	Stickiness	Plasticity
1-Ap	0-4cm	10YR 3/4	7.5YR 3/4	SANDY CLAY LOAM 25%	6-FM-SBK		T-M-V3	M-V2	5.3	D-S	MS	SS	MP
2-Bt1	4-12cm	5YR 3/3	7.5YR 3/4	SANDY CLAY LOAM 25%	6-FM-SBK	YES	T-M-V2	M-V2	5.03	C-S	MS	SS	MP
3-Bt2	12-20cm	5YR 3/3	7.5YR 3/4	SANDY LOAM 20%	5-MC-SBK	YES	P-M-11	C-V2	5.04	G-S	WS	SS	MP
4-Bt3	20-29cm	5YR 3/4	7.5YR 3/4	SANDY LOAM 20%	5-MC-SBK	YES	P-C-V2	C-11	4.87	D-S	WS	SS	MP
5-Bt4	29-36+cm	5YR 3/4	7.5YR 3/4	SILT LOAM 25%	5-MC-SBK	YES	P-MF-11	C-11	4.81		MS	SS	MP

Soil #7 (Pineapple plantation, 30 years)

Horizon	Depth	Color-Dry	Color-Moist	Texture, % clay	Structure	Clay Films	Roots	Pores	pH	Boundary	Moist Consitence	Stickiness	Plasticity
1-Ap	0-6cm	5YR 3/3	5YR 3/4	SILTY CLAY 40%	5-MC-WEG		T-M-V2	M-V2	5.25	G-S	SM	MS	VP
2-Bt1	6-12cm	5YR 3/3	5YR 3/4	SILTY CLAY LOAM 35%	5-MC-WEG	YES	P-M-11	M-V2	5.3	D-S	SM	MS	VP
3-Bt2	12-18cm	5YR 3/2	5YR 3/2	SILTY CLAY LOAM 35%	5-C-WEG	YES	P-C-11	C-V2	5.53	D-W	WS	SS	MP
4-Bt3	18-27cm	5YR 3/2	5YR 3/2	SILTY CLAY 40%	5-CO-CDY	YES	P-MF-11	C-V3	5.91	C-W	MS	SS	MP
5-Bt4	27-39cm	5YR 3/4	5YR 3/3	SILTY CLAY 45%	5-MC-WEG	YES	P-MF-11	C-V3	5.92	G-S	SM	MS	VP
6-BCt	39-53+cm	5YR 3/4	5YR 3/4	SILTY CLAY LOAM 40%	5-M-WEG	YES	P-MF-11	C-V2	5.88		SM	MS	VP

Soil #8 (Pineapple plantation, 25 years)

Horizon	Depth	Color-Dry	Color-Moist	Texture, % clay	Structure	Clay Films	Roots	Pores	pH	Boundary	Moist Consitence	Stickiness	Plasticity
1-Ap	0-13cm	10YR 3/3	10YR 3/3	SANDY CLAY LOAM 20%	5-FM-SBK		C-M-V2	M-11	5.3	G-W	MS	SS	MP
2-Bt1	13-27cm	10YR4/2	10YR 3/3	SANDY CLAY LOAM 25%	5-FM-SBK	YES	C-M-V2	M-11	5.56	G-W	MS	MS	VP
3-Bt2	27-40cm	10YR 3/3	10YR 3/2	SANDY CLAY LOAM 25%	5-FM-SBK	YES	C-C-11	M-11	5.73		MS	MS	VP

Soil #5 (Native vegetation, non-cultivated)

Horizon	Depth	Color-Dry	Color-Moist	Texture, % clay	Structure	Clay Films	Roots	Pores	pH	Boundary	Moist Consitence	Stickiness	Plasticity
1-A	0-5cm	5YR 3/3	10YR 3/4	CLAY LOAM 28%	5-FM-WEG		T-M-4 & T-M-V2	M-V2	6.45	G-S	MS	SS	MP
2-Bt1	5-16cm	5YR 3/3	10YR 4/4	CLAY LOAM 30%	5-FM-WEG	YES	T-C-4 & T-M-V2	M-V2	6.45	G-S	MS	SS	MP
3-Bt2	16-27cm	7.5YR 3/4	10YR 4/4	CLAY LOAM 35%	5-MC-WEG	YES	T-C-4 & T-C-V2	M-V2	6.55	D-S	MS	MS	VP
4-Bt3	27-39cm	5YR 3/4	7.5YR 4/4	CLAY LOAM 40%	5-MC-WEG	YES	C-MF-4 & C-C-V2	M-V2	5.67	G-S	MS	MS	MP
5-Bt4	39-54+cm	7.5YR 4/4	7.5YR 4/6	SILTY CLAY 45%	6-MC-WEG	YES	C-MF-4 & C-MF-11	M-V2	5.38		SM	VS	VP

Soil #9 (Native Vegetation, non-cultivated

Horizon	Depth	Color-Dry	Color-Moist	Texture, % clay	Structure	Clay Films	Roots	Pores	pH	Boundary	Moist Consitence	Stickiness	Plasticity
1-A	0-5cm	10YR 3/3	10YR 4/2	CLAY LOAM 30%	6-FM-WEG		T-F-4 & T-M-12	M-V2	6.03	D-S	MS	MS	VP
2-Bt1	5-14cm	5YR 3/2	10YR 4/3	CLAY LOAM 30%	6-MC-WEG	YES	T-F-4 & T-M-12	M-V2	5.81	D-S	MS	MS	VP
3-Bt2	14-26cm	5YR 3/2	10YR 3/3	SILTY CLAY LOAM 35%	6-FM-WEG	YES	T-C-4 & C-M-V2	M-V2	5.81	G-S	MS	VS	VP
4-Bt3	26-31cm	10YR 3/4	10YR 3/4	SILTY CLAY LOAM 35%	6-FM-WEG	YES	T-C-4 & C-M-V2	C-11	5.49	D-S	MS	VS	VP
5-Bt4	31-37cm	10YR 3/4	10YR 4/3	SILTY CLAY LOAM 40%	6-FM-WEG	YES	T-C-4 & C-M-V3	C-V2	5.59	G-S	MS	VS	VP
6-Bt5	37-43+cm	10YR 3/4	10YR 4/3	SILTY CLAY LOAM 40%	6-FM-CDY-WEG	YES	T-C-4 & C-M-V2	C-V2	5.48		MS	MS	VP

Distribution and Dispersal of *Miconia calvescens* DC, an invasive alien tree, in Moorea, French Polynesia

Patrick A. Bock
Department of Geography
University of California, Berkeley 94720

ABSTRACT. Field surveys conducted over two months in 1997 on Moorea found that *Miconia calvescens* DC. (Melastomataceae), an invasive alien tree from Central America, occupies most river valleys and all of the high peaks and ridges of the eastern portion of the island. Since 1993 *Miconia* has spread considerably in Opunohu valley and along the east side of the island's main ridge. A detailed study of the Putoa River suggests the important role of rivers as dispersal mechanism, as quadrat samples found most plants to be within 3 m of the stream. In addition, a permanent transect was put in place for future measurements of growth rates and invasion rates. Biological control seems to be the only way of eradicating *Miconia*, but some physical and chemical control should be implemented in the interim to protect lightly invaded areas.

KEYWORDS: biological invasion, *Miconia calvescens*, Moorea, oceanic island

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Introduction

The acute vulnerability of tropical islands to introduced species has been well documented (Cowie 1992). The tropical plant *Miconia calvescens* De Candolle provides a striking example of the success of an introduced species in a habitat suitable for growth without the limiting factors of its native environment. Already dominant over two-thirds of Tahiti, *Miconia* is presently in the middle phases of invasion on Moorea, 20 km away, where it poses a serious threat to the native flora and biological diversity of the island (Meyer and Florence 1996).

Study Species

Miconia calvescens, of family Melastomataceae, is a small tree up to 15 m tall with trinerved leaves, and panicles of white flowers, which produce dark berries 0.5-0.8 cm in diameter (Meyer and Florence 1996). It can grow in either open sunlight or dense shade in lowland and montane tropical forests receiving around 2 m annual rainfall (Gagné et al. 1992). The leaves are green with either green or purple undersides. The variety with purple undersides has long been prized by horticulturists for the beauty of its leaves and their velvety texture (in horticulture the plant is known as *M. magnifica* Triana). As a result specimens were taken from its native habitat in Central America to botanical gardens around the world (Meyer 1994).

Native Range

Miconia occurs naturally throughout Central and South America from 18°N to 26°S, from sea level to around 2000m elevation in lowland and montane rainforest. The bicolorous form now invading Polynesia occurs naturally only from southern Mexico to Costa Rica (18°N to 8°N). In its native habitat *Miconia* is a shade-tolerant tree that occupies openings in forest gaps. According to F. Almeda, *Miconia* is never common at any one site in its native range (Meyer 1996).

Seed Production and Dispersal Mechanisms

Miconia has been successful in large part because of its reproductive biology. Each panicle on a fruiting tree yields hundreds of 5-6 mm berries each containing 140-230 seeds 0.7 by 0.5 mm long, enabling a mature tree to produce hundreds of thousands of seeds per fruiting. With three peaks of fruiting and flowering per year, a mature plant can produce over a million seeds per year. These seeds can then germinate after over two years in the soil bank (Meyer 1994).

The small, light seeds are dispersed by three main mechanisms: gravity, wind, and animals, namely frugivorous birds (*Zosterops lateralis* and *Pycnonotus cafer*), rats (*Rattus exulans*), and, humans (who inadvertently transport seeds in treads of hiking boots or pots of soil among other things) (Meyer 1996). Dispersal by water is also a possibility, as seeds germinate from fruits left

floating in water over two months (Meyer 1997).

Miconia in the Society Islands

Miconia was first brought to the Papeari Botanical Garden on Tahiti in 1937 by Harrison Smith. By the 1970s it had escaped and invaded enough to warrant strong concern (Botanist Raynal named it the major threat to Tahitian vegetation) (Meyer 1996). At the same time the first populations were noticed on Moorea at the summit of Mount Mouaputa and below the west face of Mt. Rotui (Meyer 1994). Seeds are believed to have arrived via the tradewinds blowing from Tahiti, via birds, or via humans. By 1993 there were at least four areas of dense *Miconia* invasion on Moorea (Schwartz 1993).

In the Society Islands *Miconia* poses a serious threat to the native flora. The dense shade created by its overlapping leaves block sunlight from many native species. More than over 100 endemic plants are directly endangered by *Miconia* , and one plant, *Hemandia temarii*, may already be extinct (Meyer and Florence 1996).

Objectives of Study

This study had two objectives. The first was to map the distribution of *Miconia* on Moorea to define its current distribution and to examine the extent of its spread since 1993, when a distribution study was done by J. Schwartz. The second was to study the distribution and pattern of dispersal in one valley invaded since 1993 to understand how the species may be spreading or where it is most abundant.

Materials and Methods

Distribution Study

The high oceanic island of Moorea lies at 17°S, 149°W, 20 km southwest of Tahiti in the Society Islands of French Polynesia. A volcanic island of 1.5 to 2.2 million years, Moorea is remarkable for its sheer peaks and "knife-edge" ridges, which channel water down to the ocean through about ten main valleys. Rainfall over 2 meters a year for much of the island (ORSTOM 1993) supports a dense vegetation that covers most of the ground in shade.

Between September and November 1997, surveys were made on foot of the valleys and ridge lines on the eastern portion of Moorea (east of Mt. Mouroa and Opunohu Bay). Where *Miconia* plants were spotted, their height and location relative to features of the landscape were noted (for instance, in stream bed or on 85° cliff face), as well as other abundant species and interesting observations. Where large populations were present the estimated number and density as well as average height of the plants was recorded. Surveys of the exposed highlands were made both with binoculars and a telescope. In addition to plants seen firsthand, areas in the highlands were shaded according to approximations of levels seen by Dr. Tim Krantz and Dr. J.-Y. Meyer during a helicopter survey in March 1996 (Krantz 1997).

Because of the high level of invasion and patchy nature of the study species, mapping was done in broad areas rather than in absolutely precise locations to better reflect the extent of invasion. Because *Miconia* frequency generally increases towards the highlands (Meyer 96), in a valley where *Miconia* was observed, the entire watershed from the point at which the plant was first sighted was shaded according to the level of invasion observed. The levels of *Miconia* invasion were categorized according to the following scheme:

Complete invasion- Dense Monotypic stands of mature *Miconia* trees at an estimated density exceeding 10/ 10square meters
Heavy invasion- Most plants are juveniles with up to 10% mature at estimated densities between 5 - 10/10 square meters
Moderate invasion- Characterized by either 1) populations of large juvenile and adult trees in estimated densities less than 2/ 10 square meters or 2) juvenile and seedling populations with less than 2% mature in densities approaching 5-10/10 square meters where present
Preliminary invasion- Mainly seedlings with less than 10% juveniles and no mature plants in sparse densities
Isolated plant(s)- Mature plants away from any eatablished population.

For this study seedlings are defined as plants less than a meter in height, juveniles as plants between one and three meters in height, and mature plants as taller than three meters.

Dispersal Study

The Hotutea valley lies near the middle of Moorea's eastern coast (17°33'S, 149°47'W) behind the town of Afareaitu (see figure 1). The valley collects water from the immense

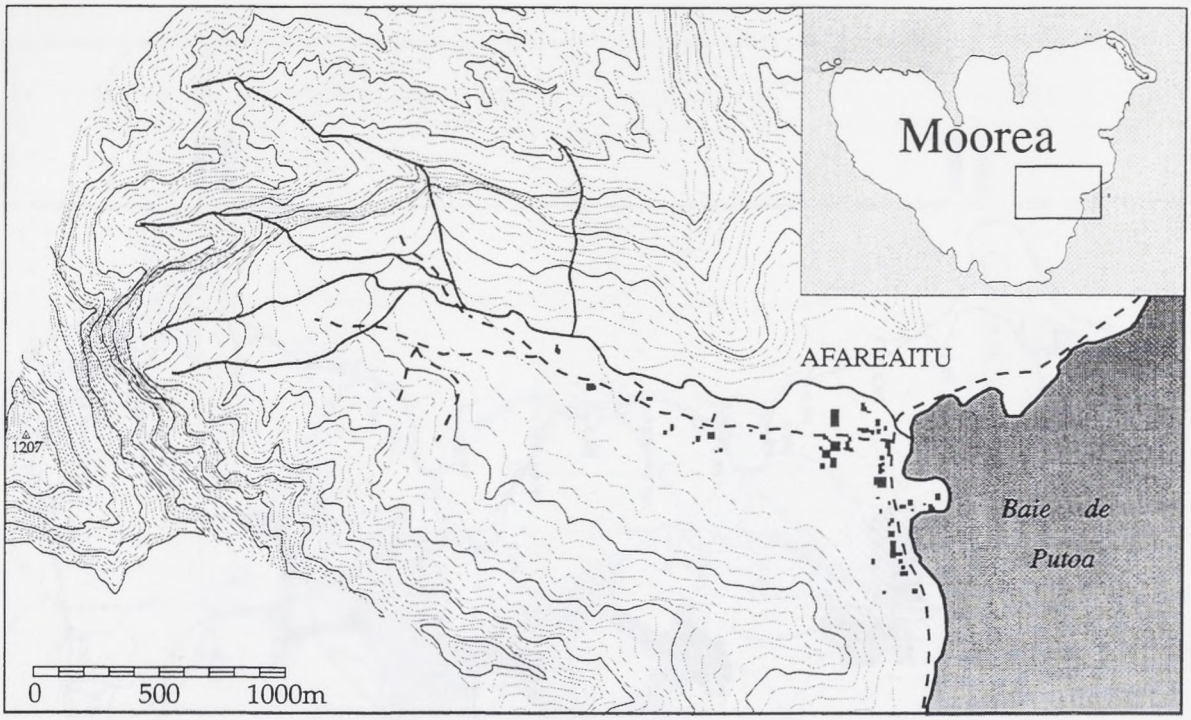

Figure 1. The Hotutea valley, site of dispersal study

Northeast face of Mount Tohiea, Moorea's highest peak at 1207 m, and the remote highlands between it and Mt. Mouaputa, and is drained by the Putoa River. The North Fork of the Putoa, which includes the popular tourist waterfall, was chosen as site for detailed observation because the *Miconia* present displays an peculiar population structure and because this valley was recommended by Schwartz in 1993 as a site for protection based on the complete absence of *Miconia*.

After surveying the length of the North Fork, quadrat sampling was done to test the hypothesis that seeds are being dispersed by the stream. Ten 10 x 10 m quadrats were placed with one edge at the stream, and the height of each plant and its distance from the stream were measured. The quadrats were placed at intervals where the plant was present from the downstream extent of *Miconia* up to the base of the falls. In one quadrat a number of plants were found on the edge of a dry stream bed. For these plants, the distance to the middle of that stream bed was recorded. It is important to note that at the time of the study Moorea was experiencing a uncharacteristic dry spell, and therefore the stream was at relatively low levels.

In a heavily invaded area just east of the waterfall, plants lying within a meter of three 15m transects were measured and recorded to sample the density and size structure of that population. The combined transects sampled an area of 90 square meters.

Finally, a permanent transect was put in place for future measurement of the spread of *Miconia*. The 50 m transect is marked at either end and at its midpoint by gray PVC pipe 32 mm in diameter hammered in the ground. It is on the eastern bank of the North Fork, roughly 20 m upstream of the confluence of the stream flowing from the valley's other waterfall (this is the second stream crossed on the dirt road leading to the "tourist" waterfall, just before the road turns off to a trail). All of the plants on the eastern bank within 10 m of the transect were measured, and their distance from the main stream recorded for purposes of relocation. (The area covered by the transect included a side stream that split off and joined back with the main stream within the 50 meters. Plants here were measured relative to the main stream to avoid confusion).

Results

Distribution Study

Miconia has invaded three valleys where it was not seen by Schwartz in 1993 (figure 2). These three, the Hotutea, Vaipohe, and Papeare, are all on Moorea's east coast. In addition, it has spread extensively down the Vaioro River valley, behind the Belvedere, and along the Rotui loop road directly behind Mt. Rotui itself.

The invasive plant was also found in a number of areas not surveyed by Schwartz.

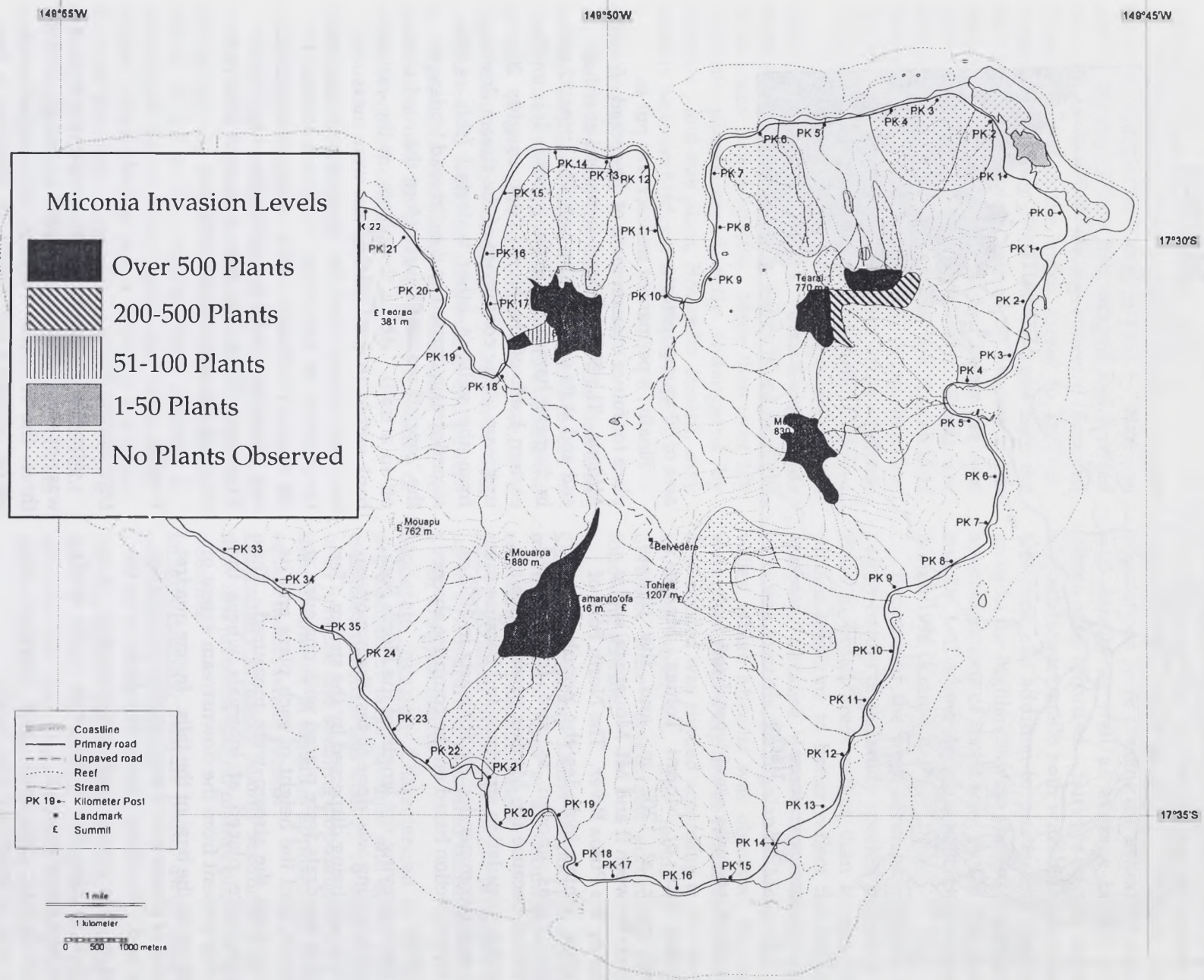

Figure 2. 1993 Miconia Distribution (after Schwartz)

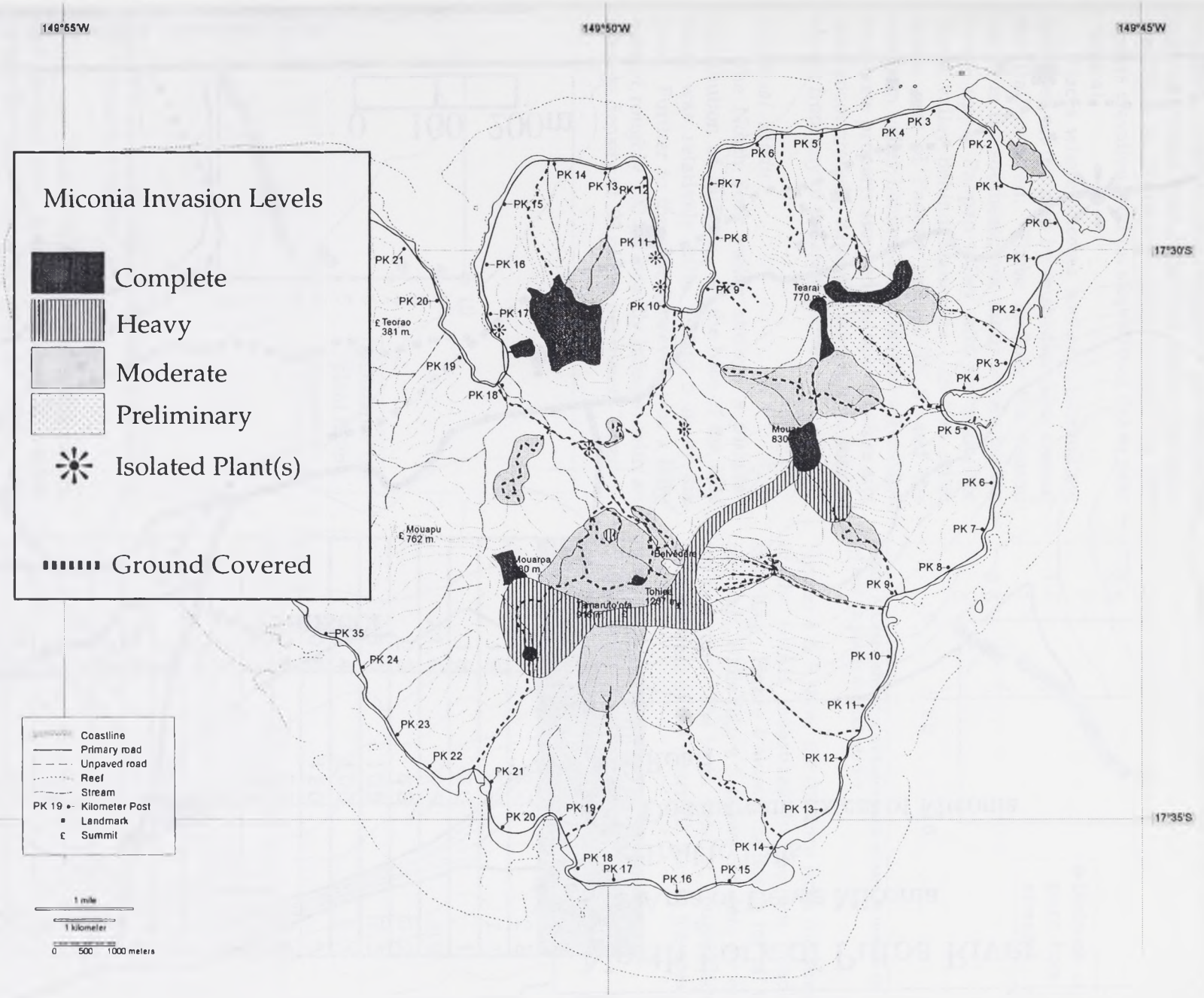

Figure 3. 1997 Miconia Distribution Map

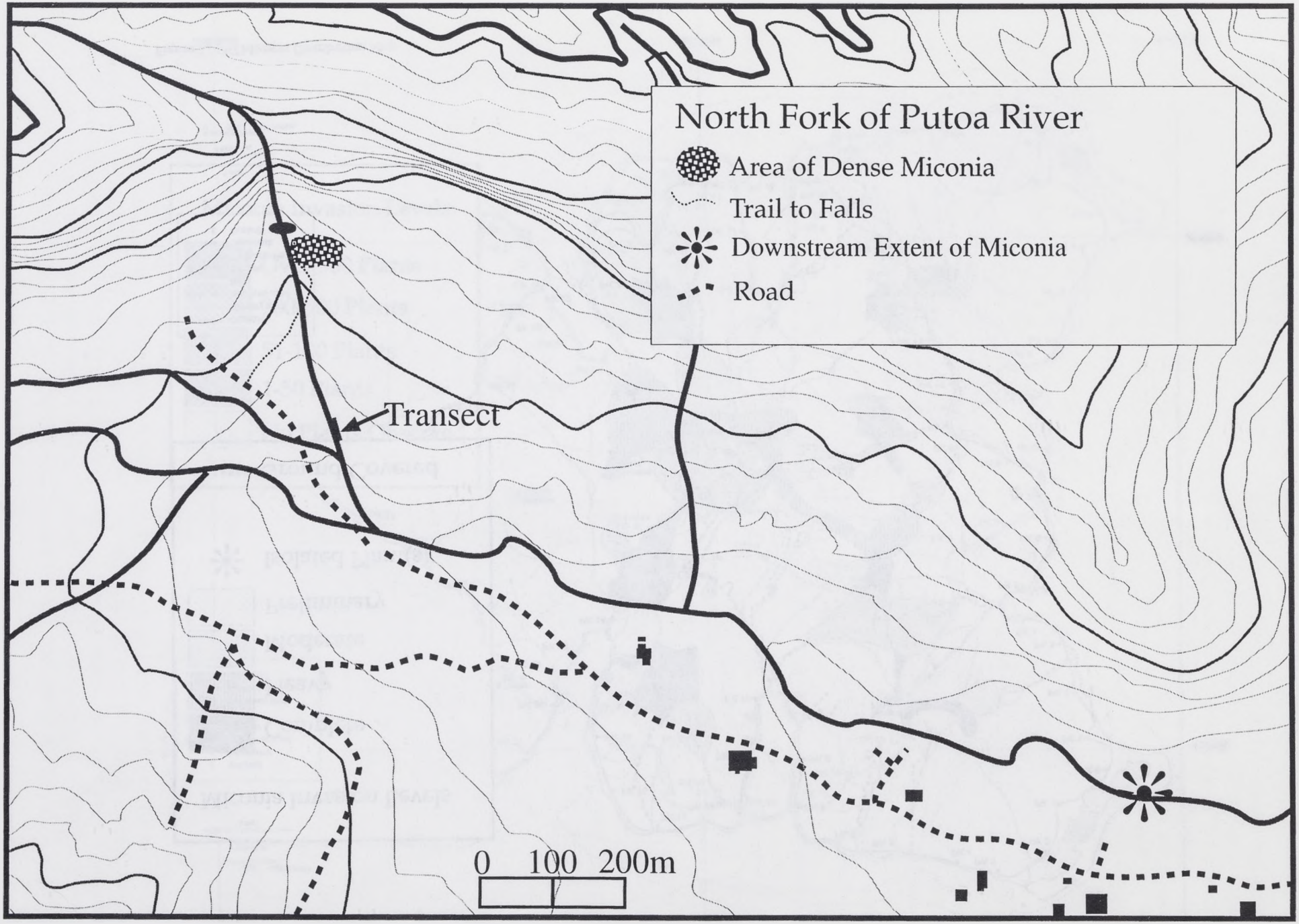

Figure 4. The North Fork of the Putoa River. Approximately 100-150 *Miconia* plants are present between the area of dense population and the downstream extent

Miconia was present in all but three of the eighteen river valleys explored on Moorea's eastern portion, and on all the major ridge tops (see figure 3). Plants were observed from 3 to 1200 meters elevation, and on slopes from flat to near vertical.

Places where *Miconia* was not observed are indicated on the map by unshaded areas around the trail covered. These include the Haumi valley in the southeast, one major stream system in the upper Paopao valley, and the Vaiterupe River valley behind Maharepa. In two other areas, east of Paopao behind PK 9, and the southern valley behind Vaire, limited access due to private property stopped the search before any was encountered. *Miconia* may not be totally absent from any of the areas above.

Dispersal Study

The North Fork valley showed a peculiar distribution of *Miconia*. At the base of the falls there was relatively little within 5 m of the pool. Further to the east, however, was a hilly area of roughly 100 m^2 heavily infested with an average density of .93 plants per meter. Three

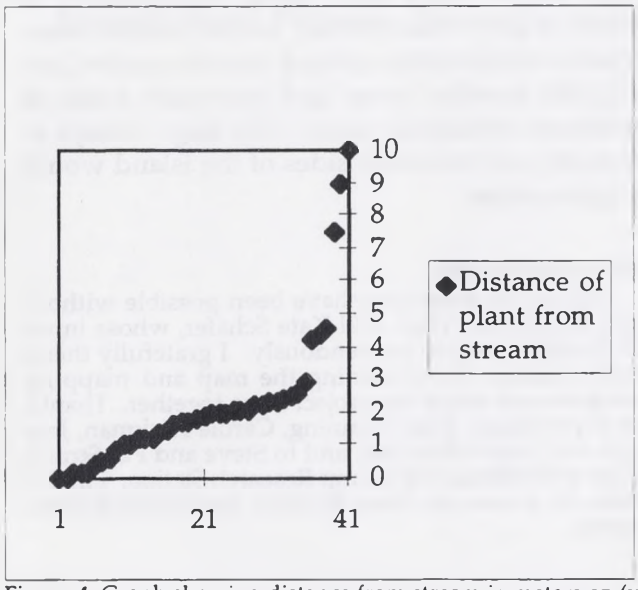

Figure 4. Graph showing distance from stream in meters on (y) axis for plants in all quadrats

plants were found on the hill across the stream, and another four spread out along a narrow stream flowing down to the west side of the falls. At about 50 m from the waterfall's base, however, all of the *Miconia* present was within three meters of the stream.

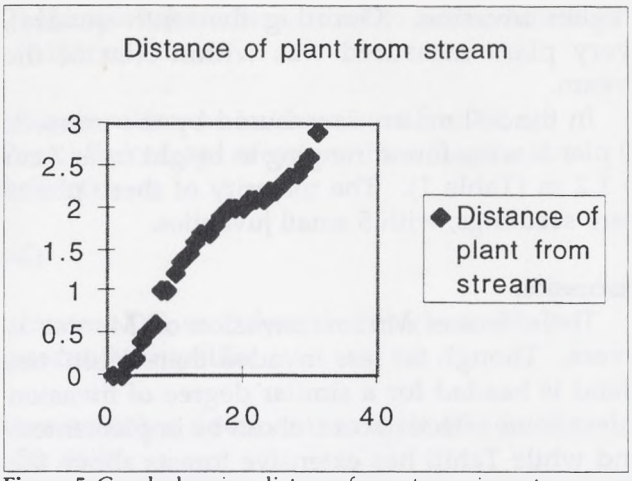

Figure 5. Graph showing distance from stream in meters on (y) axis for plants in quadrats 1-9

Figures 4 & 5 show the distance from the stream of the plants measured in the ten quadrat sampling. Figure 4 shows the totals for all ten quadrats, while figure 5 shows the data for only the first nine. The tenth quadrat, roughly 40 m from the base of the waterfall, was in the area of

Point on Transect (m)	Height of Plant (cm)	Distance from Main Stream (m)
5.1	87	2.2
19	32	1.1
19	30	1
21.6	95	3.3
23	83	6.2
23.9	105	7.3
29.4	100	5.1
30.6	120	3
30.6	28	4.6
30.7	100	4.85
31	10	4.6
31	7	4.5
31	12	0.75
34.8	17	4
36	22	1
37.2	17	3
38	105	2.1
38.3	25	2.05
38.3	45	2
38.4	50	2

Table 1. Plants along transect, measured from downstream towards the source

higher invasion. Omitting the tenth quadrat, every plant measured was within 3 m of the stream.

In the 500 m^2 area measured by the transect, 20 plants were found ranging in height from 7 cm to 1.2 m (Table 1). The majority of these plants were seedlings, with 5 small juveniles.

Discussion

The extent of *Miconia* invasion on Moorea is severe. Though far less invaded than Tahiti, the island is headed for a similar degree of invasion unless some effective control can be implemented. And while Tahiti has extensive forests above the reach of *Miconia*, Moorea's highest peaks are already invaded.

The observed distribution of *Miconia* along the North Fork of the Putoa River suggests that the river is largely responsible for the dispersal of seeds, and therefore plants. The proximity of every plant downstream of the dense hill area supports this. Seeds may have been dispersed by water to the hilly area of dense distribution as well. During storms, the heavy flow of the river combined with swirling wind sends water from the stream down on this area like rain. Further, the conspicuous lack of *Miconia* near the falls was explained by a tour guide who removes the easily visible plants to preserve a more natural appearance for his tourists.

There are doubtless dozens of other possible reasons for this distribution. One possibility is the impact of tourists, who are suspected of carrying seeds in their shoes. However, there is no *Miconia* on the trail leading to the river. The wind may be solely responsible for dispersing the seeds, but the confinement of the *Miconia* suggests otherwise (*Miconia* is only in areas touched at some point by the river water). The possibility that birds carry seeds down to the stream bed is plausible, though few birds were seen during the months of study.

The pattern of plants found only near the stream is present all along the east coast of the island at the Teavaro River, Papeare River, lower Vaioro River, and Toto valley. It has been suggested that the tradewinds have blown seeds to the west of the main, highly invaded ridge on Moorea (Schwartz 1993). The streams seem to be acting as conveyor belts carrying the seeds down the islands valleys.

Miconia's invasion of Moorea, from the highest inaccessible elevations downward, and by a variety of dispersal mechanisms, appears to be beyond control. Physical and chemical control have been deemed impossible due to the massive numbers of *Miconia* plants and the inaccessibility of the most dense areas of invasion (Krantz 1997). The only solution now seems to be biological control, and an intense search effort, especially among scientists in Hawaii, has begun. One promising candidate is a fungal pathogen *Colletotrichum gloeosporides* (Penz.) Sacc. f. sp. *miconiae*, which causes premature defoliation but only kills the plant if its stem is injured (Killgore 1997).

While biological control may be the only long-term solution, by the time it is implemented much native flora may have dissapeared or become highly endangered. In the interim some physical and chemical control must be carried out in lightly invaded areas and especially areas of significant ecological value. The large valleys at the south and southeast sides of the island would be appropriate.

Acknowledgments

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Resource Partitioning in Two Cryptic Species of Pacific Skinks *Emoia cyanura* and *E. impar* (Lacertilia: Scincidae)

Erica A. Garcia
Department of Integrative Biology
University of California, Berkeley 94720
egarc@uclink4.berkeley.edu

ABSTRACT. Two species of cryptic Pacific island skink, *Emoia cyanura* and *Emoia impar*, were studied in regards to their partitioning of habitat and food resources. These species are of particular interest because of their morphological similarity although they are not closely related genetically, and recent recognition as two separate species. Samples of skinks from sticky traps in both coast and interior forest habitats found *E. impar* in much higher relative abundance in both habitats. Using stomach flushing, segregation based on prey species was also examined. In addition, food availability at all sites was examined. Evidence suggests that these two species may segregate on the basis of microhabitat and some trends show that they may also segregate on the basis of diet.

Key words: skinks; Scincidae; diet; resource partitioning; Emoia; *Pacific island; habitat segregation; sympatry; Moorea; French Polynesia*

Introduction

In any large group of sympatric species belonging to a single genus or subfamily, careful work will always reveal ecological differences (Hutchinson 1957). Patterns of resource partitioning have been said to result from three categories of causes; competition, predation and factors which operate independently of interspecific interactions (Toft 1985). Competing reptiles segregate along one of three parameters in order of importance, habitat, food, and time (Pianka 1975). These three parameters can further be subdivided into macrohabitat, microhabitat, food type, food size, diel time, and seasonal time (Schoener 1974). Macrohabitat is considered as coast forest, interior forest, beach and disturbed habitat types whereas microhabitat includes rock outcroppings, tops of vegetation etc.

The island of Moorea, French Polynesia was a model site for this resource partitioning study between two species of diurnal skink, genus *Emoia*. The two species of focus, *Emoia cyanura* and *Emoia impar*, have just recently been described as two different species (Ineich and Zug 1991). Prior to this the two species were thought to be only *E. cyanura* (Brown 1991). The two species are morphologically similar and both species have the same color polymorphisms. The most distinct color morphs are; the striped morph, and the bronze or melanistic morph. The striped morph is dark and has three white dorsal stripes which extend from the head to the base of the tail. The bronze morph is uniformly brown. Usually morphological similarity is accredited to recent speciation but this is not the case for *E. cyanura* and *E. impar* as they are more genetically related to other species than to each other (Bruna et al. 1996a).

The morphological similarity and the fact that the two species of skink *E. impar* and *E. cyanura* occur in sympatry makes them an ideal system for examining resource partitioning. Resource partitioning, defined as the differential utilization of the physical and/or biotic environment by different species, is of general ecological interest as a mechanism allowing for the coexistence of competing species. (Auffenberg and Auffenberg 1988). Bruna et al. (1996b) explored habitat segregation between *E. cyanura* and *E. impar* on the island of Rarotonga and concluded that some amount of habitat segregation was occurring but that there were other areas needing to be further explored to better explain what enables the two species to coexist.

This study examines both macrohabitat and food type differences between *E. cyanura* and *E. impar* on an island where they live in sympatry to determine if they have developed mechanisms of resource partitioning.

Materials and Methods

Study Site

Moorea (17° 30'S, 149° 50'W) is located in the Society Archipelago in French Polynesia. It is a

high volcanic island which encompasses an area of 173 km^2 with the highest peak Mt. Tohiea at 1207m. Two main habitats surround the coast, coast forest and beach. Coast forest contains vegetation such as *Cocos nucifera* (coconut), and *Terminalia catappa* (Indian almond). The beach habitat has very little canopy cover and is bordered by vegetation such as *Pemphis acidula* (Pemphis), *Scaevola taccada* (Scaevola), and *Casuarina equisetifolia* (Ironwood). The interior forest contains vegetation such as *Hibiscus tiliaceus* (Hibiscus), *Aleurites moluccana* (Candle nut tree), *Inocarpus fagifer* (Tahitian chestnut), *Pandanus tectorius* (Screw pine), *Nephrolepis spp.* (fern), *Thelypteris spp.* (sword fern), *Teratophyllum spp.* (fern), and *Angiopteris evecta* (Tree fern).

In this study two habitat types were chosen for examination, coast forest and interior forest. For each habitat type two sites were selected. Habitats were determined by examining the dominant vegetation within and around each site. Sites 1 and 2 were located in coast forest and sites 3 and 4 were located in interior forest. Site 1 was on the east side of Opunohu Bay at PK 17.5 bordered by the bay and the main road. Site 2 was along the Gump Station nature trail at PK 11.5 bordered by a hillside and the main road. Site 3 is approximately 1 km along the Three Coconut Trail starting from the Belvedere just before the first grove of *Inocarpus fagifer* facing in a northwest direction. Site 4 is approximately 1.5 km along the Three Coconut Trail past a dry stream bed, just before the second grove of *Inocarpus fagifer* facing westward (Figure 1).

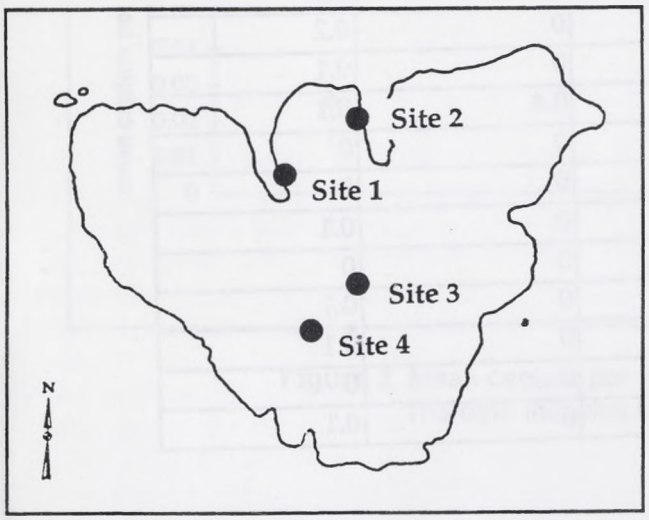

Figure 1. Map of four sites. Sites 1 and 2 are in coast forest, sites 3 and 4 are in interior forest.

Sampling

The sampling period for this study was October 24 - November 18, 1997. Similar to the procedure by Bauer et al. (1992), fourteen Enforcer® mouse glue traps and/or d-Con© covered glue traps were set out along a line transect 1 m apart. The sticky traps were checked every fifteen minutes for periods ranging from 2 to 3.5 hours. Upon capture each skink was removed from the sticky trap by greasing them with vegetable oil. Each animal was checked for coloration, snout-vent length (SVL), total length, age (adult or juvenile), weight and identified to species. Species was determined using four characters which have been shown to be diagnostic: (1) number of fused and unfused middorsal scales, (2) relative anterior loreal scale length and height, (3) presence or absence of parietal eye, (4) underbelly color (Zug 1991; Ineich and Zug 1991). Age was determined using SVL, adults range between 39-56 mm for *E. cyanura* and 40-48 mm for *E. impar* (Zug 1991).

All adult skinks were stomach flushed, meaning that water inserted into the stomach through a butterfly catheter tube washes out the contents in the stomach and those contents exit out the mouth (K. Zamudio and D. DeNardo, pers. comm.). The contents were then preserved in 70% EtOH for later examination under the dissecting scope in the lab. All skinks were then marked differently for each site before release.

In addition to the skink sampling, food availability was examined by placing insect pitfall traps at each site. Six cups filled with soapy water were set out at each site and collected 48 hours later. The contents were then transported to the lab to be sorted under the dissecting scope. The traps were used in two 48 hour periods of sampling. Insect specimens were identified to order and in some cases to family using standard texts (Boror et al. 1989), and by consulting with graduate students at the U.C. Berkeley, Division of Insect Biology.

Analyses

The Shannon-Wiener Diversity Index combines two components of diversity (1) number of species, and (2) equitability, or evenness of allotment of individuals among prey species (Auffenberg and Auffenberg 1988). A Shannon-Wiener Diversity Index was used to illustrate many comparisons of diversity; between food availability and what was actually consumed in both habitats, by both skink species; between

coast and interior forest food availability and food consumed by both skink species; and between skink species. A two-tailed T-test assuming equal variance was used to check for differences in diet between the two species of skink and to check for diet differences between habitats within a species. A mean number of prey species per skink species per habitat was calculated to illustrate differences in abundance. The catch per unit effort (total number of lizards caught per trap divided by the number of times checked) in different sites were compared using the mean number of individuals captured per trap each time checked ± standard error (Bruna et al. 1996b).

Results

Both species were found at all sites and thus in both habitats. In both coast and interior forest habitats *E. impar* was found in greater abundance than *E. cyanura*. The two species are similar in size and the striped morph was the most common color morph caught for both species. Only a few bronze *E. impar* individuals were trapped which was not enough to make any comparisons of coloration. The SVL of the adult *E. impar* individuals collected was 44.2mm ± 3.45 standard deviation (range = 38-52mm, n = 36); that of *E. cyanura* collected was 48.5mm ± 3.98 SD (range=43-56mm,n=16).

Table 1. Mean number of prey collected from stomach contents

	coast forest		interior forest	
prey spp.	***E. cyanura*(n=5)**	***E. impar*(n=10)**	***E. cyanura*(n=5)**	***E. impar*(n=12)**
Amphipoda	0.6	1.4	1.8	1.9
Isopoda	1.2	0.2	0	0.2
Formicidae	0	0.4	0.2	0
Diptera	0.4	0.3	0.2	0.5
Coleoptera	0.8	0	0	0.1
Anthribidae	0	0	0	0.1
Hydrophilidae	0	0	0	0.1
Scolitidae	0	0.1	0	0.1
Curculionidae	0.2	0	0	0
Araneae	0.4	0.6	0.4	0.3
Psocoptera	0	1.7	0	0
Hymenoptera	0.2	0.5	0.2	0.2
Homoptera	0.4	0.1	0	0.2
Fulgoroidea	0	0.2	0	0.1
Orthoptera	0	0	0.4	0.1
Cicadellidae	0	0.3	0	0
Lepidoptera	1	0.2	0	0
Neuroptera	0	0.2	0	0.1
Hemiptera	0.2	0	0	0
Dermaptera	0	0	0	0.1
Geophilomorpha	0	0	0	0.1
microgastropod	0	0.1	0	0
Acarina	0	0.1	0	0.1

The catch per unit effort in coast forest habitat ranged from 0.02 ± 0.01 (mean number of individuals captured per trap each time checked ± SE) at site 1 to 0.03 ± 0.01 at site 2. In interior forest habitat catch per unit effort ranged from 0.05 ± 0.03 at site 3 to 0.04 ± 0.01 at site 4 (Figure 2).

The diet of both species consists of a wide variety of arthropods. Amphipods were the most abundant prey species at all sites. Isopods and Coleopterans (beetles) were the most abundant prey species for *E. cyanura* in coast forest habitat. Psocopterans were the most abundant for *E. impar* in coast forest habitat. There were not any other abundant species besides amphipods in the interior forest habitat (Table 1). Also only *E. impar* consumed Acarinans, Scolitids, Neuropterans, and Fulgorideans (Table 1). A two-tailed T-test comparing the diet of the two species yielded no statistically significant results at the p=.05 level.

The pitfall traps had an overall greater diversity of species compared to the overall diet contents of skink species. The sampled *E. impar* had a greater diversity in prey species in both habitats compared to *E. cyanura* (Table 2).

Behavioral observations

At all sites marked and released individuals were sighted indicating that these skinks may have a home range. Also observed many times was two skinks running towards each other in head to head confrontation which ended each time with one of the skinks running quickly in another direction while the other skink remained indicating that these skinks may be territorial. At all sites skinks were observed most active when the sun penetrated through the canopy and much less active on windy and rainy days. Skinks were also observed climbing up trunks and branches of trees as high as 5 m, and jumping distances of about 5-10 cm between vegetation.

Discussion

The higher proportion of striped color morphs caught could be due to the fact that the striped coloration has been stated as making the animal a more confusing target for predators (Bauer 1992).

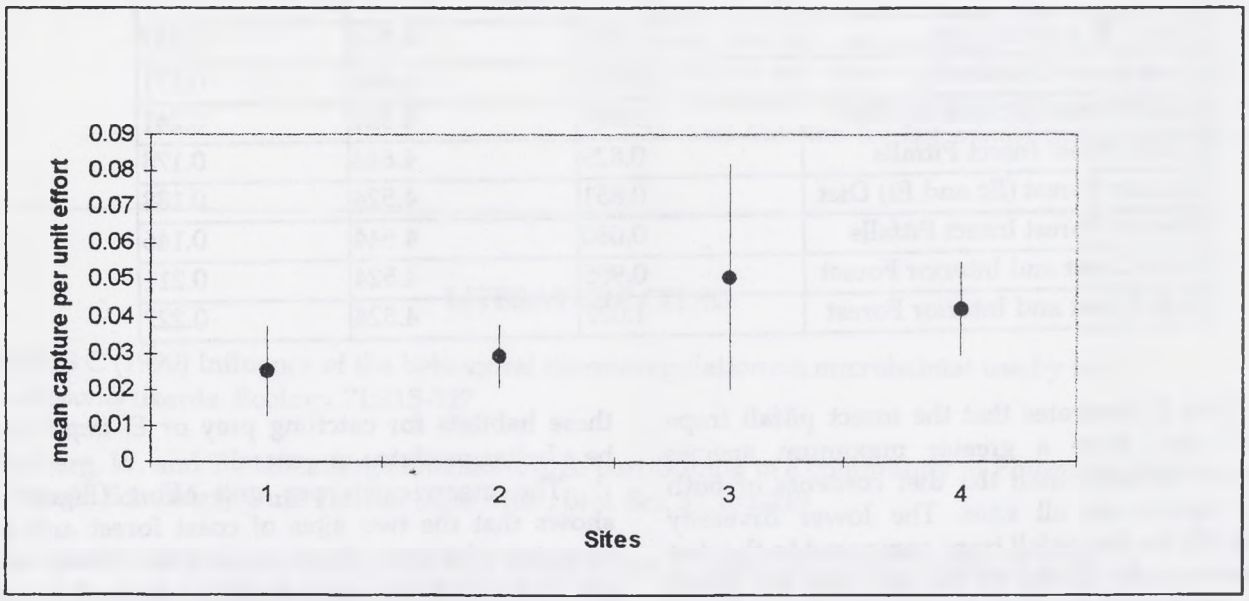

Figure 2. Mean capture per unit effort at four sites ± standard error. The data includes both *E. cyanura* and *E. impar*.

The results of the diet portion of this study did not support the hypothesis that these two species segregate on the basis of diet. The data supports the hypothesis that these skinks may well be opportunistic feeders. Dietary overlap between species is generally higher during dry periods when prey abundance is low and higher also for species that are similar in body size (James 1991). At the time this study took place Moorea was experiencing a drought and rainfall was below normal for that particular time of year. These climatic conditions may have increased the degree of dietary overlap between the two species.

Table 1 illustrates the fact that there were four prey categories that *E. impar* consumed that *E. cyanura* did not. This may be because only *E. impar* will consume these insects but a larger sample size is needed to show that this trend is statistically significant. In coast forest habitat *E. cyanura* consumed Coleopterans in relative high abundance and only *E. impar* consumed Psocopterans. These orders of insects may be areas where the two species of skink segregate but in the future a larger sample size would be needed to show this as statistically significant. Amphipods were most likely the most abundant prey species at all sites between both skink species due to their relative high abundance in nature.

Table 2. Shannon-Wiener Diversity Index
D is the information content of the sample. Dmax is the species diversity under conditions of maximal equitability and E is equitability (range 0-1).
Totals are for both coast and interior forest habitats (Ec = *Emoia cyanura*, Ei = *Emoia impar*).

	D	Dmax	E
Total (Ec and Ei) Diet	1.072	4.524	0.237
Total Insect Pitfalls	0.795	4.644	0.171
Coast Forest (Ec and Ei) Diet	1.088	4.524	0.241
Coast Forest Insect Pitfalls	0.829	4.644	0.178
Interior Forest (Ec and Ei) Diet	0.851	4.524	0.188
Interior Forest Insect Pitfalls	0.680	4.644	0.146
Ec in Coast and Interior Forest	0.955	4.524	0.211
Ei in Coast and Interior Forest	1.027	4.524	0.227

Table 2 illustrates that the insect pitfall traps at all sites have a greater maximum species diversity (Dmax) than the diet contents of both skink species at all sites. The lower diversity levels (D) for the pitfall traps compared to the diet contents could be due to the fact that the pitfall traps are biased towards insects which are found crawling or inhabiting the ground level, and do not capture flying insects which may be important components of the skink's diet. Table 2 also shows that *E. impar* sampled had a higher diversity (D) in prey species than *E. cyanura*. This may be due to the higher abundance of *E. impar* in both coast and interior forest habitats. Other hypotheses could be that *E. impar* may be more specialized in these habitats for catching prey or *E. impar* may be a better predator in general.

The mean catch per unit effort (Figure 2) shows that the two sites of coast forest and the two sites of interior forest are similar. Mean catch per unit effort was only slightly less in the coast forest habitat than interior forest habitat (Figure 2). These results of relative abundance among coast and interior forest habitats is consistent with previous studies on Fiji and Rarotonga (Zug 1991; Bruna et al. 1996b). This similarity in different Pacific island groups could support the hypothesis that the same mechanisms may be at work in causing segregation between the two species. Different optimum body temperatures,

competition and/or differences in thermoregulation activities of the two species may be some of these mechanisms.

It has been proposed that *E. impar* may be unable to tolerate the higher temperatures found in habitats lacking in canopy cover e.g. beach and disturbed forests (Bruna et al. 1996b). At all sites the canopy cover was in high percentage, but in times of sunlight penetration many skinks were sighted basking in direct sunlight. Also at times when the sunlight penetrated, a large number of skinks were seen climbing to the tops of the *Angiopteris evecta*, a type of fern which can reach heights of about 5 m. Lizards preferred body temperatures many times fall into a small well defined range governed by their physiological requirements and this could be a factor limiting microhabitat selection between species (Adolph 1990). Future studies of this system may want to consider microhabitat segregation especially in the vertical realm. It could be possible that more *E. impar* were collected in this study because all traps were set on the ground or close to ground level and *E. cyanura* may be found in greater abundance at higher points. Also optimum temperature range of the two species could be measured in the lab.

Conclusion

In summary some key findings are the trends in diet contents, which may suggest segregation between the two skink species due to competition. Also the behavioral observations compared with the relative abundance of skink species in each habitat may suggest microhabitat segregation caused by mechanisms such as behavioral specialization's for microhabitat and prey items or physiological specialization's for microhabitat and certain prey items.

Because these two species recently have been determined as distinct it may be that there are other cryptic species of skink that have not yet been recognized. A more thorough study of the Pacific islands where these species exist in sympatry may produce more informative results as to what ecological mechanisms are at work for morphologically similar species ability to coexist.

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The Effects of Nutrients and Herbivores on Algal Standing Crop in the Opunohu River, Moorea, French Polynesia

Jessica Sisco
Department of Environmental Science
University of California, Berkeley

ABSTRACT. I conducted two experiments to determine the effects of nutrients and herbivory on algal standing crop in the Opunohu River, Moorea, French Polynesia. The first experiment tested the effects of nitrogen and phosphorus on algal standing crop. The second experiment excluded herbivores to determine the effects of grazing on algal standing crop. In the nutrient enrichment experiment, a combined nitrogen and phosphorous treatment resulted in the highest mean algal biomass. Mean area grazed due to nitrogen enrichment was significantly greater than mean area grazed due to phosphorus enrichment. Mean algal biomass was significantly greater in herbivory exclosures than controls. In heavily shaded areas nutrient augmentation and herbivory exclusion failed to stimulate primary production. Light may be the primarily limiting factor in the Opunohu River. In areas of sufficient light, nutrient limitation and herbivory are significant controls of algal standing crop in the Opunohu River. As the interaction of nutrient augmentation and herbivory demonstrates, top down and bottom up controls are inextricably linked in this system.

Key words: algae; biomass; French Polynesia; grazing; herbivory; Moorea; nitrogen; nutrient limitation; Opunohu River; phosphorus.

Introduction

Tropical island streams are different from temperate streams in many respects. Streams draining tropical islands generally have lower nutrient concentrations and lower grazer diversity than continental streams (Resh pers com). There have not been many studies of community and ecosystem scale in tropical island streams (LaPerriere 1995). Temperate streams have received a great deal of attention at the community and ecosystem level recently (Vannote et al 1980, Power et al 1995, Power et al 1988, Wooton et al 1996). The result of many studies is a theoretical framework within which to examine temperate streams. In this study I set out to determine the applicability of these concepts to tropical island streams. Specifically, I examine the implications of the"River Continuum Concept" (RCC) for tropical streams, and top down vs bottom up limitation on algal standing crop.

The RCC is a framework that attempts to make generalities about how the structure and function of stream communities are shaped by the "continuum" of their physical environment (Vannote et al 1980). The source of organic inputs changes from headwaters to the mouth of the river. In general, many headwater streams are of relatively narrow channel width and riparian vegetation shades a high proportion of the stream surface area. The riparian vegetation inhibits primary production and provides a great deal of allocthonous inputs to headwaters (Vannote 1980). At downstream sites the stream channel expands and the influence of riparian vegetation is decreased. A greater area of the stream has available light and autocthonous inputs increase in downstream stretches (Vannote et al 1980). The degree of shading primarily influences the point at which the majority of inputs are autocthonous vs allocthonous (Minshall 1978). In temperate streams with sufficient light, researchers have found that primary production often is limited by nutrients, herbivory, or both (Hill and Knight 1988).

Nutrient limitation in an algal food web can be thought of as bottom up limitation and has been documented in many temperate streams, including desert, prairie, and conifer forested streams (Grimm and Fisher 1986, Tate 1990, Hill and Knight 1988, Pringle 1987). Nutrient limitation of the producing trophic level can have cascading effects, ultimately affecting the top carnivores in a system (Rosemond et al 1993). Top down controls on algal productivity and biomass are in the form of consumption by herbivores and have been documented in temperate and tropical

streams (Power 1990, Cuker 1983, Resh et al 1990, Pringle 1996). Consumption at each trophic level indirectly affects the entire food web through "trophic cascades" (Power 1990). Rosemond concluded that top down and bottom up effects were both influencing algal dynamics in a temperate woodland stream (1993).

Many nutrient enrichment experiments have documented nutrient limitation in temperate streams (Rosemond et al 1993, Tate 1990, Grimm and Fisher 1986, Hill and Knight 1988). Algal growth can be limited by nitrogen (Grimm and Fisher 1986, Hill and Knight 1988), phosphorus (Kjeldsen 1996) or both nitrogen and phosphorus (Tate 1990, Rosemond 1993). Atomic nitrogen to phosphorus ratios (N:P) have been used as support for a single limiting nutrient in numerous lotic studies (Redfield 1958). Most algae assimilate N and P at a ratio of 10-20 (Rhee et al 1978). If ambient streamwater contains an N:P ratio <10 there will exist a shortage of available N relative to available P, and P becomes secondarily limiting to algae. Conversely, if ambient streamwater has an N:P >20, P may be in short supply relative to N. Nutrient enrichment increased grazer density on artificial substrates in temperate streams (Hill and Knight 1988), illustrating the dynamic relationship of nutrients and herbivory. Herbivory often reduces standing crop of algae in streams (Pringle 1996, Power 1992).

The focus of this study was to determine limiting factors of algal standing crop in the Opunohu River, Moorea (17° 31'S, 149° 55'W), French Polynesia. A nutrient augmentation experiment was conducted for 20 days. A herbivory manipulation experiment was conducted for 25 days.

Methods

Study Site

The study site consists of a 1.5 km stretch of the Opunohu River, Moorea, French Polynesia. Moorea is an island of basaltic origin, which tend to be low in N content and have moderate levels of P (Tolliver, *pers com*; 1997).

Site one is adjacent to the Belvedere road at the Marae Titiroa. The first site can be reached by a trail that begins at the informational sign at the marae. This site is a series of short riffles and small pools. Mid-stream velocity averages 0.22 m/s and mean discharge is 0.049 m^3/s. The canopy is dominated by *Inocarpus fagifer* with some cover provided by *Hibiscus rosa-sinensis*. Canopy cover is approximately 60% at this site, with mosses and ferns abundant. The streambed is composed mainly of boulders with some cobble and sand. Site 1 has a great abundance of diatoms which are clearly visible, particularly on large boulders, and very low algal biomass. Periphyton was observed only on two occasions. This site is at a relatively high elevation (122 meters) and is above most anthropogenic influence.

Site 2 is located just downstream of the first bridge on the Opunohu-Pao Pao road. This site has many pools connected by a few riffles. Mid-stream velocity averages 0.18m/s and mean discharge is 0.068 m^3/s. The canopy is a mixture of *Inocarpus fagifer* and *Hibiscus rosa-sinensis*, which provides approximately 35% cover. The streambed at this site is mainly gravel with some cobble. Diatoms were not abundant by visual observation at this site. Algae tends to be visible as an epilithic film at site two. Three species of algae have been documented in the Opunohu River, *Schizothrix mexicana*, *Mougeotia genoflexa*, and *Hildenbrandia rivularis* (Shiley 1992). Site two is at an elevation of 12 meters and there is a great deal of agriculture in the immediate vicinity and in upstream areas. The agriculture consists of large scale monoculture plots and managed forestry, which receive sporadic fertilization.

Physical and Chemical Characteristics of the Opunohu River

Several parameters were monitored over a two month period (10 October 1997 to 20 November 1997) in an effort to determine limitations on algal standing crop in the Opunohu River. Four subsamples of water were taken at 2.5 m intervals parallel to stream flow at each site, and mean values were reported. Dissolved oxygen, pH, total dissolved solids and conductivity were measured using a Corning meter (Table 1). In addition, mean velocity, discharge, and water temperature were also monitored weekly (Table 1). Water samples were transported to Berkeley and analyzed for total nitrogen content, total phosphorus content, and N:P atomic ratio using the Kjeldal procedure (Bradstreet 1965).

Table 1.

SITE	DO $\%O_2$	pH	°C	canopy cover %
1	94	7.05	23.5	60
2	90	6.88	25.0	35

Table 1. Mean water quality values.

Natural Algal Standing Crop

Percent cover of algae was estimated on 3 occasions. Algal standing crop was not consistently high enough to measure biomass, therefore percent cover was used as an estimate of changes in standing crop. At each site, ten transects were delineated perpendicular to stream flow at 0.5 meter intervals. Quadrats of 0.09 square meters were placed at two randomly chosen points along each transect. Percent cover of algae was visually determined within each quadrat, and mean values were reported for each site. Because this study focused on green algae, diatoms were not included in percent cover estimates.

Nutrient Manipulations

Nutrient manipulations were conducted for a period of 20 days (31 October 1997 to 19 November 1997) to determine if nutrient limitation influences algal standing crop in the Opunohu River. Artificial substrates with enriched nutrients were constructed out of terracotta roofing tiles. The tiles were 46 cm in length and had a width of 21 cm at one end and narrowed to 16.5 cm at the opposite end, creating a total surface area of 684.16 cm^2. Petri dishes with a volume of 71.3 cm^3 were filled with 1.8% agar solution containing four varying nutrient concentrations. The four treatments were: 1) 0.5 mol/L NaNO3 (+N), 2) 0.1 mol/L KH2PO4 (+P), 3) 0.5 mol/L NaNO3 and 0.1 mol/L KH2PO4 (N+P), 4) and no nutrients (C). Three petri dishes were attached to each tile, creating a total solution volume of 213.9 cm^3 per variate. A total of sixteen tiles were introduced to the stream on 31 October 1997. Tiles were anchored in the stream by pounding rebar into the substrate and wiring the tiles to the rebar. Eight tiles were placed at site one and eight tiles were placed at site two. Each group of 4 replicates was arranged in a diamond configuration with the control tile at the upstream point, the N and P tiles were downstream from the point, parallel to each other, and the N + P tile was at the downstream point of the diamond. Tiles were oriented in the stream to maximize diffusion of nutrients over the downstream end of the tile. Other than canopy cover, physical and chemical variables were relatively constant between groups (Table 1). After 20 days, tiles were removed from the stream. An area of 144 cm^2 was scraped from the downstream end of each tile using an entomological scalpel. Algal biomass was scraped onto preweighed filter papers and dried in a plant drier for 24 hours and mean treatment values reported. Area grazed was estimated on each of the nutrient treatments. Due to the prevalence of gastropod grazing, and the density of individuals (see discussion), area grazed was quantified only if it was unquestionably due to gastropod grazing. Gastropods in the Opunohu River create distinct patterns in periphyton as a result of their grazing, which facilitated identification of gastropod consumption of algae in the nutrient treatments (Boyer, pers. com.; 1997). A clear plastic grid was placed over nutrient tiles to estimate area grazed. The number of grazed squares were quantified, where each square was 6.25 cm^2, and area grazed of each tile was estimated.

Herbivory Experiments

Herbivory manipulations were conducted for a period of 25 days (25 October 1997 to 19 November 1997) to determine if grazing was influencing algal standing crop in the Opunohu River. Ceramic tiles were introduced as an artificial substrate for algal growth. The tiles were 20 cm long and 10 cm wide. Cages were constructed to exclude all algivores. The cages consisted of 18 mm metal wiring with 3 mm window screening surrounding it. Cages with one end open were also placed in the stream to control for cage effects. Ceramic tiles were placed in the stream to measure natural algal standing crop. The tiles were divided into six groups. Each group had a closed cage, an open cage, and a tile without surrounding structure. The variates were arranged randomly within their groups. Three groups were placed at Site One and three groups were placed at Site Two. Physical and chemical variables were relatively constant between groups (Table 1).

Statistical Analyses

Data from natural algal standing crop measures were analyzed by a two factor (site and date) analysis of variance. Nutrient manipulation data from site two were anlyzed by ANOVA. Herbivory manipulation data were averaged over

both sites and analyzed by ANOVA. When significant differences were found by ANOVA, the Tukey-Kramer test was employed.

Results

Nutrient Manipulations

Nutrient augmentation did not stimulate algal growth at site one. At site 2, the nitrogen and phosphorus tile had the greatest mean algal standing crop (Fig. 3), although it was not significantly higher than the control. The nitrogen tile had evidence of significantly greater grazing than the phosphorus tile (Fig. 4; $F=9.4120$, 3, 4 df, $p<0.0276$). Mean N and Mean P concentrations were very low throughout the study period (0.1642 mg/L and 0.1635 mg/L, respectively). The N:P atomic ratio of ambient streamwater ranged from 1.026 to 5.279 during the study period

Grazing Manipulations

The closed cages had significantly greater mean algal standing crop than both open cages and lone tiles (Fig. 4; $F=8.92$, 2, 14 df, $p<0.0032$). The closed cages had greater numbers of Chironomid (midge larvae) individuals than the open cages and the lone tiles (Fig. 5) although the difference was not statistically significant.

Disturbance

An extremely high flow event occurred 9 October 1997 and flow remained relatively low until termination of the study . Mean natural algal standing crop increased significantly (Fig. 2; $F=15.8534$, 2,3 df, $p< 0.0001$) during the period of low flow which followed the high flow scouring event.

Discussion

Total algal growth (both natural and manipulative) was negligible at site 1 (Fig. 2, 3, 4, 5), suggesting that another factor is limiting algal growth at this site. The fact that there was no natural algal cover initially at site 1 creates some doubt as to whether there were sufficient colonizers available for the manipulations. Perhaps over a longer period of time, colonization of site 1 manipulations might have occurred. It is also possible that light is controlling algal standing crop at site 1. Site 1 has approximately two times more canopy cover than site 2 (Table 1). Light is primarily limiting in many temperate headwaters and could be limiting periphyton at site 1 (Vannote et al 1980, Hill and Knight 1988). Light manipulations in the Opunohu River would be an ideal way to test this hypothesis.

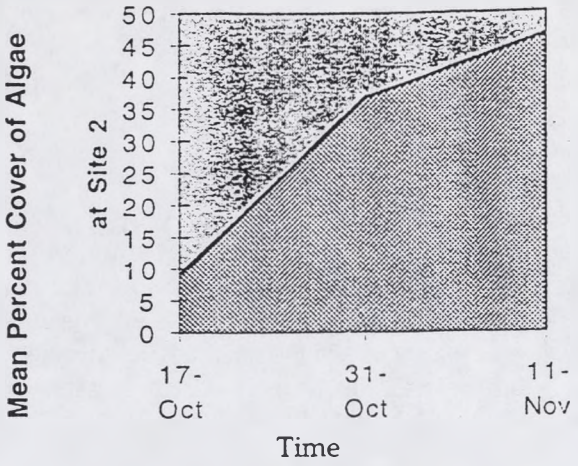

Fig. 2. Mean percent algal cover at site two during the study period. Scouring event occurred on 9 October 1997.

Natural Algal Standing Crop

High flow has been observed to scour periphyton and "reset" river systems (Power et al 1996). A heavy rain period occurred 9 October 1997 in the Opunohu Valley which might have reduced algal standing crop. Algal biomass increased significantly during the 4 weeks of relatively dry weather following the high flow event (Fig. 2). Typically, a high flow event disrupts small to medium sized substrate and periphyton is subsequently impacted. Many grazers require a longer time period to recover from scouring floods than periphyton, which allows high periphyton accrual immediately following these disturbances (Power et al 1996).

High flow events can also provide a pulse of nutrients to the stream system through leaching and runoff from the land. It is of particular

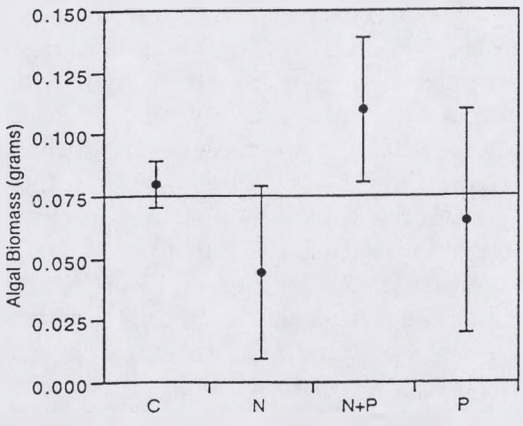

Fig. 3. Algal biomass (means ±SE) vs nutrient treatment, where C=control; N=nitrogen, P=phosphorus; N+P=nitrogen and phosphorus.

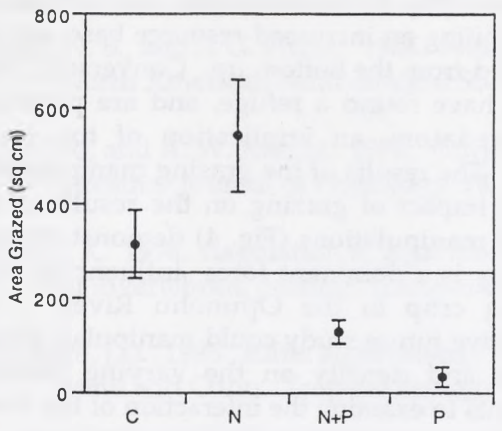

Fig. 4. Area grazed (means ±SE) vs nutrient treatment, where C=control; N=nitrogen, P=phosphorus; N+P=nitrogen and phosphorus.

interest that site 2 is surrounded by agriculture. High flow events might deliver nutrients in the form of agricultural fertilizer and organic inputs to primary producers. It is clear that algal standing crop increased in the dry period following disturbance, but the mechanisms behind this growth require deeper investigation.

Nutrient Manipulations

There was no algal growth as a result of nutrient manipulations at site 1, therefore, the following discussion of nutrient manipulations refers to site 2. The N+P treatment exhibited the highest mean algal biomass (Fig. 3), suggesting that nutrients limit algal standing crop in the Opunohu River. The N+P treatment was not significantly greater than the control treatment, although statistical significance might have been achieved with greater sample size (n=2). The N treatment and P treatment both resulted in relatively low mean algal biomass (Fig. 3). Dual nutrient limitation has been documented in instances of similar experimental design where single N and single P additions fail to stimulate growth, but combined N+P additions increase algal growth (Tate 1990, Rosemond et al 1993).

The low +N biomass value (Fig. 3) might be explained by the extremely high area grazed on the +N treatment (Fig. 4). It appears that N stimulates algal growth, but this stimulation is not represented in standing crop values because herbivores are preferentially grazing this treatment. Preferential grazing of plants with high N content has been documented in terrestrial systems (Mattson 1980). As a result of increased nutrient concentrations, plants frequently allocate more energy to growth and less to herbivory defenses, making them more susceptible to grazing. Although this shift in allocation increases turnover rate of primary producers and ultimately increases algal growth (Chapin, *pers com* ; 1996). The extremely high area grazed on the +N treatments, along with the high biomass value on the N+P treatment suggests N has greater influence on algal productivity and standing crop than P. Primary and secondary limitation by nutrients has been observed in temperate prarie streams (Tate 1990). It is believed that by augmenting primarily limiting nutrient values, algal growth is increased, and the secondarily limiting nutrient is taken up and is subsequently in short supply. Tate found that upon addition of N, P became secondarily limiting to primary productivity in a temperate stream (1990). The mean N:P ratio (2.22, range=1.02-5.28) throughout the study period supports the hypothesis that N is primarily limiting. In the Opunohu River, the algal biomass and grazing patterns suggest primary limitation by N and secondary limitation by P, although a manipulation with greater sample size and more conclusive results are neccessary to support this hypothesis.

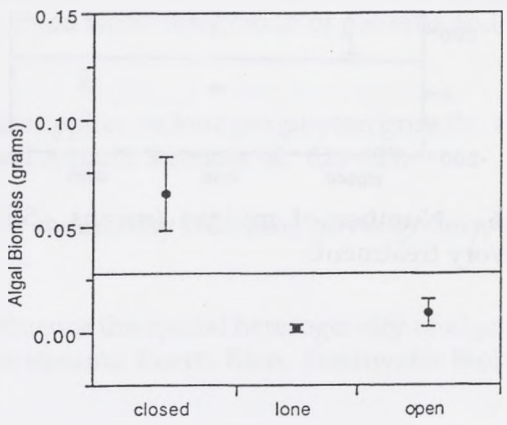

Fig. 5. Algal biomass (means ±SE) vs herbivory treatments.

Grazing Manipulations

Gastropod molluscs were the most frequently observed group grazing on natural and artificial substrates. The abundant families of gastropod molluscs in the Opunohu River are Neritidae and Thiaridae, which have been documented as algal grazers (Resh 1992). There

are two abundant families of crustaceans in the Opunohu River, Atyidae and Palaeomonidae (Resh 1992), which were observed grazing on enriched treatments on a few occasions. Tube dwelling Chironomids, order Diptera, were observed grazing on treatments occasionally. In addition, small gobie individuals were observed on enriched substrates, but it was unclear whether they were grazing or not.

Grazing significantly decreased algal standing crop in the Opunohu River (Fig. 5). Resh et al documented that Neritid snails reduce algal standing crop, they observed grazing halos in the periphyton surrounding individuals (1990). Cuker found that grazing snails reduced algal standing crop in artic lakes, but increased primary production (1983). It is unfortunate that primary production data were not obtained from these manipulations because it would be interesting to relate primary production to responses of higher trophic levels. Future experiments could be designed to isolate the effects of gastropod grazing on algal standing crop and productivity.

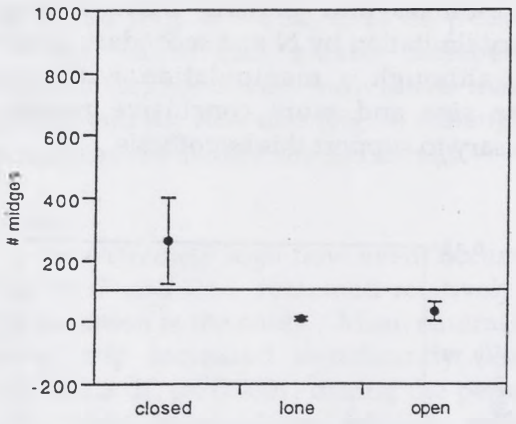

Fig. 6. Number of midges (means ±SE) vs herbivory treatment.

The greater number of midges in exclosures (Fig. 6) could indicate that consumers are exploiting an increased resource base and are controlled from the bottom up. Conversely, these grazers have found a refuge, and are protected from predators, an implication of top down control. The results of the grazing manipulations and the impact of grazing on the results of the nutrient manipulations (Fig. 4) demonstrate that herbivory is a dominant force influencing algal standing crop in the Opunohu River. An informative future study could manipulate grazer biomass and density on the varying nutrient treatments to examine the interaction of top down and bottom up controls in the Opunohu River.

Conclusion

Light plays a strong role in algal standing crop limitation in the Opunohu River as it does in many temperate streams. In areas of the Opunohu River with sufficient light, top down and bottom up controls become increasingly important. Disturbance in the form of high flow creates a bare substrate on which these factors control algal standing crop to varying degrees.

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Diurnal Behaviors of *Anguilla marmorata* in Streams on Moorea, French Polynesia

Celina E. Salazar
Department of Geology and Geophysics
University of California at Berkeley
Berkeley, CA 94720

ABSTRACT. This research characterizes the behaviors of *Anguilla marmorata*, and establishes a diurnal time budget for the behaviors. It tests the hypotheses that (1) there is a diurnal pattern of behavior and (2) hiding activities are the most common type of behavior. The first hypothesis is strongly supported that *A. marmorata* do exhibit diurnal patterns of behavior. Peak visibility of eels is in the late afternoon between 4:30 PM and 5:00 PM when there is an average of 9 to 10 visible eels per study site. There is a secondary peak in the morning between 8:30 AM and 9:30 AM, when there is an average of 5 visible eels per study site. The lowest point is between 11:15 AM and 12:15 PM when there are fewer than two eels visible per study site. This data suggests that eel visibility may be affected by the available shade and sun. *A. marmorata* eels engage in one of 15 behaviors when visible. These behaviors occur in the sun 1.1% of the time and in the shade 98.9% of the time. Chin perching is the most frequent behavior. It leaves the eel exposed, and away from its crevice, disproving the second part of the hypothesis. Chin perching behavior increases exponentially throughout the day and suggests that the behavior may be dependent upon the time of day. This study contributes to the knowledge of the basic biology of *Anguilla marmorata*, a species of which little was known about its behavior.

Keywords: *Anguilla marmorata*, Eels, Fish Behavior, Animal Behavior, Nocturnal Animals, Diurnal Activity, Moorea, Society Islands, French Polynesia, Field Research.

Introduction

Anguilla marmorata is a tropical species of fresh water eel. It is found in Japan, South Africa, the Marquesas Islands, and in all streams on Moorea, French Polynesia. The species is believed to have evolved in the rivers of Malagasy in the western Indian Ocean (Moriarty 1978).

Individuals of *A. marmorata* have a very distinct profile, with a flat forehead, and small mouth. From the top, the snout appears pointy. These fish can be recognized by their spotty brown skin and anal fin which reaches halfway up its body. Water is passed through their mouth and gills are used to breathe. Their lack of large scales allows them to also breathe through their skin, and they can remain out of the water for 48 hours provided their skin stays moist (Moriarty 1978). It is reported that "on rainy autumn nights when silver -stage eels feel the urge to migrate to the sea, they can easily wriggle through sodden fields to escape from land-locked ponds into nearby rivers" (Usui 1974).

In Moorea, French Polynesia, *A. marmorata* have a biomass of 261kg/ha (Marquet 1991). They have little or no competition from other fish and they eat mollusks, crabs, insects, crustaceans, fish, rats and other *A. marmorata*.

Much is known about eel physiology, but very little is known about eel behavior. They are reportedly nocturnal and difficult to study (Moriarty 1978). The purpose of this study is (1) to characterize the behaviors of *A. marmorata*, and (2) to establish a diurnal time budget for the behaviors. This study tests two hypotheses: (1) A diurnal pattern of behavior exists, and (2) hiding activities are the most common type of behavior.

Methods

This study was conducted between November 4th and 21st, 1997 at three locations in Moorea, French Polynesia. The surface flow of all the study site rivers is on the order of 0.05 m/s.

Site 1 is at the village Urufara in Opunohu Bay between PK 19 and 20 (Figure 1). This site is on the west side of the intersection of the Urufara River with the main paved road. The river is an average of 7 meters in width and the site is 7 meters in length from the bridge. The average depth of water is 30 cm. The substrate is primarily silt, with some cobble and boulder.

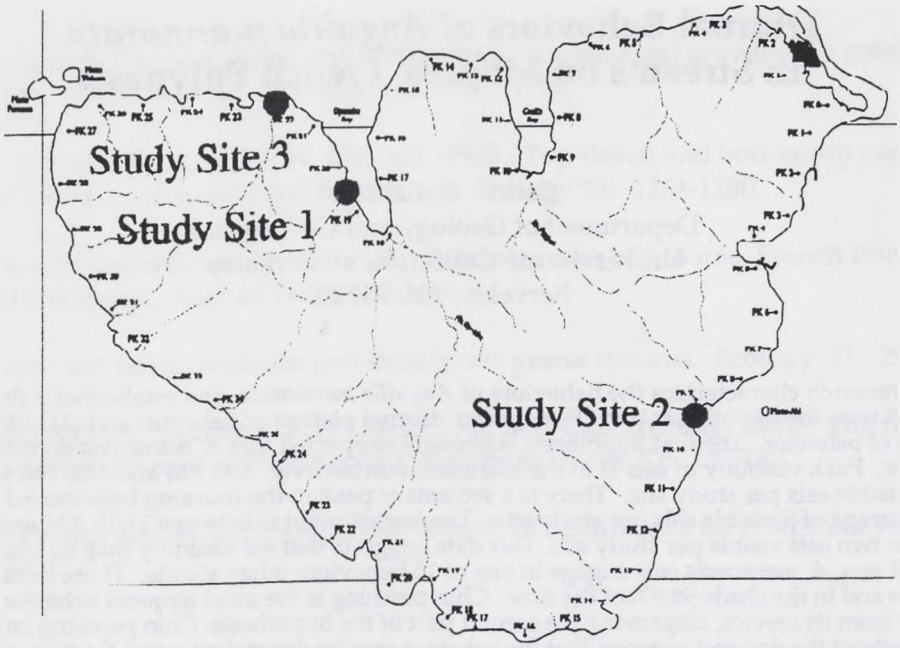

Figure 1. Location of study sites in Moorea, French Polynesia.

Site 2 is at the village Afareaitu, on the eastern side of Moorea at PK 9. The 9m by 9m site is on the western side of the intersection of the main paved road with the Putoa River. It consists primarily of cobble, but some boulder and silt are also present and there is a large concrete structure covering $8m^2$ of the substrate. The water depth is ~50 cm (Figure 2).

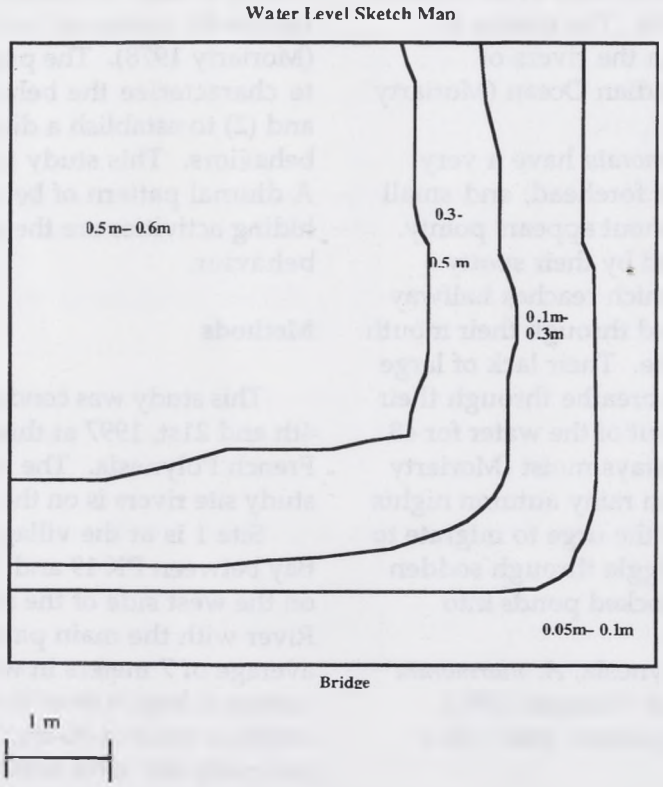

Figure 2. Water level of study site 2: The Putoa River in Moorea, French Polynesia.

Site 3 is at the village Papetoai in Opunohu Bay at PK 22. The public road by the Papetoai post office is taken to access the site which is adjacent to the northern most house on the eastern bank of the Vaihana River. The site is 8m by 8 m and the water depth is 15 cm. The substrate is primarily cobble and organic debris.

Extensive preliminary observations were made to characterize the behaviors of *A. marmorata*. Thereafter, behaviors of visible *A. marmorata* were recorded every five minutes between 8:00 AM and 5:00 PM. It was recorded whether or not the behavior took place in the sun or shade, and when one eel engaged in more than one behavior ("duplicate"). At the end of selected days, canned mackerel or fresh fish was placed into the stream and the visible *A. marmorata* eels were counted. This average number was assumed to be the population of the site.

The number of "average visible eels" was calculated by totaling the number of visible eels for each time slot, subtracting any "duplicates", and dividing the total by the number of data sets for the time slot. For the percentage of visible eels from the total, the time slot was totaled, multiplied by 100, and then divided by the sum of each study site data set times the eel population. The same procedure was used for individual behaviors, as well as for activities which took place in the shade and sun. Percentages of diurnal eel behavior were calculated by taking the number of visible eels for each behavior divided by the total number of visible eels.

Results

There is strong support that *A. marmorata* exhibit diurnal patterns of behavior. Peak visibility of eels is at late afternoon between 4:30 PM and 5:00 PM when there is an average of 9 to 10 visible eels per study site. There are also secondary peaks in the morning at 8:30 AM and 9:30 AM, when the average of visible eels is between 5 and 6 per study site. The lowest point is between 11:15 AM and 12:15 PM when there are less than two eels visible per study site. At 12:00 PM the percentage of visible eels is ~10%, and at 5:00 PM it is ~65% (Figure 3).

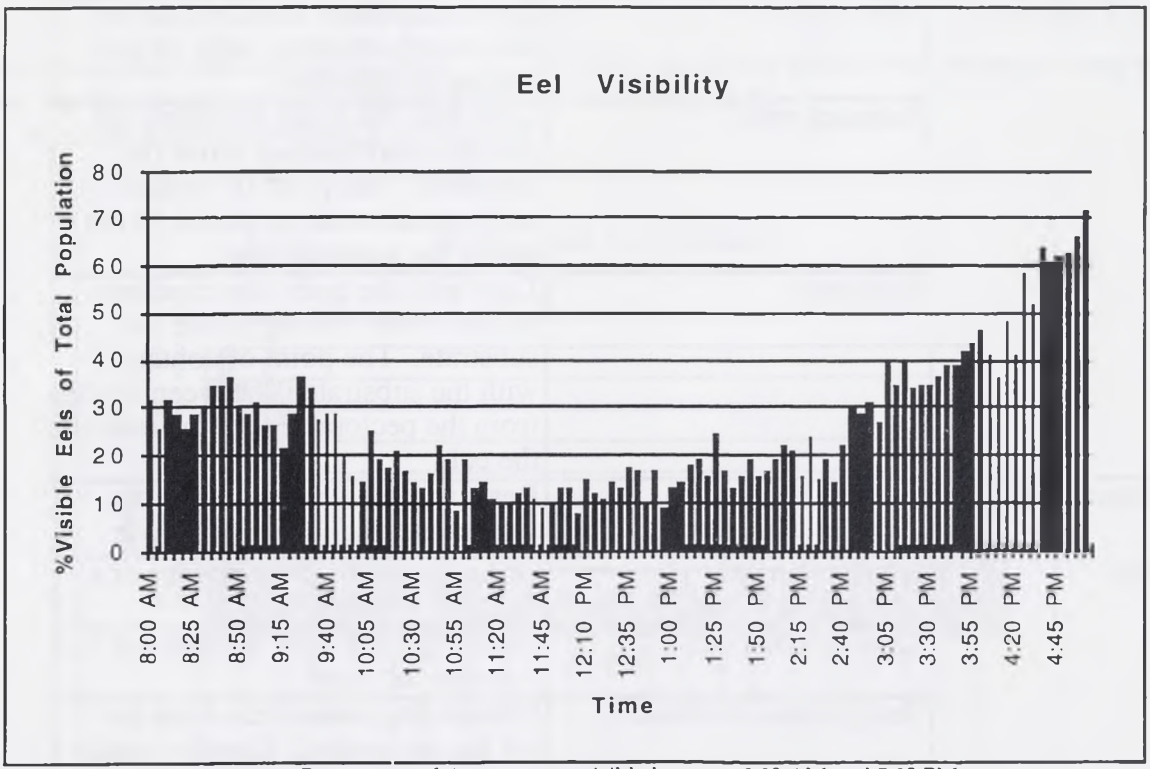

Figure 3. Percentage of *A. marmorata* visible between 8:00 AM and 5:00 PM.

A. marmorata eels engage in one of 15 behaviors when visible. These are described in Table 1.

Table 1. Diurnal behaviors of *Anguilla marmorata* .

Category	Behavior	Description
Hiding Behaviors	Poking head out	Protrudes the head, while keeping the length of its body protected within a crevice or burrow.
	Tail sticking out	Protrudes tail from a burrow, while keeping the head protected within the burrow.
Swimming Behaviors	Swimming slowly to moderately	Swims at a rate of ≤ 1 undulation of the eel body/ second.
	Swimming quickly	Swims at a rate > 1 undulation of the eel body/ second.
	Entering crevice	Swims into burrow, which may or may not cause splashes on the stream surface.
	Exiting crevice	Swims from burrow so that the whole body is visible.
Searching Behaviors	Looking to surface for food	The head quickly floats to the surface when a small object falls into the stream, or stream surface.
	Snooping under cobble	Uses snout to feel underneath the stream substrate, whether it is cobble, organic debris, or some other debris.
Perching Behaviors	Chin perch	Lays completely stretched out on the stream substrate, with its jaw resting on substrate.
	Stomach perch	Lays with the body stretched out, and the head floating above the substrate. The point of contact with the substrate is within 10 cm below the pectoral fins.
	Hip perch	Lays with the body stretched out and the head floating above the substrate. The point of contact with the substrate is between 11 cm from the pectoral fins to the end of the eel.
Interactions With Other Eels	Head to head	Rests with its nose touching or very close to another eel's nose.
	Biting other eel	Biting another eel on the face or a fin.
	Chasing other eel	Swims quickly after another eel for a second or more.
	Being bitten or chased	Passive activities over which the eel has no control. Usually results in a reaction such as swimming quickly.

In an average day, when *A. marmorata* is visible, it chin perches 40.19% of the day, pokes head out of crevices 36.32%, swims slowly 7.64%, sticks tail out of crevice 7.56%, stomach perches 2.06%, enters crevices 1.78%, hip perches 1.44%, exits crevices 0.98%, swims quickly 0.48%, is chased or bitten by other eels 0.42%, bites other eels 0.33%, rests head to head with other eel: 0.27%, chases other eels 0.25%, snoops under cobble 0.16%, looks to surface for food: 0.11% (Figure 4).

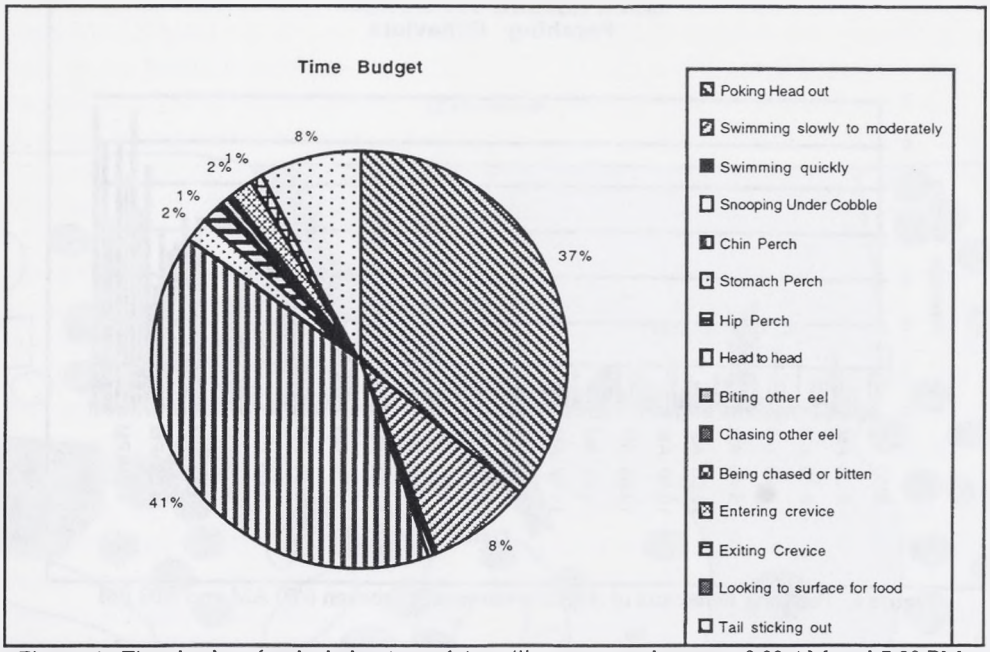

Figure 4. Time budget for the behaviors of *Anguilla marmorata* between 8:00 AM and 5:00 PM.

Between 8:00 AM and 9:00 AM there are an average of 4 to 5 eels poking heads out of their crevices. By noon, there is an average of less that 0.5 eels, and by 5:00 PM the average raises to 3 eels (Figure 5).

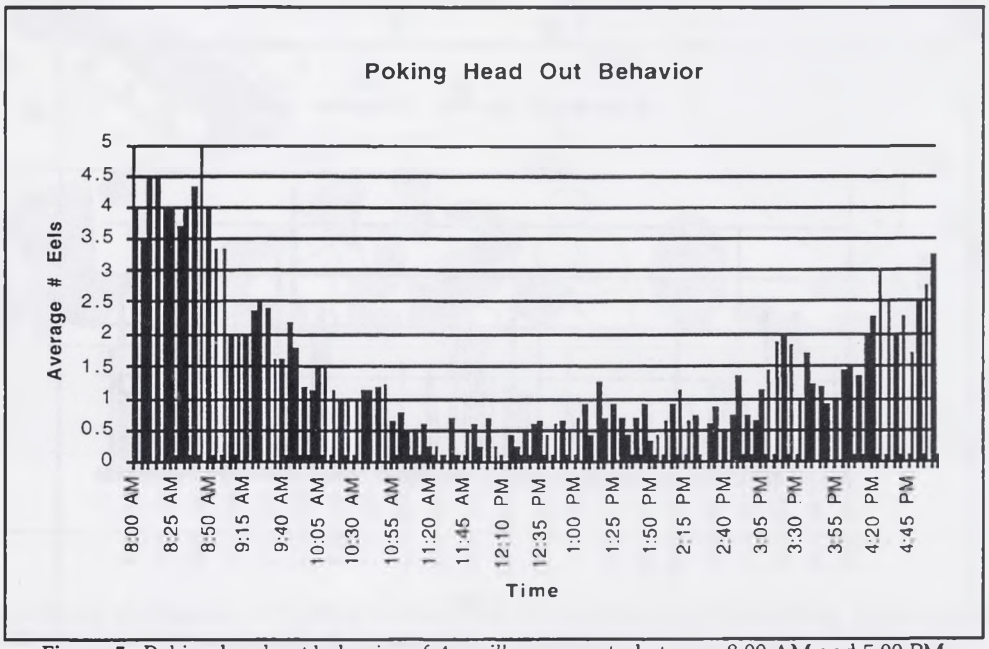

Figure 5. Poking head out behavior of *Anguilla marmorata* between 8:00 AM and 5:00 PM.

Snooping was observed only between 10:00 AM and 3:00 PM. Chin Perching increases throughout the day. Hip perching and chin perching have no apparent diurnal patterns.

As a whole, the perching behaviors increase throughout the day (Figure 6).

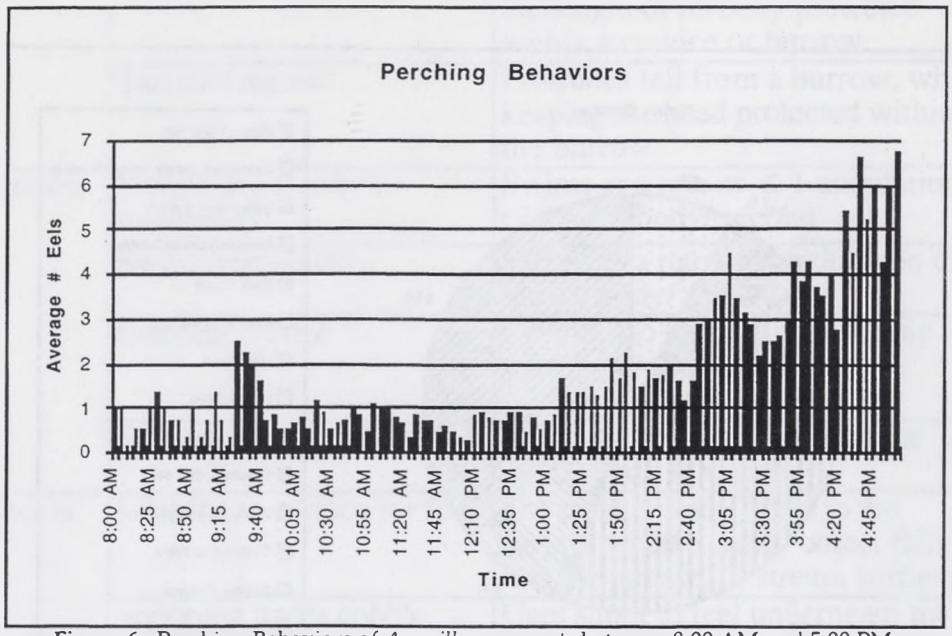

Figure 6. Perching Behaviors of *Anguilla marmorata* between 8:00 AM and 5:00 PM

There is no apparent pattern in the head to head behavior. Although the biting and chasing behaviors are concentrated at midday, both have an average of less than 0.15 eels. Entering crevices is not observed from 8:00 AM to 8:50, from 1:40 PM to 3:00 PM, or from 4:00 PM to 5:00 PM. Exiting of crevices is most frequent in the morning and late afternoon, with the lowest point of activity at noon. The peak is at 4:45 PM, when the average number of eels is 0.66. Looking to the surface of water for food is observed between 10:30 AM and 12:25 PM. There is no apparent pattern in the tail sticking out behavior or in the swimming behaviors (Figure 7).

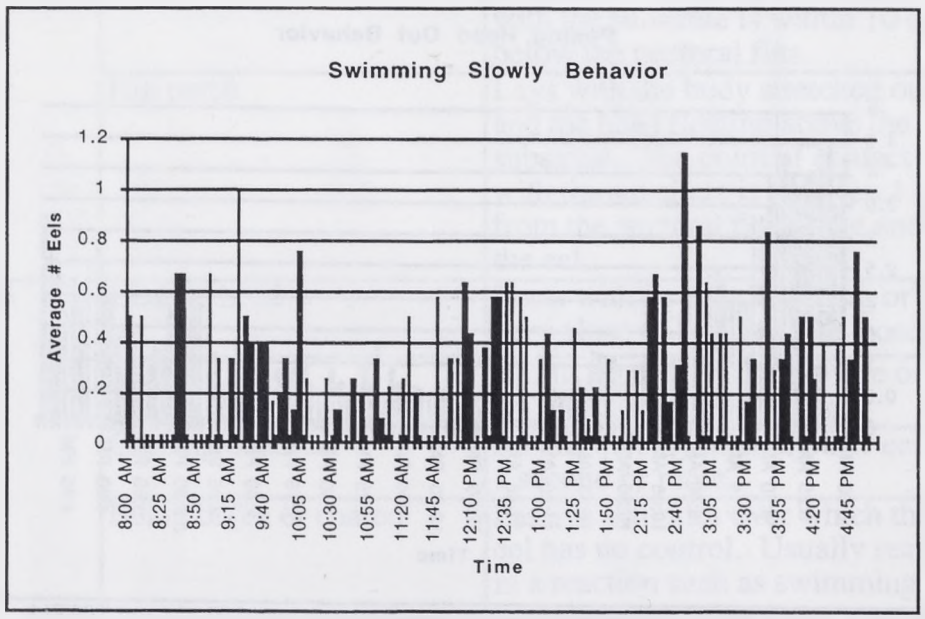

Figure 7. Swimming slowly behavior of *A. marmorata* between 8:00 AM and 5:00 PM.

Visible behaviors occur in the sun 1.1% of the time and in the shade 98.9% of the time. Behaviors which take place in the sun occurred between 9:15 AM and 12:45 PM and behaviors in the shade occur all day long.

An example of the diurnal behaviors of an individual *A. marmorata* eel at study site 2 is shown in Figure 8.

Figure 8. Sketch map of substrate with path of an individual *A. marmorata* eel at Putoa River, between 11:00 AM and 2:00 PM. (1) Exits crevice. (2) Stomach perch. (3) Chin perch. (4) Hip perch. (5) Chin Perch. (6) Enters Crevice

Discussion

Contrary to popular belief, *Anguilla marmorata* eels are not exclusively nocturnal. Over 2500 individual behaviors were observed during the course of this study, suggesting that *A. marmorata* behave diurnally.

The parabolic shape of total eel visibility (Figure 3) suggests that visibility of eels is dependent upon the availability of shade and sun. The eels are highly visible in the mornings and late afternoons, when the sun is at its lowest. At noon there are less eels visible probably because there is less available shade. Moriarty (1978) confirms that eels avoid bright light. Only nocturnal and bottom-living fishes, such as the burbot and the barbel have more retina rods than the eel. Because of this, eels have limited vision capacities in the daytime.

It is surprising that chin perching is the most frequent behavior. This is an exposed behavior (as opposed to hiding) which leaves an eel vulnerable while away from its protective crevice. The fact that the behavior increases exponentially throughout the day is also surprising, being that total eel visibility peaks both at the beginning and end of the day. This suggests that the perching behavior may depend directly upon the time of day, rather than on available sun and shade.

Eels' dependence upon time, rather than light has been observed by others as well. In Northern Europe scientists and fishermen have found that the peak migration runs take place at the last quarter moon, when the early part of the night is dark. Even when the cloud cover masks a bright moon, the eels still migrate during the last quarter. Statistical analyses of eel catches have raised doubts as to whether light alone is responsible for the monthly lunar rhythm in eel migration (Moriarty 1978). The question is raised whether or not the eel is dependent upon the light, or upon an internal calendar.

The poking head out of crevice behavior was second most frequent which is not surprising. Based on initial observations, it was suspected to be a frequent behavior. Some days it was the only behavior which was observed at all. The average number of eels engaged in this behavior is highest in the morning, lowest at noon, and peaks again at late afternoon (Figure 5). The numbers of eels are lower in the afternoon, perhaps, because more are engaged in perching behaviors.

Entering of crevices is not observed in the morning, afternoon, or late afternoon. One explanation is that the eels take advantage of the shaded areas at these times, and do not seek protection from the crevices. However, we know from the poking head out behavior that the crevices are, indeed, occupied at this time. An alternate explanation may be that the space to poke heads out of the crevices is already occupied and the exposed eels would rather be outside than pushed to the back of the crevice.

Different sizes of *A. marmorata* were observed biting and chasing, suggesting that small eels chase large eels just the same as large chase small. *A. marmorata* is bitten by other eels 0.42% of the time, and bites other eels 0.33%, and chases other eels 0.25%. It seems that these should be cause and effect, and that the number of bitten eels and chased eels should total to 0.58. However, *A. marmorata* was not always the only eel involved. At Papetoai, one individual *A. megastoma* was present and it was observed being bitten and chased by *A. marmorata* repeatedly. It was only rarely observed in the shade, and never seen sharing crevices with *A. marmorata*. This individual was never observed biting or chasing any *A. marmorata* eels. This suggests that there may be some territorial behaviors which occur between the different species of eels, and dominance of one over the other.

Head to head behavior does not appear to be an aggressive activity. The eels do not move from one another, but share a common space. Similarly, during perching behaviors, the eels sometimes stack up one on top of the other. This can be seen during the head poking out behavior as well, but it was not clear from my observation whether or not the eels choose to stack, or if space is merely limited inside the burrow. According to Tesch (1977), several eels will squeeze into the same crevice even when others are available.

Looking to the surface for food is a behavior that has most likely been induced by humans who feed eels. The eels are accustomed to being fed and are not afraid to swim right up to humans. When something falls into the water naturally or unnaturally, a nearby eel will look up to see what fell in the stream.

I observed people feeding eels very frequently, and this could have an affect on their overall behaviors. I always stopped data collection until approximately 20 minutes after feeding ceased. However, the length of time for which the eels behave abnormally after feeding is not known; It could be 20 minutes to a lifetime.

Snooping under cobble was not frequently observed. It remains a question whether or not it is a behavior that has been induced by humans.

Activities took place in the sun only between 9:15 AM and 12:45 PM. Perhaps this is because there is less shade at these times and there is a greater chance of being in the sun.

Future research on A. marmorata:

Do *A. marmorata* eels have an internal clock, or are they responsive to light only? An experiment manipulating light and using time could be conducted in the lab to determine this. Special attention should be given to the documentation of cloud cover and in the field. Also, a study could be conducted on the correlation between water depth and perching behaviors. Is there competition for space to poke heads out of crevice? There are still many unanswered questions about the interactions of *A. marmorata* with other species such as *A. megastoma* and *A. obscura*. Moriarty (1978) says it is very difficult to determine the sexes in specimens of 30 cm and greater, but it will be very valuable information when future study is conducted and should be attempted in the lab.

Conclusion

Anguilla marmorata's visible diurnal behaviors exhibit a distinct pattern. Therefore, my hypothesis was proven that a diurnal behavior pattern exists. However, it is unknown if this pattern is a factor of the time of day, time of year, or sunlight present.

The most common behavior is an exposed activity, which disproves the second part of my hypothesis. I expected that the most common activity would be a hiding activity since eels hide from the sun. Instead, the chin perch, an exposed behavior, is the most frequent of all behaviors.

Contrary to the belief that eels are difficult to see in the day, over 2500 activities were recorded, which is neither "occasional" nor "by chance" as Moriarty (1978) claims. Eels did not stay buried away in their crevices as he stated. During daylight hours they engage in at least 15 distinct behaviors which follow distinct patterns. Knowledge of these behaviors and time budget provide a richer understanding of the biology of *Anguilla marmorata*.

Acknowledgments

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Distributional Patterns in Moorean Waterfall Macroinvertebrates

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

davebors@ocf.berkeley.edu

ABSTRACT. Cascade faces were studied to determine if there was a pattern to the distribution of organisms and what that pattern is. Water flow was found to be variable throughout the study sites and is not a major factor on the distribution of organisms. Type of cover present was a significant factor for *Simulium sp.* larvae and pupae, thiarid snails and for amphipods. Full-time cascades were found to have less diversity than those that run intermittently. Topography was also identified as being important, but quantitative data could not be analyzed.

Keywords: Moorea, waterfall, stream, cascade, macroinvertebrate

Introduction

Volcanic islands have long fascinated biologists for their unique fauna. Few animals make it to islands and even fewer are able to actually colonize them. Within volcanic streams lives a collection of mainly marine derived species who have found a way to adapt to the ways of life in the fresh water. These organisms are most likely exploiting the increased productivity of tropical fresh waters(McDowall et al. 1987). Exploiting these bountiful waters are the gastropods, fish, and other macroinvertebrates. Like the fish, most marine derived macroinvertebrates continue to have an obligate salt water life stage.

Most studies involving tropical cascades have focused on the stream gobies, known for their ability to climb straight up the shear faces. Though the fish may be relatively unique in the fish world, many other organisms also have adapted to life in the fast moving waters. Life in the streams has created many innovations and changes in the lives of organisms. Flow is known to affect metabolism, respiration, feeding biology and many behavioral characteristics(Statzner et al. 1988). Animals whose behaviors are controlled by the stream flow are known as rheotaxic.

When working in tropical streams, one must not only consider the unique fauna, but also the unique habitat. Upon approaching the face of a cascade it is clear that the organisms are not distributed evenly across the face. Therefore the waterfall habitat must be broken down into several microhabitats. What is the major influence on organismal distribution on the cascade face???

Materials and Methods

Four sites were chosen on Moorea, French Polynesia. Two of the sites are full time streams: Putoa and Vaioro, and two of the streams are not full-time: Teavaro and Belvedere(See Figure 1). Fulltime streams are always running, even during the dry times. The parttime streams of the other hand dry up in places during between rainfalls. This means they provide a discontinuous opportunity for organisms to advance up the stream. Also makes it possible that the locale a particular organism is living in will dry up if the rain does not keep falling. This provides a unique chance to look at the faunal distributions in relation to desiccation.

Putoa:

The largest of the cascades used in the study, Putoa falls is on the Putoa river which drains into Putoa bay on the Eastern edge of the island. The face faces south and is exposed to the sun nearly all day long. A wide arc, surrounding the pool, of nearly 50m is swept down to low grasses from high winds, leaving the face very exposed. The falls are approximately 80m tall and 48m wide at the base. The main flow is restricted to the west side of the face.

Vaioro:

Vaioro falls is just North of Putoa and also empties into Putoa Bay. It is a tall narrow face rising about 70m on its final drop. At the base, the falls are only about 18m wide. The face faces East giving it sunlight for half of the day. These falls are more popular with the tour groups and has a deeper pool than the Putoa site.

Teavaro:

Teavaro has a narrow shoot, 2m, and is about 50m tall. This is one of the dry faces where the water nearly stops in the dry season. It is on the East side of the island between Plage de Temae and Vaiare. The face of the cascade faces east.

Belvedere:

Belvedere is located up the second stream bed starting along the 3 Coconut trail out of The Belvedere. The face is about 40m tall and faces North. The face is part of a cliff at the base of Mt. Toheia and is about 12m wide. Belvedere becomes extremely dry at times, with over 50% of its face dried up completely.

Sampling Procedure:

To sample the waterfall face, quadrats were used measuring 30 by 30cm. The quadrats were stacked in groups of three: the bottom quadrat starting at the waterline and the top of the third one approximately 1m above the waterline. The location of the quadrats were chosen to give an accurate representation of the falls as a whole. The main channels on the face were chosen along with any areas which appeared as important representatives of the face. Once the quadrat was positioned, the location was marked on a map and sampling commenced. The macroinvertebrates were then counted and recorded. Along with the numbers of individuals, the percent and type of cover was also recorded.

Flow:

A five liter olive oil bottle with a square bottom was used to collect the water coming down the face. The bottom was cut off and one edge was held up against the face so that all water coming down was collected. The water was collected for 30s and then the volume was measured using a graduated bottle. For places where the water flow would fill up the jug in less time, the water was allowed to fill for a shorter amount of time and the volume divided by the time to get the flow rate. All data were reduced to L/s.

Statistics:

Single variable ANOVA tests were run to test the distribution of water flow on the faces both between groups of three and between faces. This data was then compared between dry and wet sites using a T-test. The number of organisms found were run through regressions with the flow rate. A Pearson Product Moment was calculate for the macroinvertebrates to see if there was any exclusion of species by others. Shannon indexes were calculated and then compared using T-tests. All statistics were run on SigmaStat and graphed on SigmaPlot(Jandel Corporation).

Results

In total, sixty-nine quadrats were sampled on four waterfalls faces. Many species were found on all four faces. The only correlation was a positive one found between the black fly pupae and larvae(BFP and BFL), genus *Simulium sp.* with a correlation coefficient of .3556 and a p-value of .00272.

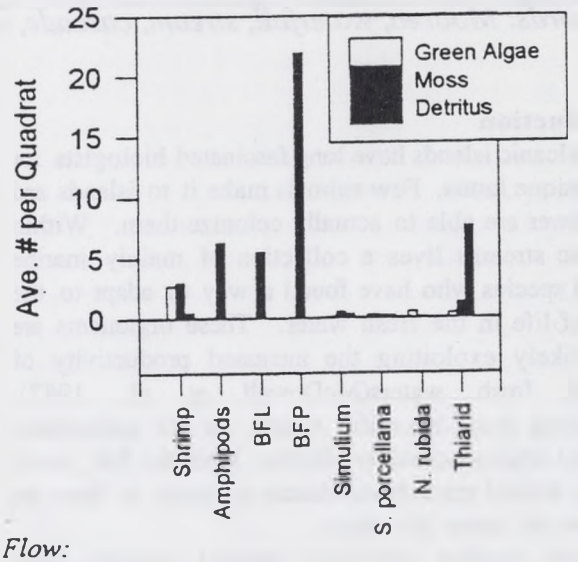
Species:

Dry cascade faces were found to have a higher diversity index than the wet cascade faces.

The J' values were significantly higher for the dry falls than they were for the wet falls with a p-value of <.0001.

Dominant cover was a factor in the distribution of several of the study organisms: amphipods, black fly larvae and pupae, and Thiarid snails(figure 2).

Figure 1. Cover preferences of 8 studied organisms



Flow:

Statistically significant variation was found in the groups of three quadrats. The variation between cascade faces was not significantly different either. The variation in flow rates was between dry and wet faces using a t-test were not significant.

Combined:

Regression tests using flow versus species data were not significant for any face, but some possible trends were noticed in the data. Nor was there a significant correlation between flow rate and any one species studied.

Discussion

Species:

The diversity indexes calculated for the cascades suggests that the periodically dry cascades have a wider variety of habitats for organisms to live in. This is apparent when one is sampling on the face. There are definite patches of wet and dry spots as well as large variations in flow. Also seen on the dry faces, but not

included in my study are many terrestrial species including: ants, centipedes, skinks, geckos, and several species of millipede. Many species of flying insects were also noted on the dry cascade faces. The dry faces seem to serve as a meeting place between the land and the river where organisms from both worlds can interact.

Cover was found to be important in distribution to several species included in my study. Amphipods, black fly larvae and pupae, and thiarid snails all had a preferential habitat where they were most often found on the face. All but the thiarids preferred the dense moss covering, most likely because it provides some protection from the hydraulic strains of the falling water. Only one amphipod was found not in the mossy cover, suggesting that they are either feeding in the moss or they are using it for safety. It was noted while exploring the faces that amphipods would seek moss as cover when approached while exposed, most likely the moss provides protection from predators. The thiarids were found to prefer habitats where detritus dominates. It is quite possible that they are eating the detritus or they are seeking a place where the flow is not so strong and the detritus just happens to come out of suspension in the same spots.

Flow:

The water flow through the quadrats was found to be significantly different both across the face and down the groups of three quadrats used to sample. This demonstrates that there is too much variation on one face to distinguish it from another on just on the basis of flow. This is important because it helps explain the discontinuous distribution of species when moving up from the waterline. Water flow is highly dependent on the topography of the face. Data were collected on topography, but was not able to be analyzed completely. A topographic map of one quadrat is included to give an understanding on how the organisms were related to topography in their distributions(Figure 3). Most organisms were found in the channels and grooves in the quadrats, where the more variability in the topography there was generally more animals present. Water gets channeled along ridges on the face. Filter feeders such as the black fly larvae and pupae were almost exclusively found in these microfalls. In these small habitats the flow is nearly laminar making filter-feeding easier. When the cascade dries up, there are left pockets of water in the indentations on the face. These pockets hold many shrimp during the low flow days. In one such pocket I found 19 shrimp.

Interesting Finds:

There were some interesting and thus far unexplained finds on the cascade faces. Truly a unique environment for the study of organisms. I found several species of snail that have yet to be identified. It is still up in the air whether they are terrestrial or aquatic. Many other terrestrial species were also found on the faces. A surprising find was that of an

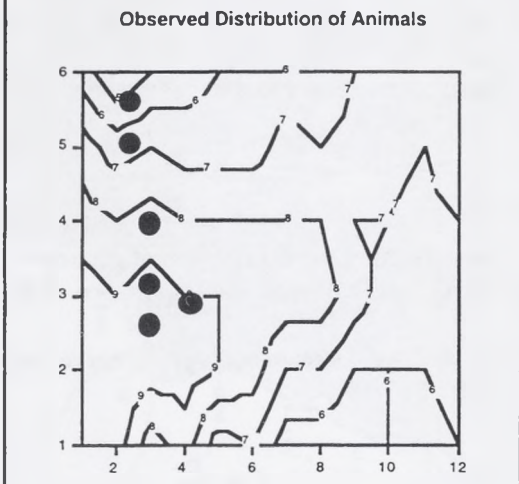


Figure 3. Observed distribution of organisms on a quadrat. Higher numbers mean a deeper recess.

Anguilla megastoma found 1.2m above the pool and 4m to the side of it. The eel was protruding from a hole and apparently dead, but slithered back in when prodded. It is believed that this individual has been sighted twice because of the small area and one being found on the ground at nearly the same spot on a previous trip to the face. Also exciting was finding that above what I consider a full-time cascade, Putoa, there exists an intermittent one with a fauna that seems very close to that of the intermittent sites I studied. A full sampling was not able to be performed here, but a small collection was made and they seemed to match.

Conclusion

There are a lot of ideas that can be produced from this study, but further work is needed to pin down exactly what is controlling the distribution of organisms. Topographic data needs to be analyzed on a fine scale and a more rigorous data collecting regime needs to be employed. Individuals' locations should be recorded as well as their presence in the quadrat. Complete collections of all organisms in a quadrat including the plant material would also be helpful in getting a more complete look at the face. A further look at some of the cascades and maybe looking at some of the other ones on the island would give a better picture and more data with which to draw comparisons. A better understanding of the lower reaches of the streams would also be good in understanding what happens to these organisms when their river dries up or drastically increases flow.

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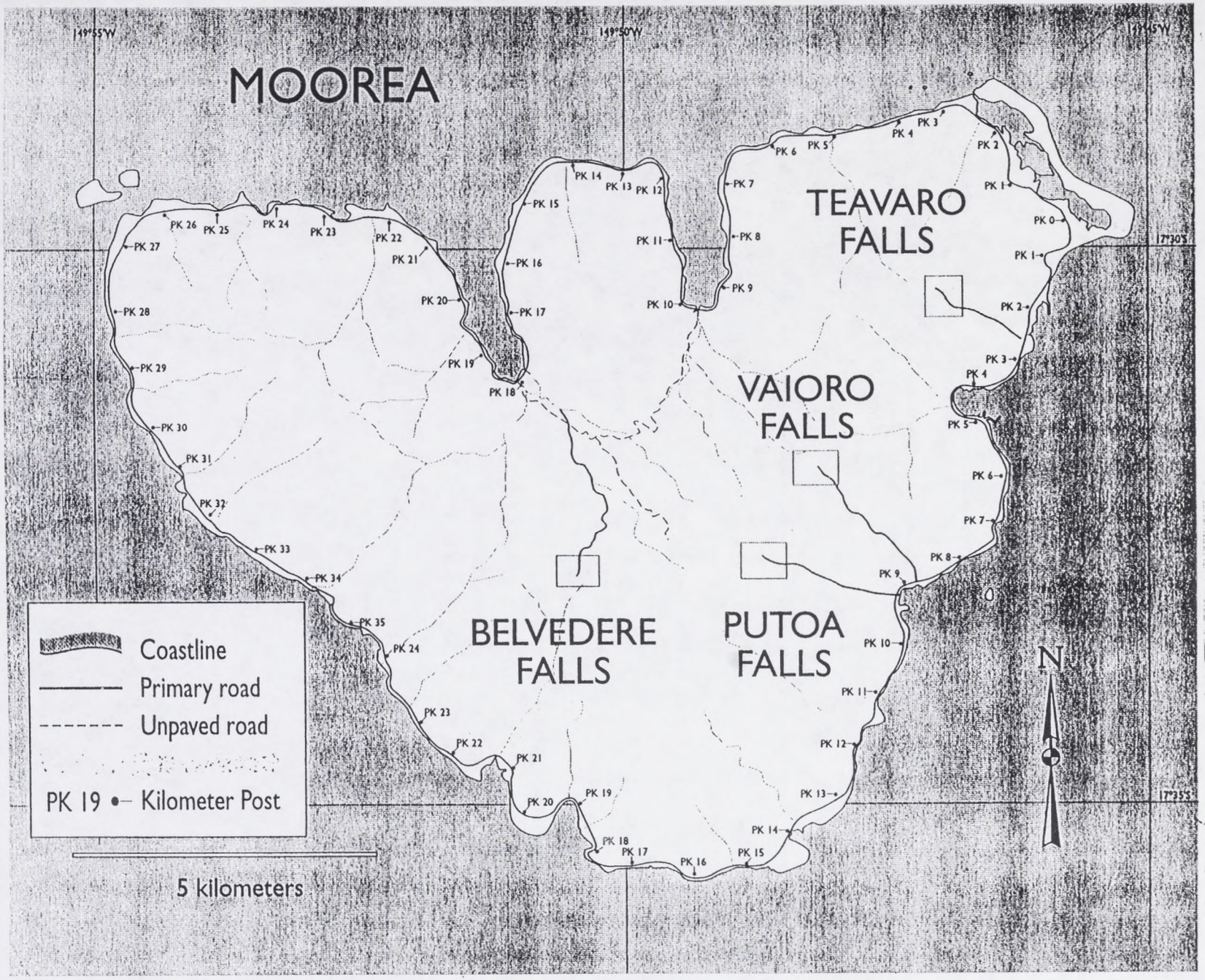


Figure 1. Study sties on Moorea

Comparative Study of the Effects of Land Use Practices on the Opunohu and Pao Pao Rivers, Moorea, French Polynesia

Heather S. Cooley
Molecular Environmental Biology
University of California, Berkeley, 94720

ABSTRACT. The Opunohu River and Pao Pao River were compared on the basis of sediment and nutrient loading levels from 14 October 1997 to 13 November 1997, during periods of high and low flow. Water samples were collected at a total of eight sites along both rivers , filtered on a 42 μm filter, and air dried. Samples were also analyzed for total nitrogen and phosphorus concentration using the Kjeldahl procedure. The results indicated that the sediment load was substantially higher in the Opunohu River than in the Pao Pao River. The nitrogen and phosphorus loading levels, however, were not significantly different. This suggests that the Opunohu River is not pristine relative to the Pao Pao River.

Key words: land use practices, Moorea, Opunohu River, Pao Pao River, sediment load, nutrient load

Introduction

Numerous studies have suggested that the sediment and nutrient transport of a river is affected by the watershed land use practices (Richey et al. 1991). The bay into which the river drains is subsequently impacted, the extent of which is a function of the type and intensity of the land use activity, as well as the ability of the particular system to recover. Sediment and nutrient transport are of particular concern in areas near coral reefs. Eutrophication and sedimentation have resulted in the overgrowth of macroalgae and the subsequent death of corals (Banner in LaPointe et al. 1992) This phenomena has been documented worldwide and is becoming of increasing concern with the worldwide decline in coral reef health.

In Moorea, French Polynesia, studies on the effects of onshore development activities have been conducted on Pao Pao Bay, using the supposed pristine quality of Opunohu Bay as a basis for comparison (Moraney 1994; London & Tucker 1992). This assumption, however, has been formulated solely from visual assessments of the bays.

The Pao Pao region is characterized by the presence of hotels and the town of Pao Pao. Agriculture, primarily pineapple cultivation, is also practiced in the valley. The Opunohu region, however, looks relatively undeveloped, as there are few houses and only one inconspicuous hotel. The drainage basin does, however, include a significant amount of agricultural land. Unfortunately, previous researchers have not considered agriculture as a form of development. This bias is likely a consequence of the emphasis on point sources, e.g. effluent pipes, and the failure to recognize the importance of nonpoint sources, e.g. agriculture, as significant contributors to pollution.

The purpose of this study was to compare the freshwater inputs into

Pao Pao Bay and Opunohu Bay on the basis of nutrient and sediment loading levels. The emphasis was placed on assessing which land use practices on a regional scale had a greater impact on these levels.

Materials and Methods

Study Sites

Moorea (17° 30′ S, 149° 50′ W, pop. 11,000) is located in the south central Pacific within the Society Archipelago of French Polynesia, approximately 25 km northwest of Tahiti. It is a high volcanic island that is 1.2 million years old. Moorea is triangular in shape and is surrounded by a barrier reef with a lagoon 500-1500 meters wide. The reef front is intersected at 12 passes which correspond to the principal valleys (Galzin & Pointier 1985). The primary means of economic support on the island is tourism.

The climate in Moorea is tropical, with daily temperature fluctuations greater than average seasonal fluctuations. There are two distinct seasons: a cool, dry season from June through September and a hot, humid rainy season from October through April. The dominant winds are the trade winds, which approach the island from the northeast.

This study focused on the Opunohu and Pao Pao Valleys, both located on the north side of the island and separated by Mt. Rotui (Figure 1). Although both valleys are subject to similar wind and wave conditions, they have been subject to very different patterns of development. The history and cultural significance of the Opunohu Valley has had a tremendous impact

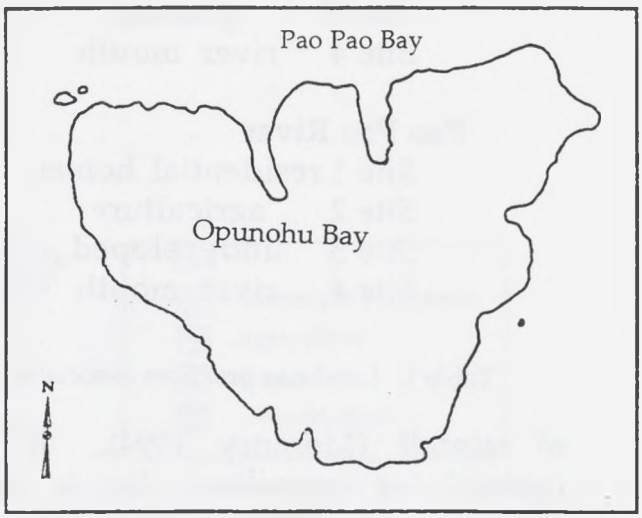


Figure 1. Location map of Opunohu and Pao Pao Bays

on the current land use practices within the region. Polynesians view Moorea as a fish with Mt. Moua Puta as the eye and the Opunohu Bay as its abdomen (opu nohu means belly of the stone fish in Tahitian) (Galzin & Pointier 1985). In pre-European times, the Opunohu Valley was the primary religious center of the Windward Islands, which is evident by the numerous maraes in the area. The region was colonized by Germans after European arrival, but was purchased by a wealthy American family during the early 20th century. The Territorial Authority bought the area in the 1950's with a stipulation that prevented the division of the land. The valley was eventually turned over to the Rural Economy Bureau for management. The valley includes an area of 28.5 km^2 and receives an average of 3200 mm/year

Site	Land Use Practice	Source of Inputs
Opunohu River		
Site 1	undeveloped	weathering/atmospheric deposition
Site 2	agriculture	fertilizer
Site 3	grazing	feces/urine
Site 4	river mouth	overall inputs from valley
Pao Pao River		
Site 1	residential homes	trash/sewage
Site 2	agriculture	fertilizer
Site 3	undeveloped	weathering/atmospheric deposition
Site 4	river mouth	overall inputs from valley

Table 1. Land use practices associated with each site and dominant source of inputs.

of rainfall (Moraney 1994). It is optimal for agriculture due to the presence of fertile soils and a minimal slope. Today, the region has become a center for agricultural development, including forestry, horticulture, aquaculture, and grazing (Galzin & Pointier 1985).

The land use practices within the Pao Pao Valley are more focused on tourism and human settlement than those of the Opunohu region. The Pao Pao Valley includes an area of 16.8 km^2 and receives an average of 2800 mm/year of rainfall (Moraney 1994). The town of Pao Pao, with a population of approximately 800, is situated at the head of the bay and extends the entire length of the river. Coconut and pineapple plantations are also scattered throughout the valley. In addition, the bay itself is lined with hotels that release sewage into the bay.

Eight sites were sampled, four along the Opunohu River and four along the Pao Pao River. Four subsites were randomly chosen at each site at 2.5 meter intervals parallel to the stream. These intervals were marked so they could be sampled at each time interval. Water samples were collected for all tests at mid-stream and mid-depth as suggested in the 1982 Environmental Protection Agency guidelines. Each subsite at a particular site was treated as a replicate for which a mean was calculated. The sampling period extended from 14 October 1997 to 13 November 1997 during periods of high and low flow and consisted of five sampling dates. Sites were chosen as representatives of the land use practices in each valley (Table 1; Figure 2 and 3). These sites are described beginning at the most upstream site and proceeding toward the mouth of the river.

Opunuho River Sites

The first site along the Opunohu River is located near the marae Tetiiroa. It is a second-order stream that consists of alternating pools and riffles. Canopy cover is approximately 50% and is dominated by Tahitian chestnut (*Inocarpus fagifar*). Ferns and moss are also found in the surrounding area. At the time of sampling, very few algae were present, but diatoms were abundant. Some shrimps and snail

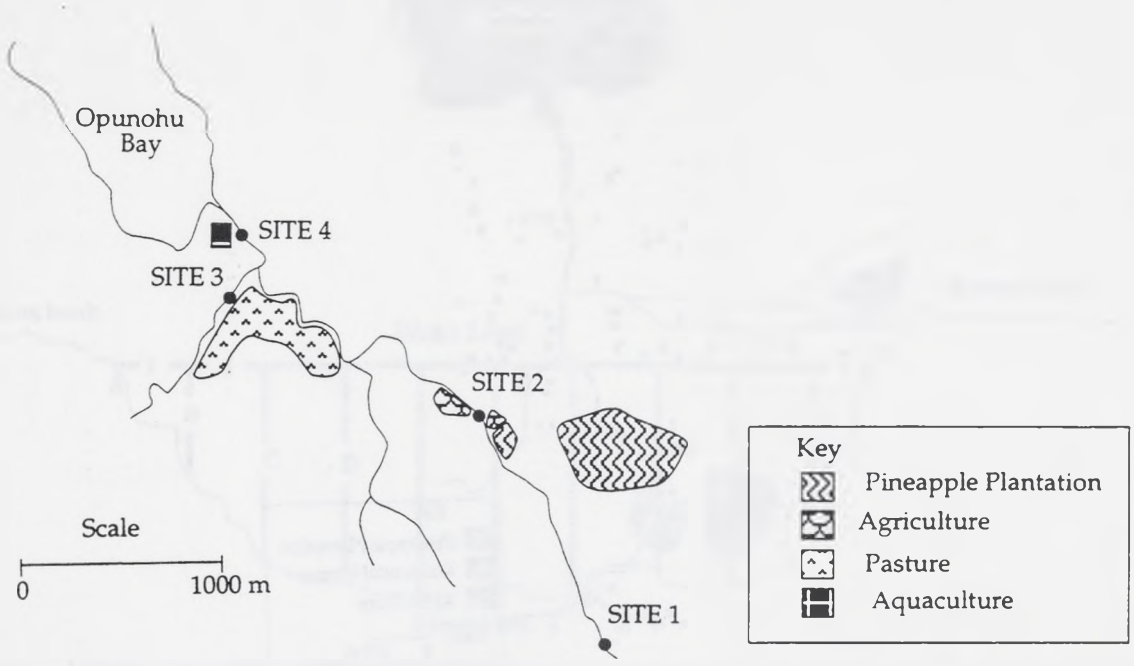


Figure 2. Location of study sites along the Opunohu River in relation to land use practices.

eggs were visible. The substrate consists of boulders, cobble, and gravel. There is very little development above this site, thus patterns and trends are assumed to be independent of human activities.

The second most upstream site was on a tributary off the main road to Pao Pao. It is just downstream of a small road bridge and adjacent to agricultural fields, where papaya and taro are cultivated. The field to the southwest was recently planted with taro seedlings. The site also receives runoff from pineapple plantations that are located in the surrounding area. There are fewer diatoms than the first site, but more algae is present. The site consists of riffles and the substrate is cobble and gravel. Canopy cover is approximately 35% and is dominated by Tahitian chestnut and hibiscus (*Hibiscus spp.*).

The third site is located on the main road to the Belvedere, a well-known lookout point of the two bays. It is on a tributary and is approximately .4 km from the mouth of the river. The canopy is open, but a closed canopy of hibiscus is found immediately upstream and downstream. The substrate consists of gravel and silt. An orange bacterial mat, with an areal extent of approximately $15m^2$, was visible during the low flow period after heavy rains. Algae is also present within the bacterial mat and within the main path of the stream. Few diatoms are present. Cattle and sheep graze in the fields immediately adjacent to the site.

The fourth site along the Opunohu River is located about 100 meters from the mouth of the river where tidal influences are reduced. The canopy is open, but the riparian vegetation is dominated by hibiscus.

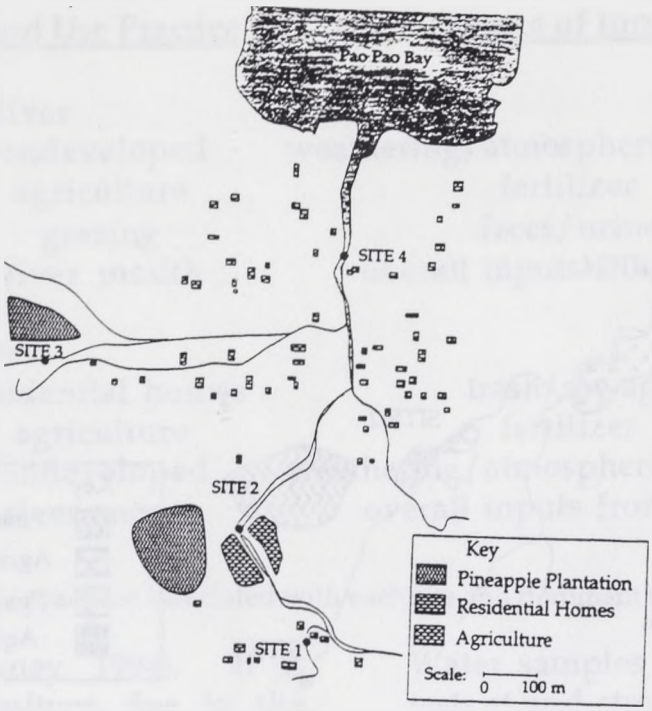


Figure 3. Location of study sites along the Pao Pao River in relation to land use practices.

The substrate consists of silt. Shrimp farming is practiced in the surrounding area. This site indicates the overall input to Opunohu Bay.

Pao Pao River Sites

The first site along the Pao Pao River is immediately upstream of a small bridge. The banks have been severely altered from their natural state, i.e. they have been reinforced with large boulders and planted with ornamentals. The canopy is essentially open and the substrate consists of silt. Small fish and freshwater eels are present. Residential homes are located in the immediate area and any inputs are attributed to this source.

The second most upstream site is immediately adjacent to a number of irrigated fields. The cultivated plants include eggplant, carrots, cabbage, and onions. Pineapple plantations are also present on the surrounding slopes. The canopy is open, but hibiscus and Tahitian chestnut are found immediately upstream and downstream. Cobble, gravel, and silt dominate the substrate. Algae is present.

The third site is located on a small tributary off the main channel on the north side of Mt. Rotui. The stream consists of a series of pools and cascades. The substrate is predominately boulder and gravel. Root masses from the riparian vegetation extend into the main flow of the stream. Canopy cover is 50% and consists of hibiscus. Diatoms are abundant, while algae is absent. Although some pineapple plantations are found in the surrounding area, this site is the least impacted by human activities.

The fourth site is located adjacent to an elementary school and is approximately 200 meters upstream from the mouth of the Pao Pao River. The canopy is open and there is essentially no riparian vegetation. The river bank has been reinforced by large boulders. The substrate is

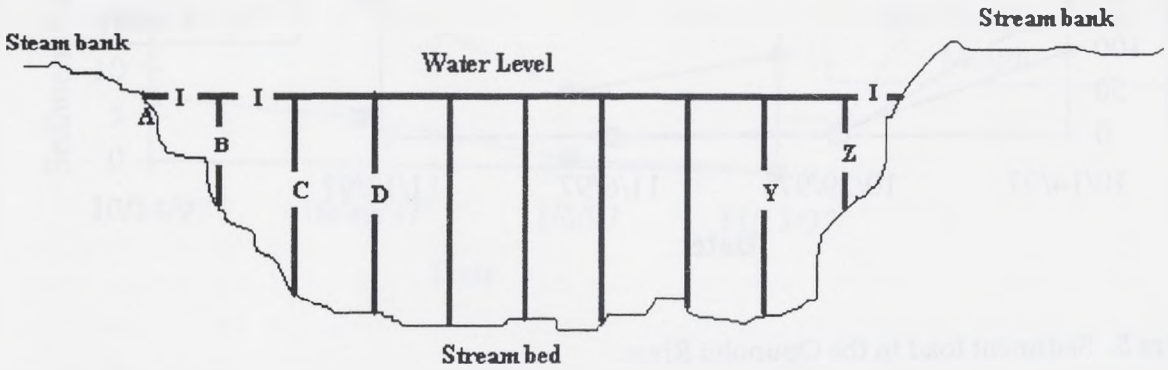


Figure 4. Method for determining cross-sectional area of a stream reach. A, B, C, D, etc. represent the depths at various points and I represents the interval between two adjacent depth measurements.

predominately silt. No algae or diatoms are visible. This site represents the overall inputs to Pao Pao Bay.

Discharge (Q)

A transect was established between two stream banks, perpendicular to stream flow. Thedepth at various intervals was measured (Figure 4). The cross-sectional area (A_{xs}) was then calculated by the equation

$$A_{xs} = I_1[(A+B)/2] + I_2[(B+C)/2] + I_3[(C+D)/2] + \ldots + I_n[(Y+Z)/2]$$

where A, B, C, D, etc. are the depth measurements and I_n is the interval between two adjacent depth measurements.

The surface velocity (v_{sf}) was measured by taking the average time that sticks required to travel a specified distance of the stream (n=5). The mean flow velocity (v_{mf}) wascalculated by multiplying v_{sf} by .6 (Hamilton and Bergersen 1985). The discharge (Q) was calculated by the equation

$$Q = A_{xs} \times v_{mf}$$

(Jeffries and Mills 1990). A_{xs} and v_{sf} were measured at approximately the same point at each site for every sampling date.

For the fourth site along the Opunohu River, a reference A_{xs} was determined by taking the depth at one meter intervals from a kayak. From the shore, the edge of the river was located. Because access to both sides of the river was not possible and the depth profile is symmetrical across the width of the river, the change in the width due to changes in flow at subsequent sampling dates was assumed to be consistent on both sides of the river. The elevational difference between the reference edge and the new edge was measured and was assumed to be constant for all points along the width of the river.

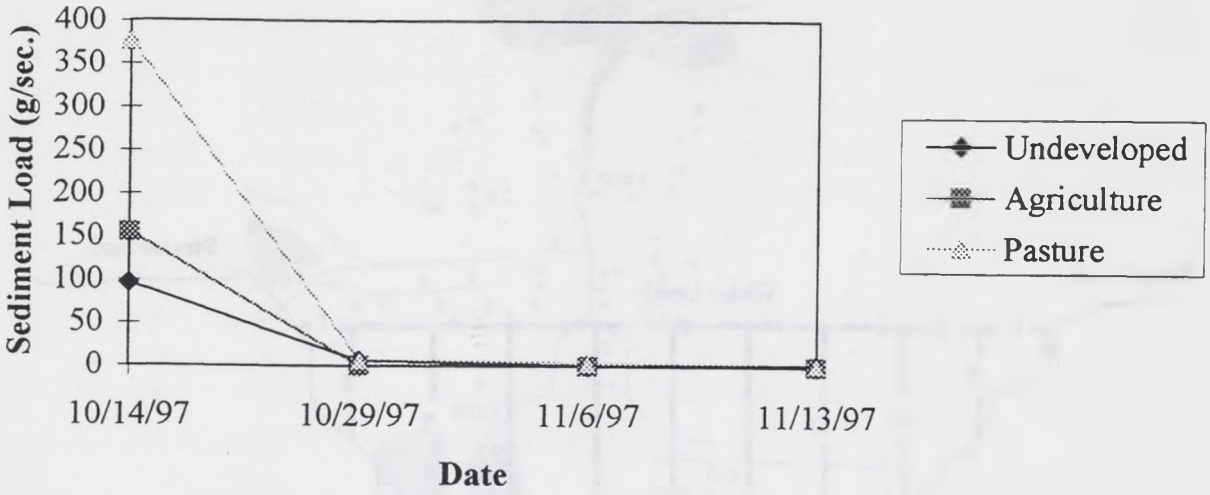


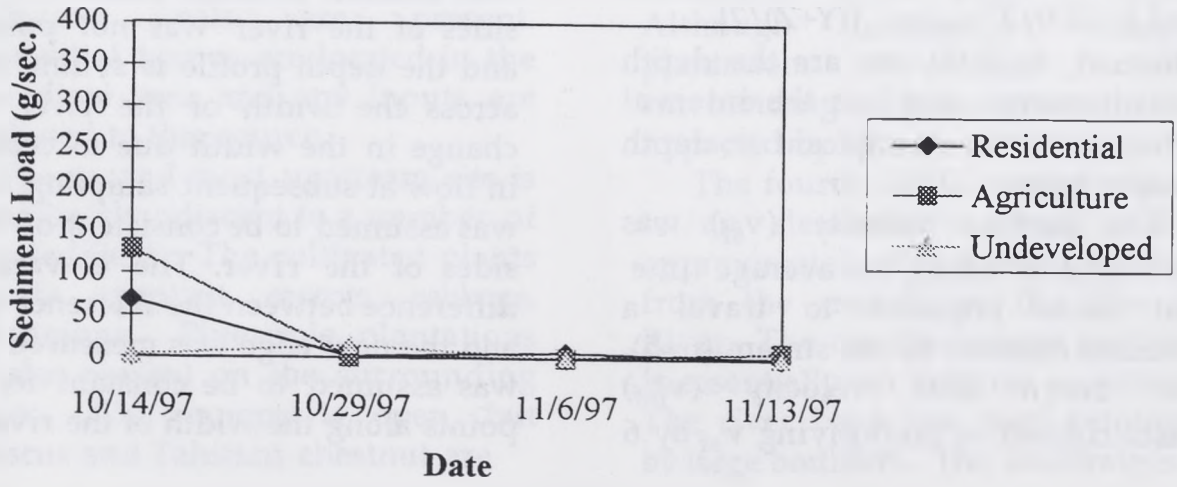
Figure 5. Sediment load in the Opunohu River.

The corrected depths were then used to determine the new A_{xs}.

Nitrogen and Phosphorus Measurements

A preliminary nitrate concentration was determined for each site using a Chemets® nitrate kit. In addition, 60 ml water samples were collected at each subsite. The samples were frozen and transported to UC Berkeley. Upon arrival in Berkeley, the samples were digested according to the Kjeldahl procedure in Tracy Benning's laboratory to obtain total nitrogen and phosphorus concentrations (Bradstreet 1965). The samples were then auto-analyzed at Stanford University. Nutrient concentrations were multiplied by the discharge to obtain nutrient load, expressed in mass per unit time. A Student's t-test was performed for each sampling date to determine if there was a significant difference in the mean nutrient loading levels between the rivers (n=12).

Figure 6. Sediment load in the Pao Pao River.



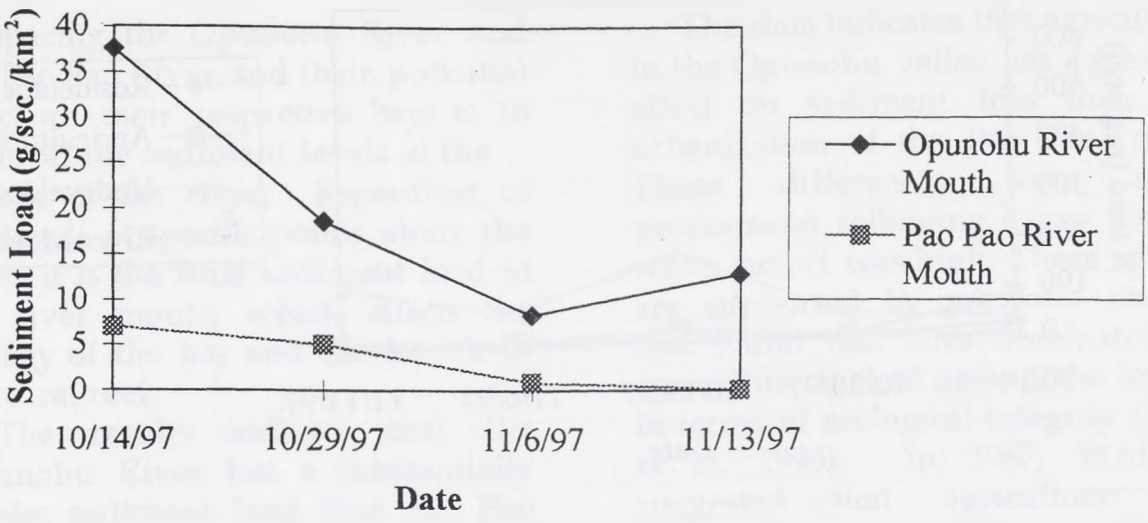


Figure 7. Sediment load at the Opunohu and Pao Pao river mouths.

Sediment Load

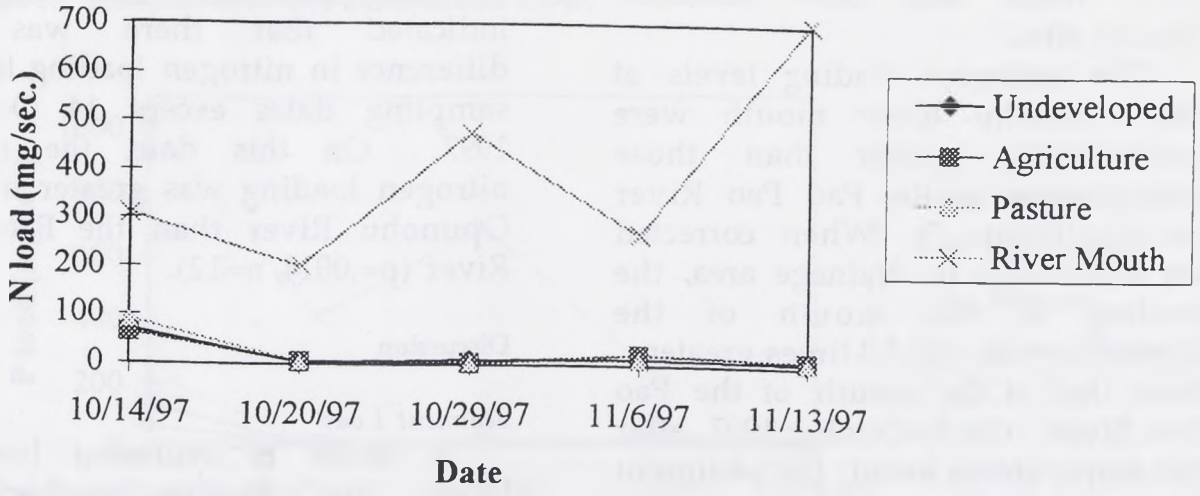
Water samples were collected at each site from midstream and mid-depth and filtered through a pre-weighed 42 μm filter. The filtered samples were air-dried and then weighed again. The sediment concentration was calculated and then multiplied by the discharge specific to that site and sampling period to obtain the sediment load.

Results

Sediment Load

Along both the Opunohu River and Pao Pao River, sediment load declined over time at all sites. (Figure 5 and 6). The sediment loads were highest after the storm event on 12 October 1997 and 13 October 1997. This storm event represented the first heavy rains of the season

Figure 8. Nitrogen load in the Opunohu River.



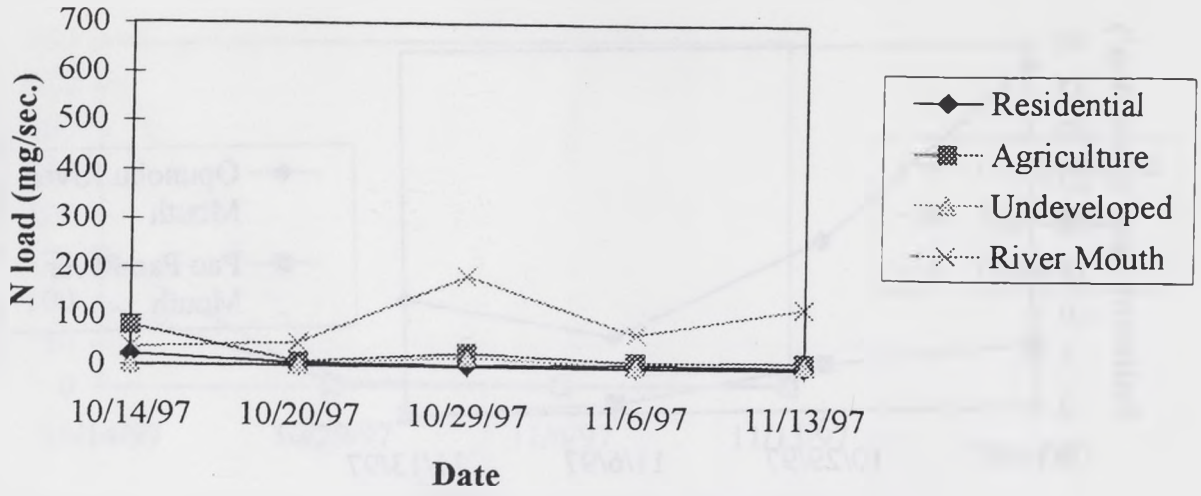


Figure 9. Nitrogen load in the Pao Pao River.

and was followed by a period of heavy river discharge.

On the Opunohu River, the highest sediment loads were found at the mouth of the river, whereas the lowest levels were recorded at the undeveloped site (Figure 5). The sediment loading levels at the pasture were initially twice those of the agricultural site, but both approached and maintained low levels by the 29 October 1997.

Along the Pao Pao River, the highest sediment loading levels were found near the agricultural site and the lowest was at the undeveloped site (Figure 6). By the 29 October 1997, there was little variation among sites.

The sediment loading levels at the Opunohu River mouth were substantially greater than those encountered at the Pao Pao River mouth (Figure 7). When corrected for differences in drainage area, the loading at the mouth of the Opunohu was still 5.3 times greater than that at the mouth of the Pao Pao River. On 14 October 1997, after the major storm event, the sediment plume in the Opunohu Bay appeared to be three times greater than the plume in Pao Pao Bay.

Nutrient Load

At all sites except the river mouths, the nitrogen and phosphorus levels were at their peak during the first sampling period (Figure 8-11). The greatest variation in nutrient levels among sites occurred during this period of high flow. Nutrient levels were more erratic at the mouths of the rivers.

The Student's t-test indicated that there was no significant difference ($p<.05$) in phosphorus and nitogen loading between rivers for all sampling periods. The test also indicated that there was no difference in nitrogen loading for all sampling dates except 14 October 1997. On this date, the mean nitrogen loading was greater in the Opunohu River than the Pao Pao River ($p=.0014$, $n=12$).

Discussion

Sediment Load

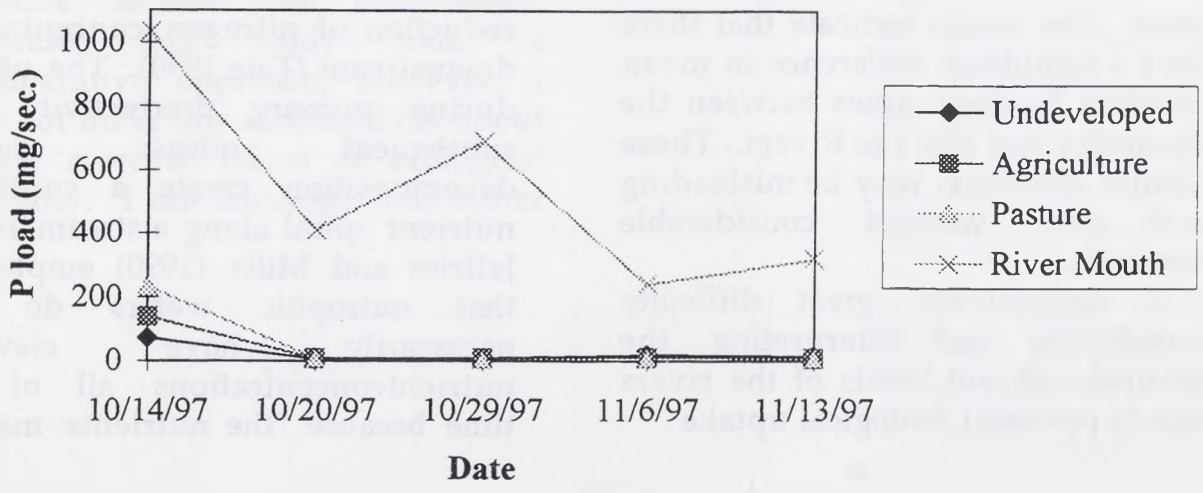
In terms of sediment loading levels, an effective method of

comparing the Opunohu River and the Pao Pao River and their potential effect on their respective bays is to focus on the sediment levels at the mouth of the river. Regardless of the levels at specific points along the river, it is the final sediment load at the river mouth which affects the biology of the bay and the health of the coral reef.

The results indicate that the Opunohu River has a substantially greater sediment load than the Pao Pao River. The elevated sediment load in the Opunohu River, however, may be due to both natural and anthropogenic causes. Because the Opunohu catchment is approximately 1.7 times larger than the Pao Pao catchment, the total amount of discharge and potential sediment loss is naturally greater in the Opunohu valley. By correcting the sediment load to obtain a value per unit area, however, we can compare the amount of sediment lost for the same unit of area. This value would enable us to minimize natural variation and assess how land use at the larger spatial scale affects a given area.

The data indicates that agriculture in the Opunohu valley has a greater effect on sediment loss than the urbanization of the Pao Pao valley. These differences were more pronounced following heavy storms when runoff was high. These results are supported by previous studies that found that sites dominated by agriculture ranked among the lowest in terms of ecological integrity (Roth et al. 1996). In 1967, Wolman suggested that agriculture and grazing have a greater impact on sediment yield than urbanization. Agricultural practices such as tilling and ploughing break up the soil structure and subsequently cause erosion. An important consideration when assessing the impact of agriculture is to examine the intensity of agricultural practices, i.e. the use of fertilizers and heavy machinery. Grazing can also lead to erosion as a result of the physical compaction of the soil and the removal of ground cover. Cattle and sheep create paths and tracks which lead to hillside instability. Urbanization, however, results in the creation of impervious surfaces

Figure 10. Phosphorus load in the Opunohu River.



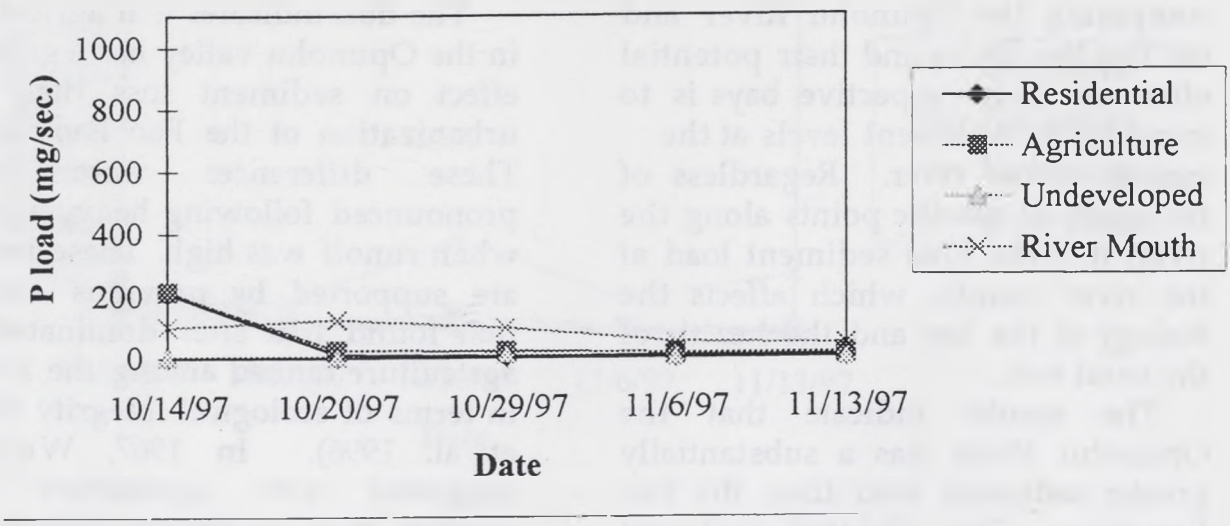


Figure 11. Phosphorus load in the Pao Pao River.

and a decline in sediment yield as the area becomes more stable (Knighton 1984).

The future of the Pao Pao River, however, is questionable. Within the Pao Pao Valley, there is a demand for more agricultural land, primarily for the cultivation of pineapple. Because available space is limited, many farmers have opted to plant on steep slopes. This practice, however, can be disastrous because it may lead to substantial increases in erosion.

Nutrient Load

By monitoring the nutrient loading levels at multiple sites, I obtained an average loading for each river. The results indicate that there isn't a significant difference in mean nutrient loading values between the Opunohu and Pao Pao Rivers. These results, however, may be misleading and thus warrant considerable research.

I encountered great difficulty quantifying and interpreting the relative nutrient levels of the rivers due to potential biological uptake and release. At the agriculture sites on both rivers and the pasture site on the Opunohu river, there was a noticeable increase in algal standing crop after the first sampling period. A microbial or fungal mat, measuring fifteen meters by one meter, was also observed at the pasture site. This mat is typically associated with nutrient inputs due to grazing (Lawson pers. comm.). The algal and microbial growth may have depleted the nutrients in the immediate area so that their concentrations would be undetectable. The biotic uptake of nitrogen by algae and possibly riparian vegetation may be an important mechanism of the reduction of nitrogen concentration downstream (Tate 1990). The uptake during primary productivity and subsequent release during decomposition create a continual nutrient spiral along a stream reach. Jeffries and Mills (1990) emphasize that eutrophic waters do not necessarily have elevated nutrientconcentrations all of the time because "the nutrients may be

gleaned and utilized by the plants, especially algae, so quickly that amounts at any instant are undetectable". This phenomena may be even more pronounced on a volcanic, tropical island where nutrient levels are typically low (Marquet 1991).

This study was initially designed to monitor sediment and nutrient loading levels relative to localized land use practices. This approach, however, ignores the dynamic nature of a river ecosystem and factors, such as biological activity, which may influence these levels. Riparian vegetation, for example, regulates sediment transport and moderates terrestrial inputs of nutrients from agricultural sources (Osborne & Kovacic 1993; Lowrance et al. 1984) Esser and Kohlmaier (1991) suggest that the "input over the entire watershed and load at the river mouths are not equivalent, because of the processes occuring along the rivers and their floodplain". Roth et al found (1996) that measures of land use at larger spatial scales, i.e. at catchment levels, were a superior predictor of

Conclusion

The nutrient and sediment loading values suggest that the Opunohu River is not pristine relative to the Pao Pao River. Because this study took a comparative approach, however, I can not make any assumptions about either river in terms of ecological integrity. I can conclude that either the Opunohu River is more impacted or the Pao Pao River is less impacted by anthropogenic activities than originally assumed. It may be helpful for future studies to focus on the use of biological organisms as indicators of stream health.

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Causes of Spatial Variation of a Fringing Reef in Paopao Bay, Moorea, French Polynesia

Devon Muto
College of Natural Resources
University of California, Berkeley 94720

ABSTRACT. Several factors can effect the development and the community structure of a coral reef. This main objective of this study is to describe characteristics of a fringing reef in a bay and to identify the major factors which are influencing its composition. 37 20 m^2 areas were surveyed on the reef flat of the fringing reef along the eastern side of Paopao Bay, Moorea (French Polynesia). Algae and coral genera were identified and percent cover was recorded. In addition, substrate type and cover along with Echinodermata and Holothurian abundances were noted. Through regression scatter plots, patterns were observed which identified the inputs of rivers as the overriding influence on coral communities in the bay. This contradicted previous work on other bays in which the confinement and energy conditions within the bay governed the development of the reef assemblages.

Introduction

Bays are often described as being subject to numerous influences. They have been noted to possess higher variations in tides, temperature, salinity, and turbidity (Ketchum, 1983). In addition, they are most often affected by multiple human activities. Suprisingly, the coral reefs of these unique environments have attracted few studies.

Possible effects on coral reefs of both natural and anthropogenic origins have been well documented over the past years. Natural stress such as those which result from storms, volcanoes, temperature, sea level, predation by *Acanthaster planci*, sedimentation, and El Nino events can result in large amounts of changes or mortality in the reefs (Grigg and Dollar 1990; Brown and Howard 1985; Pearson 1981). Other studies reviewing impacts on reefs such as sedimentation (from construction, dredging, wastes), sewage, nutrient enrichment, and toxic dumping or spills, displayed the destruction that humans have caused on reefs throughout the world (Johannes 1975; Rogers 1990; Karlson and Hurd 1993; Connell 1997).

Practically all of the research for these studies were conducted on reefs which causes were known and effects were to be discovered. The objective of this study is to analyze the effects on a reef in a bay by looking at spatial variation and patterns, and then to deduce the cause or causes of those characteristics.

Materials and Methods

The study was conducted in a bay on the north coast of Moorea (17° 30'S; 149° 50'W), one of the Society Islands (French Polynesia). Moorea is a triangular shaped high island with the circumference of 61 km and 134 km^2 of land. The north shore of the island consists of two deep bays similar in size and shape. The study area was along the east side of Paopao Bay, the eastern most of the two bays (Figure 1). This bay is approximately 2.5 km long from bay head to the bay mouth and has an approximate average width of 550 m. The mouth of the bay is effected by Avaroa Pass (300 m wide and 60 m deep) in the barrier reef located directly north of it. A patchy fringing reef which connects to the lagoon's fringing reef at the bay's mouth begins 100 m from the bay head on the east side and further north on the west side. Steep volcanic mountains boarder the bay to the east and west, and a large valley containing the Paopao River which flows into the bay head is to the south. The watershed of the valley's river contains numerous pineapple plantations, and between 150 and 200 residences. Another river, much smaller in size, enters the bay in a cove about 600 m from the bay head in the east side. The shore and coastal strand along the east side of the bay and around the bay head are populated by hotels, markets, restaurants, and numerous residences. The west side of the bay remains practically completely undeveloped.

Distances from the mouth of the Paopao River along the fringing reef on the eastern side of the bay were calculated by using a topographic map of the area. 36 50 m long stretches were calculated along the reef starting at 350 m from the river mouth. A study site was selected at random within each stretch to ensure that the entire length would be represented. At each site a 2 m × 10 m area parallel to the reef crest was studied by placing a 1 m × 1 m quadrat with a 10 × 10 grid throughout it 20 times (Figure 2). This area was located 2 m inshore of the reef crest

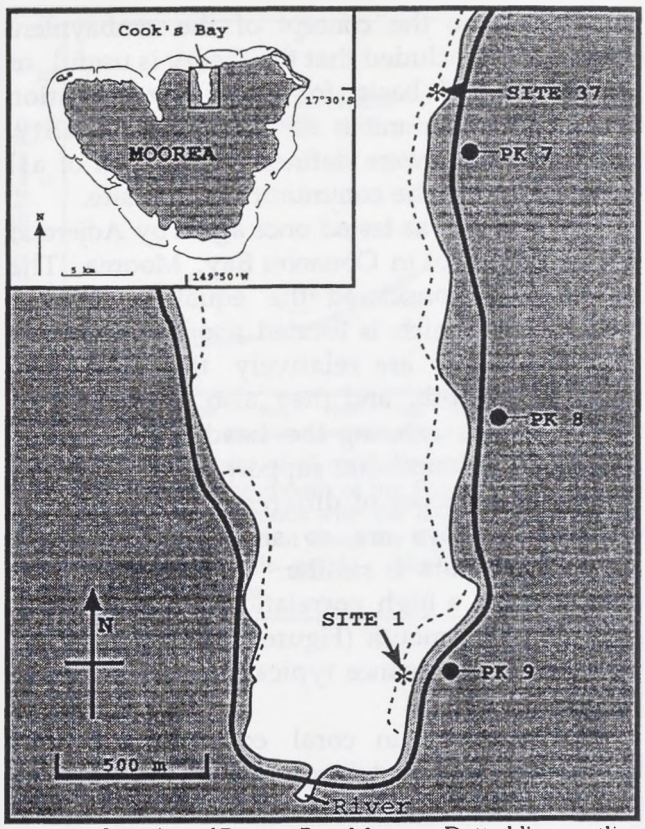

Figure 1. Location of Paopao Bay, Moorea. Dotted lines outline the edge of the patchy fringing reef which is found along both sides of the bay. Site 1 was the southern most point and site 37 was the northern most point along the fringing reef. The river which is refered to at the bottom is Paopao River.

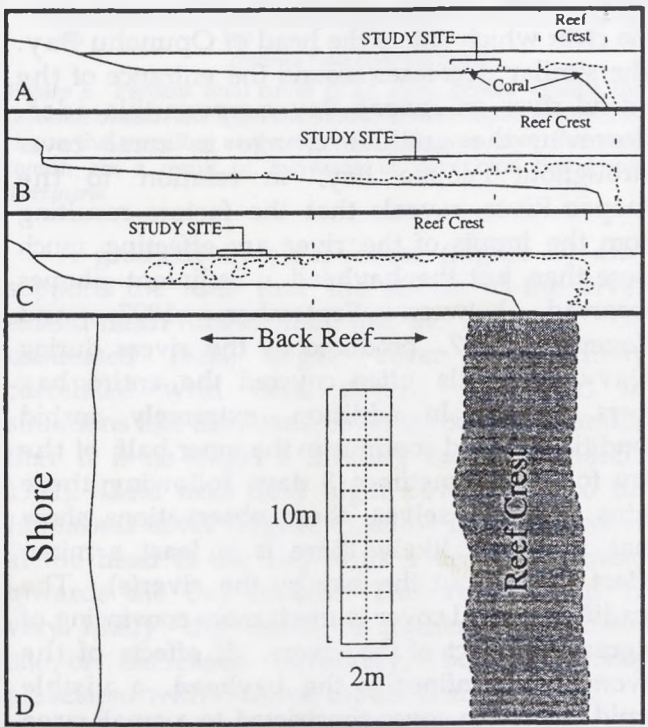

Figure 2. Location of study sites in relation to reef crest. A,B, and C show a profile position of study area when reef crest size and characteristics vary. D represents an overhead of the parrallel position of the site to the reef crest.

community on the back reef area. The reef crest characteristics varied along the fringing reef, therefore, in order to standardize the testing area, the 2 m measurement started at the point where there was a visible difference on the inshore side in the reef crest community (Figure 2).

Within each quadrat, genera of coral and algae were identified and for each genus percent cover was calculated. Substrate was classified as either sand/mud or dead coral, and percent cover of each was also calculated. Percent cover values represent a 2-dimensional view from directly above the quadrat. Topography of the area and mass, height, and density of corals and algae are not represented. Counts were also made for all echinoderm and Holothurian species visible from directly above within the quadrats. In addition, an estimated average depth was recorded for each quadrat. Data from the 20 quadrats, at each site, were grouped to give a total for the entire studied area at that site. In order to determine the differences along the reef, representative values for each site were plotted in relationship to their distance from the river mouth. All other data to be analyzed were also subjected to a normal x/y scatter plot. Any patterns or correlations were analyzed for relevance with r-square values.

Results

A total of 8 genera of corals were identified among the 37 study sites. These were *Porites, Psammocora, Pocillopora, Montipora, Acropora, Montastrea, Pavona, Leptastrea,* and *Fungia.* 4 uncommon species or genera of coral were not identified. Algae genera identified along the reef included: *Halimeda, Dictyota, Galaxaura, Porolithon, Padina, Turbinaria, Ventricaria.* 3 genera or species of algae with low occurrence were not identified. The species of echinoderms occurring in the study sites were those of sea urchins only: *Diadema savignyi, Echinothrix calamaris, Echinothrix diadema,* and *Echinometra mathaei.* Two species of holothurians, sea cucumbers, were recorded within the study sites. .

Total coral cover was found with an increasing gradient away from the Paopao River mouth (Figure 3). Data was fitted with a polynomial line which reached a minimum where the smaller river enters the bay. Only

data for the genus *Porites* was comparable for all sites. Other genera were either restricted to only 2 or 3 sites or had values too small with too much variation to have significantly meaning. *Porites* were found at all sites, except for 3, and normally dominated in comparison to the cover of all other coral genera. This dominance decreased in proximity to the mouth of the second river and also at the mouth of the bay (Figure 4).

Although algal cover was extremely variant, a trend much similar to the inverse for that of coral cover could be seen (Figure 5). Algal cover was found to be greatest closer to the river mouth and decreased gradually moving away from that point. The cover does increase just slightly for sites near the mouth of the bay. *Halimeda* and *Dictyota* were the two most common genera observed. However, near the mouth of the smaller river a species of sea grass completely dominated. Also, *Turbinaria* became increasingly the more dominant genera closer to the mouth of the bay. At a few other sites, relatively uncommon genera were found to have the most cover. Like the coral data, only one genera, *Halimeda*, of algae was consistent enough to be analyzed between all sites. Percent cover values for *Halimeda* revealed a slightly decreasing trend away from the river mouth (Figure 6).

Identification of sea urchin species in the field was extremely difficult. The main reason for this is that many of the individuals were found in small crevices or holes in the substrate which restricted intensity of inspection. To account for this all species, except for *Diadema savignyi*, were grouped for a total urchin count at each site. *D. savignyi*, was an easily identifiable species and had a total count of 3 individuals for all of the sites. The total urchin counts contained extreme variability which hid any trends that existed. Data for the counts of the holothurians was also much too sporadic for any trends or correlation to be seen.

Discussion

In 1944, Miyadi *et al.* offered the term "embayment degree" to describe the factors of confinement and energy conditions which effect coral reef communities in bays. They reported three categories to recognize a change in benthic communities throughout a bay: weak, medium, and strong embayment degrees from the bay head to the mouth respectively. Several studies on bays in Ryuku, Japan and Palau, Micronesia were summarized by Horikoshi (1988), who related those works to the concept of the embayment degree. He concluded that the theory is useful on a more general basis for describing "location factors" of communities at any given locality. Location factors were defined as the sum of all factors effecting the community at that site.

The theory was tested once again by Adjeroud and Salvat (1996) in Opunohu Bay, Moorea. The bay is often considered the equal to that of Paopao Bay, which is located about 4 km to the east of it. They are relatively the same size, shape, and depth, and they also have a river similar in size entering the head of each bay. Patterns were found that supported the theory of three distinct zones of different characteristics. Because the bays are so similar, it similar. Overall, the data is similar: 1) coral cover was found to have a high correlation to the distance from the river mouth (Figure 3); and 2) *Porites* displayed a dominance typical to fringing reefs (Figure 4).

The decrease in coral cover and *Porites* dominance found by Adjeroud and Salvat closer to the river entrance were not consistent with diverse and populous communities found in locations of "high embayment degree" in studies cited by Horikoshi (1981,1988). This discrepancy was determined to be a result of stress due to temperature, salinity, and turbidity changes from the river which enters the head of Opunohu Bay. The similar decreases around the entrance of the second river on Paopao Bay supports this idea. However, the gradual change in coral cover throughout Paopao Bay, in relation to the Paopao River, reveals that the factors resulting from the inputs of the river are effecting much more than just the bayhead. Sediment plumes observed between September, 1997, and November, 1997, produced by the rivers during heavy rain falls often covered the entire bay (pers. obs.). In addition, extremely turbid conditions would continue in the inner half of the bay for 1 to sometimes 3 days following these rains. By themselves, these observations show that it is very likely there is at least a minor effect throughout the bay by the river(s). The gradient of coral cover is much more convincing of a greater impact of the rivers. If effects of the rivers were confined to the bayhead, a visible rapid change in cover constricted to a small area would be much more likely. However, the gradient of coral cover seen in Paopao Bay is gradual and is throughout the entire bay.

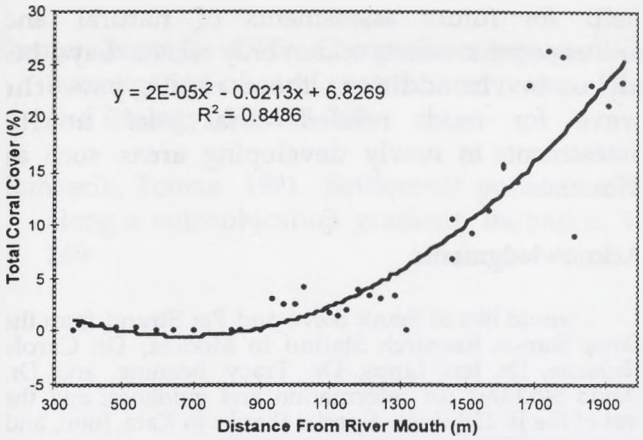

Figure 3. Percent cover of all coral genera combined, against distance of site from the mouth of the Paopao River. Bottom of polynomial fit corresponds with the location of the second river entrance. The percent cover for the genus *Porites* looks extremely similar to this graph. Mostly because of the dominance by that genus.

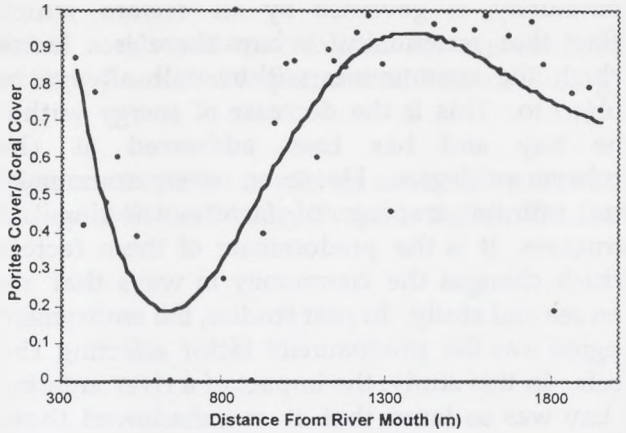

Figure 4. Dominance of the genus *Porites* against distance of site from the mouth of the Paopao River. Dominance is calculated by dividing the percent cover of genus Porites and dividing it by the percentage of total coral cover. The large drop at approximately 600m corresponds with the location of the second river entrance.

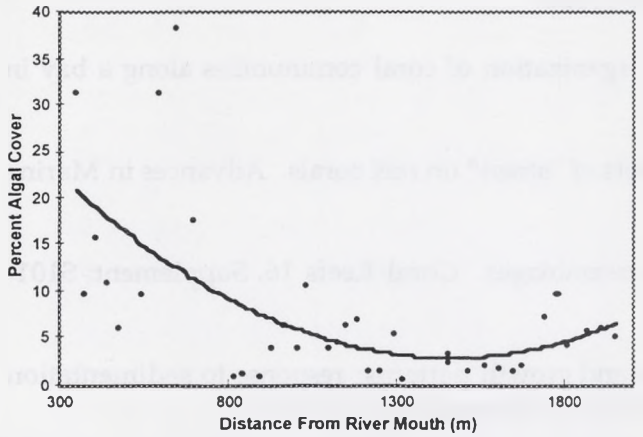

Figure 5. Percent total cover of all algae genera against the distance of each site from the mouth of the Paopao River. The rise in the trendline at the furthest distances from the river mouth are a result of increases in cover for the genus *Turbinaria*.

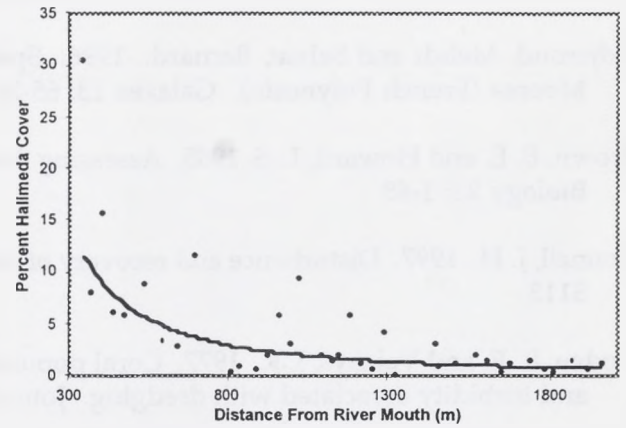

Figure 6. Percent cover of the genus *Halimeda* against the distance of each site from the mouth of the Paopao River. *Halimeda* grows on both sandy and hard substrates, and was the only genus of algae recorded along the entire fringing reef.

A gradient in algal cover (Figure 5) also supports the idea that the effects of the river extend much further than just the bayhead. On unstressed reefs, algal cover is normally correlated with coral cover. However, in situations like this, coral cover is reduced so much that it is no longer a limiting factor (Tomascik 1991). Data from total algal cover and also for *Halimenda* cover (Figure 6), show increased cover at the head of the bay with a decreasing trend towards the bay mouth. This relationship is very likely the result of nutrient enrichment and/or decreased herbivory, both normally associated with riverine inputs (Tanner 1995).

Although Paopao Bay is certainly effected by the Miyadi factors of confinement and changing energy conditions (which Adjeroud and Salvat deemed dominant in Opunohu except for the bay head), evidence suggests that the effects resulting from the rivers are larger than previously stated. There are 4 possible reasons which may explain the difference in opinion on the impact of rivers on bays between this paper and that of Adjeroud and Salvat (1996): 1) there *is* an actual difference between Opunohu Bay and Paopao Bay; 2) Adjeroud and Salvat looked at species richness and diversity, whereas this study calculated coral cover; 3) Adjeroud and Salvat only had 8 sites within the bay, this one had 37; and 4) Adjeroud and Salvat compared transects of the fringing reef, this study compared select 20 m^2 sites on the back reef.

The gradient in Paopao Bay supports Horikoshi's adapted concept of the embayment degree which must take into account all factors of a locality. The populations and make up of any

community, is governed by all factors which effect that community. In bays there is a factor which the communities within will always be subject to. This is the decrease of energy within the bay and has been addressed as the embayment degree. However, every community has infinite amounts of factors affecting its structure. It is the predominate of these factors which changes the community in ways that we can see and study. In past studies, the embayment degree was the predominant factor effecting the reefs. In this study, the impact of a river entering a bay was so large that it overshadowed those effects of energy conditions the bay. Understanding these different factors can greatly help for future assessments of natural and anthropogenic effects on not only reefs in bays, but all reefs. In addition, these results pave the wave for much needed coral reef health assessments in newly developing areas such as Moorea.

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The Morphology of Tuarea Fringing Reef, Moorea, French Polynesia

Ryan Petterson
Dept. Geology, U.C. Berkeley, 94704

ABSTRACT. On the southern tip of Moorea lies the bay of Atiha. Inside the bay lies Tuarea Fringing reef. This reef is abnormal in both its location and morphology. Forming with the general morphology of a barrier reef, including an algal ridge and spur and groove topography, Tuarea fringing reef is of unknown origins. In order to document this feature, a map was made depicting the lagoon, ridge, and spur and grooves. Profiles were made to compliment the plan map. Detailed observations were also made of the surface features of the reef. In addition to the documentation of the reef, several scenarios are presented as to the possible origin of the reef. The reef may be a depositional feature, upon which a thin veneer of calcareous and fleshy algae have grown. There is also evidence to support the idea that it is relic reef growth that as a result of change in the environment shifted to algal growth. The actual shape and location of the reef are most likely due to wave patterns generated by the very shallow pass directly seaward it.

Key words. Fringing reef, morphology, spur and groove, algal ridge.

Introduction

Moorea, located in French Polynesia, is a high, steeply dissected volcanic island with a continuous barrier reef around it. This reef is broken only by several major passes. On the south western tip of Moorea is the pass of Avarapa and its accompanying bay, Atiha. The southern tip of this bay is a small, non-descript projection called Tuarea Point. Around this point has formed a well developed fringing reef. In 1977, Steers and Stoddart stated that coasts protected by barrier reefs are often void of fringing reefs, and that fringing reefs were generally simple reefs with simple explanations. Tuarea fringing reef has the apparent morphology of a second barrier reef, which Guilcher (1988) noted to be absent in the Societies as a result of low tidal range (~30cm), narrow lagoons and no wide passages on the windward side of the islands. Tuarea reef defies both statements. Not only has it formed within the lagoon of a barrier reef, but it has extremely well developed facies, including spur and groove formations.

Though rare, double barrier reefs are not unheard of. The double barrier reef of North Bohol (Philippines), described by Pichon (1977), is perhaps the most well known. Pichon's origin of Bohol was one of subsidence and favorable tidal currents. The two barriers were mostly sandy accumulations, characterized by a low energy environment.

This is not the case with Tuarea. With unfavorable tides and a high energy environment, it requires another explanation. In the interest of better understanding reef formation in general and thereby helping to preserve them, it becomes of interest to determine and document the controlling factors in the development of the Tuarea fringing reef.

Materials and Methods

The mapping was founded on a system of 1m rebar posts hammered into the reef crest at measured distances and compass bearings. Distances and bearings were taken from points on the framework to features of interest (rock and sand interfaces, spur and grooves, etc.). Profiles were made from the shore to the seaward edge of the reef crest and across the shallow spur and groove formations. This was done using a tripod, level, transect tape, stadia rod, and more 1m rebar stakes. The surveys were backsited to the benchmark located near Kilometer post (P.K.) 18. This benchmark is part of a system of benchmarks near almost all of the P.K. markers. The profiles were taken perpendicular to the coastline to a specified post in the framework already setup and across a characteristic well developed region of the shallow spur and groove. The additional rebar stakes were used to "leapfrog" with the tape along the length of the profile. The bearings of the profiles were taken and tied into the plan map of the reef. The data were complemented by the topographic map of the island of Moorea, several

high altitude aerial photographs, and snorkeling expeditions around the ridge crest, both seaward and landward. Depths around the seaward edge of the reef were measured using a commercially purchased depth gauge.

Results

Inner Lagoon

The landward edge of the lagoon is an artificial seawall constructed of large boulders. The lagoon floor is composed primarily of coral sand and small debris, with accumulations of larger coral rubble apparent at the northern end of the lagoon. In the middle and to the south, *Porites* heads are present in the lagoon, even forming micro-atolls in the shallow water. The southern and northern extremes of the lagoon are shallowest, no more than 1 meter in depth. The middle of the lagoon reach a maximum depth of approximately 2 meters (figure 2). A lack of *Diadema* in the inner lagoon, as well as on the reef flat and fore reef, was also noted.

Reef Flat

The transition from the lagoon to the reef flat is demarcated by an abrupt change in elevation, and moves from a sandy to a rocky carbonate structure. The reef flat ranges from 10 to 30 meters in width. The widest areas being at the northern and southern extremes and the narrowest in the middle, corresponding to the areas of least and greatest spur and groove development respectively. The reef flat is dominated by *Sargassum sociale*, *Turbinaria ornata*, and *Dictyota bartayresiana*. Several other species characteristic of low flow back reef are also present (figure 2). The flat itself is interspersed with depressions and furrows. The furrows are no more than 50 centimeters deep and run roughly normal to wave direction. They originate at the heads of grooves and continue through the backspur moat, across the reef flat and occasionally reach the inner lagoon waters on the other side. The path varies from furrows to tunnels with no recognizable pattern.

Boulder field

On the reef flat, behind the zones of less well developed shallow spur and groove formations, a boulder field is present (northern and southern extremes, fig. 1). The boulders of coral rubble are often as big as 50 centimeters in diameter. The fields also contain pieces of coral rubble that are very wide and flat, characteristic of deep water growth forms.

Back-spur moat

From the ridge crest the surface of the reef slopes into a depression between the ridge and the *Porolithon* encrusted spurs that runs, in some fashion, the entire length of the spurred crest. This depression, or moat, is highly irregular, sometimes flowing into the outer lagoon and sometimes connected to it by furrows or tunnels. The moat itself is up to 1 meter deep. Where the moat opens into the outer lagoon *Hydrolithon* islands often occur (figure XXXX). These islands are no more than 10 meters from the reef proper, and the depths between the islands and the reef are no more than 2 meters.

Shallow spur and groove

On the outer lagoon side of the moat, pink *Hydrolithon* encrusting algae replaces the *Sargassum* and *Turbinaria* that cover the reef flat and algal ridge. *Hydrolithon* is the dominant genus on all of the shallow spurs. The spurs are irregular in frequency, but show a fairly consistent pattern of amplitude (figure 3). The maximum depth between the spurs and off the ends of the spurs is consistently around 1 meter and at low tide the *Hydrolithon* encrusted tops stand roughly 10cm out of the water. The orientation and shape of the spurs is also irregular, showing only a general trend towards orientation normal to wave direction. The sides of the spurs are vertical to overhanging and are sometimes so close to each other that the overhanging sides become incipient tunnels. The grooves between the spurs are characterized by a distinct lack of algae, perhaps the only location without it. They are instead filled with gravel sized and smaller grains of coral debris.

Fore Reef

Beyond the shallow spur and groove formations the fore reef is once again dominated by algae. *Sargassum sociale* and *Dictyota bartayresiana* provides a near total algal cover, with the latter often epiphytic on the former. The topography of the fore reef is made up of coral rubble and has a gently decreasing slope until it reaches the sandy bottom of the lagoon floor at 7 to 10 meters. At the interface between the fore reef structure and the outer lagoon floor 5-6 large *Porites* heads are present. These helmet shaped heads range in size from just under 1 meter in diameter and less than a meter high to more than 3 meters in diameter

and 2 meters high. The heads are growing inuneven plates, each superceding the previous one.

Outer lagoon

The outer lagoon reaches depths of over forty-four meters and contains, at its edges, what appear to be basaltic out crops, though this was not confirmed. The pass in the outer barrier reef is approximately 200 meters wide and a mere 3.5 meters deep.

Comparison with Afareaitu reef

The morphology of Tuarea fringing reef is very similar to a fringing reef formation in the bay of Afareaitu. The reef at Afareaitu is much less defined, however, than Tuarea. The crest, as well as the shallow spur and groove formations, are only marginally visible. The inner lagoon is approximately 50 meters wide and no more than 50 centimeter deep at low tide. The outer lagoon is 36 meters deep and the pass is 4.4 meters deep. The pass at Afareaitu and the pass at Atiha are the only major passes that are of depths this shallow. The next shallowest pass is perhaps 30 meters deep. In addition, these two bays possess the only fringing reefs of the afore mentioned morphology that are known on the island of Moorea.

From aerial photography, it can be seen that a wave pattern, often present in passes, is exacerbated in the bay of Afareaitu. This is presumably due to the shallow pass and the wide width of the barrier, which is causing a defraction pattern that appears as two distinct wave propagations originating from the edges of the pass. The shallow pass decreases the wave length and, in doing so, increases the effect of the wave defraction and reflection off of the edges of the pass. The point at which these two arcs cross is directly in line with the reef formation under observation.

Discussion

The lack of live coral growth is particularly interesting because this reef appears to be characteristic of high levels of coral growth, i.e. the pronounced reef crest and spur and groove. This offers two possibilities. Either the environmental conditions causing the extreme reef growth drastically changed after the reef had reached its present form, or our ideas about the formation of reef structures need to be reexamined.

It is altogether possible that a shift in environmental conditions has taken place in the recent past to cause the coral to die and the algae to flourish. This could be natural changes or anthropogenic disturbances. This would mean that the conditions in the lagoon were extremely favorable reef growth at one time.

Tuarea reef could also be a veneer of algal and minimal coral growth upon a preexisting erosional platform. Similar structures were noted by Steers and Stoddart (1977). This platform could be a result of waves continuing to erode even after the barrier reef was fully developed due to the pass directly out from Tuarea point.

Adey and Burke (1976) described a similar fringing reef on the island of Martinique in which the coral growth had given way algal growth at some point in the past. They described a reef characterized by a lack of corals on the ridge section. In its place was dense covering of fleshy algae on a carbonate substrate. This *Sargassum* dominated platform was given the term "Fleshy algal pavement." These fleshy algal pavements have been described at several places in the Caribbean but have not been described in the Indo-Pacific. The reef structure described by Adey and Burke was also typified by high productivity and turbidity, but low populations of *Diadema* and parrot fish.

Adey and Burke concluded that the low populations of *Diadema* (and possibly parrot fish) precipitated the heavy growth of macro-algae. The lack of *Diadema* on the reef seemed to be a result of high levels of deposition filling in the large porosities that *Diadema* habitate and over exposure to rough water (Adey and Burke 1976).

It would be of interest to determine if a similar lack of Diadema exists on the fringing reef at Afareaitu so as to further correlate the two sites and thereby increase our understanding. If more similarities between the two reefs and the two passes could be demonstrated it would lend more support to a causal relationship between the reefs and the passes. Unfortunately, the exact nature of the relation between the phenomena of Tuarea Fringing reef and the extremely shallow pass is unclear, though there is evidence to support a relation.

For example, there are three possible outcomes of the wave crossing; they are aligned trough to trough, they are aligned trough to crest, or they are somewhere in between. If they are trough to trough the waves will amplify, creating higher wave energy. If they are trough to crest, the two wave patterns will cancel each other out.

leaving no wave energy (Bearman 1989). If the waves are amplified, the increased wave energy could cause increased coral growth in response, thereby extending the reef toward the outer lagoon. If the waves are canceling each other, the decreased energy in this zone could lead to increased deposition of coral rubble on the reef. If the waves were causing increased reef growth a negative feed back system would be set up in which the propagating spit of coral reef would cause wave refraction around itself, thereby increasing sedimentation and reducing coral growth. This leaves the possibility of cancellation of wave energy and deposition a more likely hypothesis.

The different depths in the inner lagoon are most likely a result of this same wave energy pattern, differentially depositing and removing sediment. It can be seen that the areas of shallower inner lagoon correspond with the areas of little or no spur and groove formation. Whereas the deep parts of the inner lagoon are directly behind the most defined regions of spur and groove formation. The reef flat as well seems to work in relation to wave energy. The widest reef flat zones are grouped with the shallow inner lagoon and the lack of spur and groove.

Much more definitive conclusions could be made concerning this reef with more detailed observations. The most helpful of these would be to core the reef, both on the ridge and on the spurs. In addition a more detailed survey of the fringing reef at Afareaitu would be beneficial.

Acknowledgments

This paper would not have been possible without the help of Carole Hickman, Jere Lipps, and David Stoddart. Thank you. I also thank John Herr, Sarah Boyer, and especially Kate Schafer. For without them I would still be waiting on the side of the road, with my trusty and ever jovial assistant, Dave Borslein, at my side still begging for more. A special thanks goes out to the consortium of governmental conspirators who managed to keep things going straight when it seemed as though all would fail.

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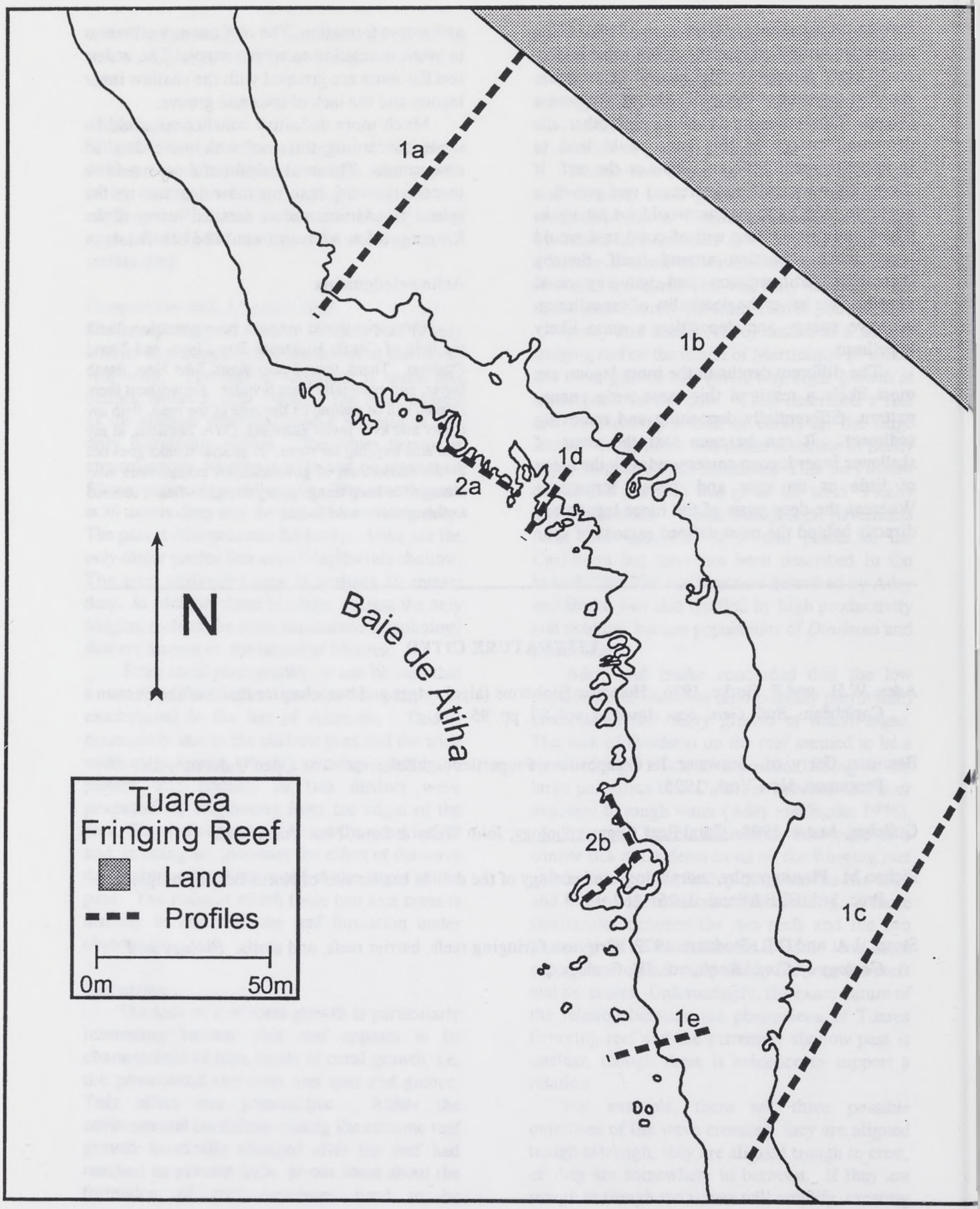


Figure 1. Plan map of Tuarea Fringing Reef, with profile transects labeled.

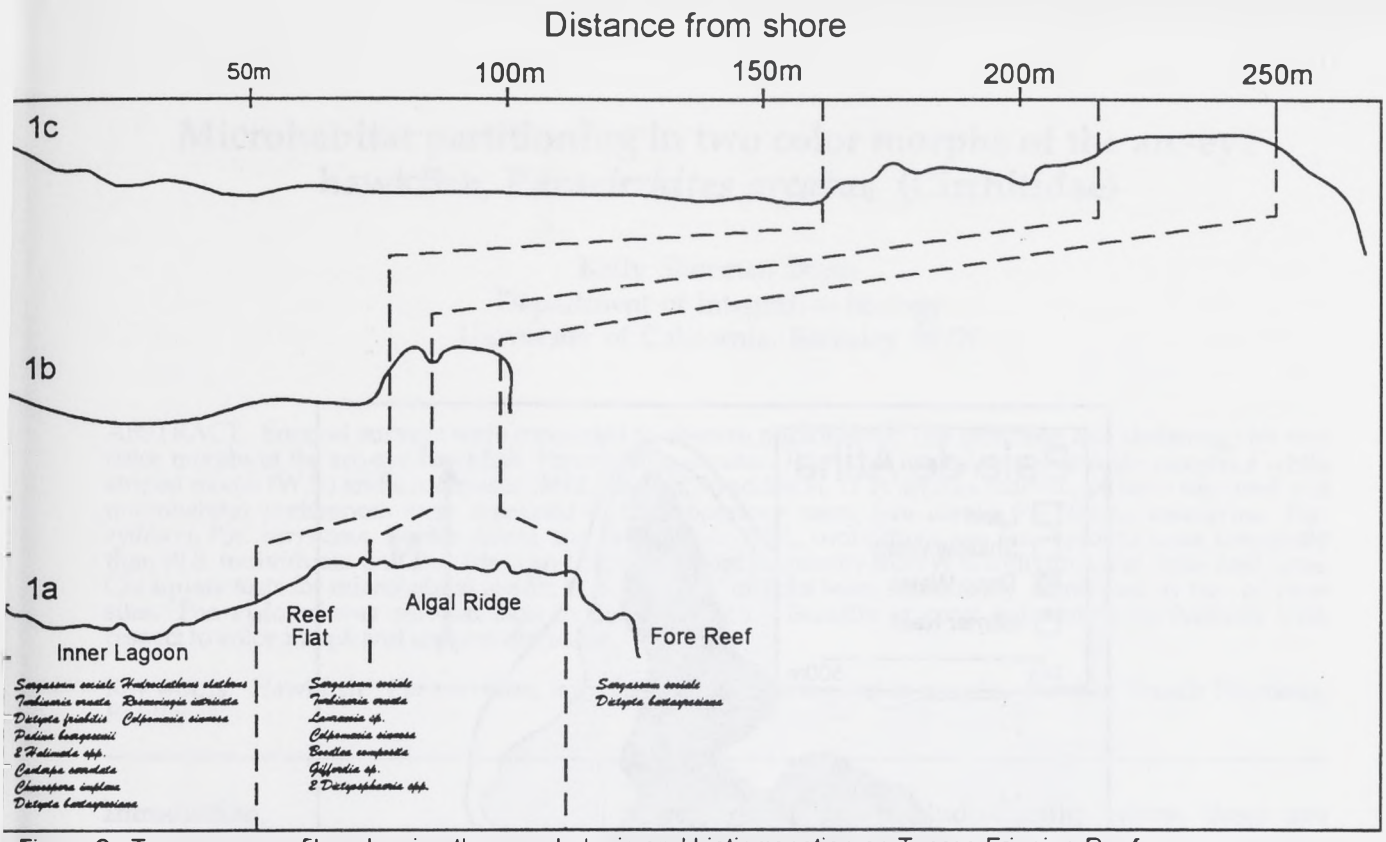


Figure 2. Transverse profiles showing the morphologic and biotic zonation on Tuarea Fringing Reef.

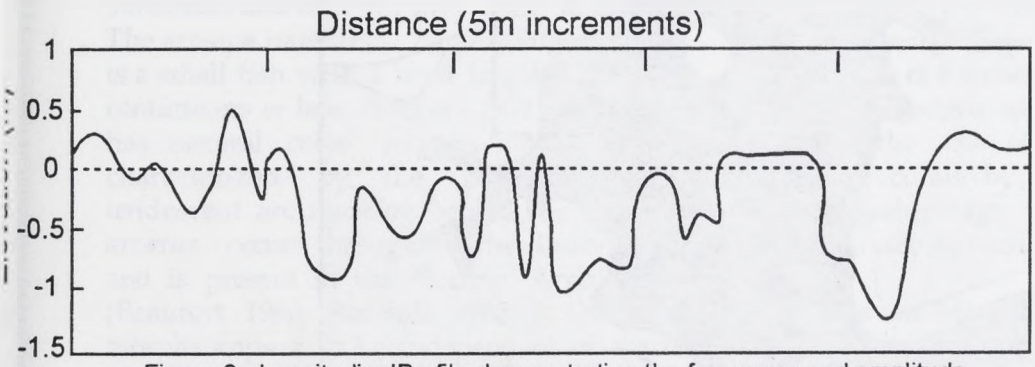


Figure 3. LongitudinalProfile demonstrating the frequency and amplitude of shallow spur and groove formations on Tuarea Reef.

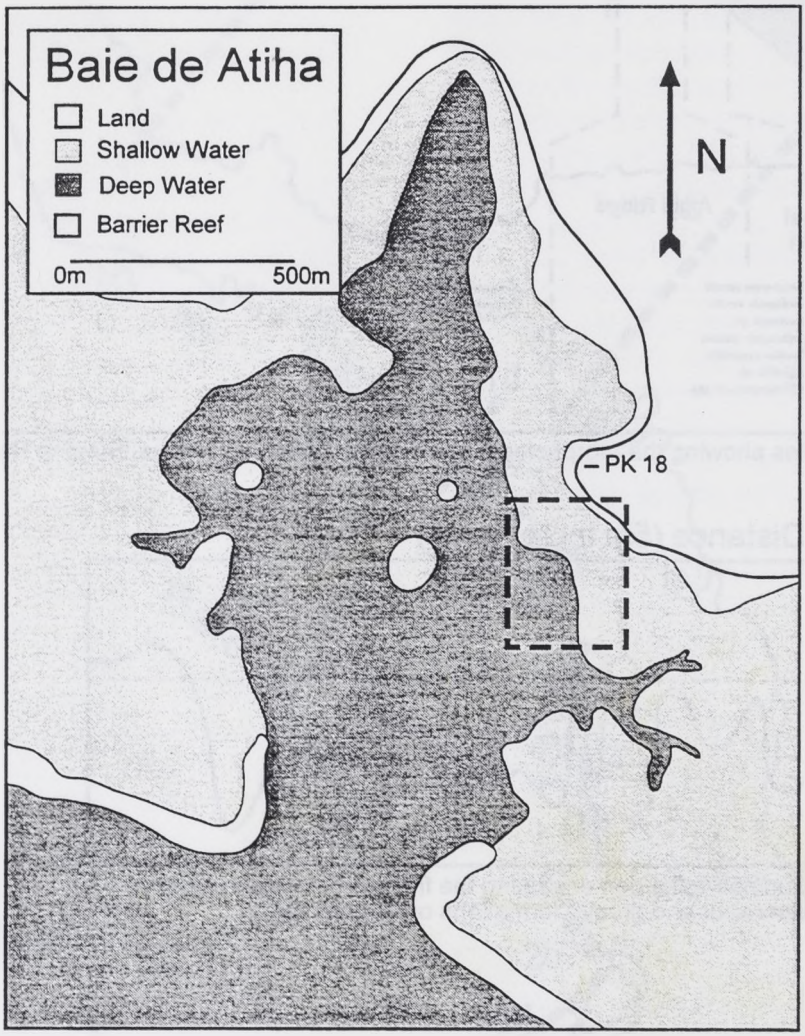


Figure 4. Bay of Ahtia with Tuarea Fringing Reef in inset.

Microhabitat partitioning in two color morphs of the arc-eye hawkfish, *Paracirrhites arcatus* (Cirrhitidae)

Kelly Sherman Boyle
Department of Integrative Biology
University of California, Berkeley 94720

ABSTRACT. Snorkel surveys were conducted to observe microhabitat use (perching and sheltering) by two color morphs of the arc-eye hawkfish, *Paracirrhites arcatus*. *P. arcatus* has two common color morphs, a white striped morph (W.S.) and a melanistic (MEL) morph. In addition, 11 *P. arcatus* individuals were captured and microhabitat preferences were examined in the laboratory using live corals: *Pocillopora meandrina, Poc. eydouxi, Poc. verrucosa, Porites lobata,* and dead coral. MEL individuals use *Poc. eydouxi* more frequently than W.S. individuals and *Por. lobata* and dead coral less frequently than W.S. individuals at three field sites. Chi square tests for microhabitat use for W.S. vs. MEL morphs were statistically significant at two of three sites. *Poc. eydouxi* was selected most in the laboratory. Benefits of coral substrate microhabitats with respect to color morph and size are discussed.

Key words: Hawkfish, *Paracirrhites,* microhabitat partitioning, color morphs, Moorea, French Polynesia, *Pocillopora*

Introduction

Hawkfishes (Cirrhitidae) are lie-in-wait predatory fish. Hawkfish perch on substrates and wait for prey items to appear. The arc-eye hawkfish, *Paracirrhites arcatus*, is a small fish with a total length (T.L.) 11.1 centimeters or less. (Meyers 1991). *P. arcatus* has several color morphs but is always characterized by the presence of an irridescent arc marking behind the eye. *P. arcatus* occurs throughout the Indo-Pacific and is present in the Society Archipelago (Beaufort 1940; Randall 1963). The color morphs appear to be independent of sexual identity (Randall 1963) or maturity of the fish (Sadovy and Donaldson 1995).

The use of different perches or microhabitats, such as species of live corals, dead coral, and rock, may provide different levels of benefit for hawkfish. Hawkfish may be more inconspicuous on certain perch colorations and some perches may have a dual function as a shelter from potential predators. DeMartini (1996) found that in Hawaii, the branching coral *Pocillopora meandrina* was the most commonly used perch by *P. arcatus* and its use may be the result of the protection the branched coral fingers provide when potential predators of *P. arcatus* are present. Elsewhere in the Indo-Pacific, *P. arcatus* has been seen using other branching corals which are not common in Hawaii, such as *Acropora* sp. and *Pocillopora* sp. (DeMartini and Donaldson 1996). In other areas of the Indo-Pacific, where there are several common branching corals present, the partitioning of live coral microhabitats may be different. Branching corals may afford different benefit depending on the size and color morph of *P. arcatus*..

The objective of this study was to examine the use of different species of branching corals by *P. arcatus* in Moorea, Society Archipelago, French Polynesia, with respect to size and color morph of the fish.

Materials and Methods

Microhabitat Partitioning

Surveys were conducted at three different sites (Appendix 1) within the lagoon of Moorea, Society Archipelago, French Polynesia: the north-east corner of Cook's Bay (Slim's reef), Plage de Temae, and Motu Ahi. Surveys were conducted for 25, 45, 50, or 70 minutes at a time using snorkel gear. The surveys were conducted on separate areas of the reef at each site to avoid surveying the same fish individuals, except at Plage de Temae, where data from separate days covered the same site area. This was done because the study site was restricted in area and *P. arcatus* density was lower relative to the other sites.

Hawkfish occurrence was determined visually using a search image based on the shape of the fish and its perching behavior to minimize sampling bias for either color

morph (DeMartini and Donaldson 1996). Color morph of the fish (WS or MEL) and the coral the fish was first seen perching on or hiding in, was recorded. Size estmates of total length (T.L.) were recorded, initially using visual estimates, and later on using estimates with a measured rule by measuring the perch area the fish was last seen on (McKaye 1977). All data were recorded on plastic slates and transcribed upon returning from the field.

Habitat Preference

Hawkfish individuals were captured from north east Cook's Bay by using a net and chasing them out of coral with a ruler. Captive fish were kept in an outdoor, flow-through aquarium. The coral species, *Pocillopora meandrina, Poc. eydouxi, Poc. verrucosa* and *Porites lobata,* and pieces of dead coral were used as microhabitats for the laboratory environment. Microhabitats were placed between 30 and 50 cm. from each other and the composition of controlled microhabitats was changed eight times over 24 days (Appendix 3) to minimize artifacts of location in the aquarium on habitat use decisions. Sizes of some corals were augmented by adding several small corals to the existing corals and total quantity of some coral species was changed by using different pieces of coral or by adding more pieces (Appendix 3). This was done to minimize the effect of coral size on habitat decisions.
Microhabitats within the aquarium were quantified by surface area. Surface area of branching corals (*Pocillopora* sp.) were approximated by calculating the hypothetical surface of the space encompassed by the tips of the branches. The surface area was computed by using the average diameter, AD [(L x W x H)/3] (Kuwamura et. al 1994). The height of the coral was estimated by averaging four finger-depth measurements within the center of the coral and four random measurements along the perimeter. Length and width (and height in *Porites lobata*) were measured directly.

Eleven fish were used in the laboratory study. Fish were in the aquarium individually and in pairs. The fish that were kept in pairs were introduced as pairs and later separated, or introduced as individuals and later a second fish was added (Appendix 4). Total length of each fish (TL) and color morph were recorded before introduction to the aquarium (Appendix 4) The occurrence of each fish on a particular coral or on dead coral was recorded at half hour intervals and whether or not the fish was perched on top, hiding within the coral or beneath the coral. Occurrences outside the controlled microhabitats were recorded but not considered in the analysis.

Statistical Analyses

Chi square tests (Sokal and Rohlf 1987) were used to analyze the uses of coral between both color morphs of *P. arcatus* in the field. At Slim's reef and Motu Ahi, total occurrences were used because there was no overlap in study site. At Plage de Temae, the median number of each color morph of fish on each microhabitat category were used (DeMartini and Donaldson 1996).

Unpaired one-tailed t-tests were performed for size data of W.S. and MEL morphs, and for size data of W.S. individuals using the branching corals *Poc. meandrina* and *Poc. eydouxi.* T-tests were not performed on sizesMEL morphs using the *Poc. meandrina* and *Poc. eydouxi* because too few MEL morphs (n<4) were found on *P. meandrina* at any site.

Significance was denoted by P values of $\leq$ 0.05.

Electivity for microhabitats as perches and shelters within the laboratory were measured using the Strauss' (1979) linear index of selection, $L = (r_i + p_i)$, where r_i = the relative use of the ith perch or shelter and p_i = the relative amount of the ith microhabitat (DeMartini 1996). $-1 < L < +1$, with negative values indicating avoidance and positive values indicating selection of a substrate. Variance of L was estimated using: $\text{var } L = [(r_i)(1- p_i)]/ n_r + [(p_i)(1- p_i)]/ n_p$, in which n_r = the number of times a microhabitat was used (measured occurrence of sheltering or perching) and
n_p = the total amount of microhabitat use (observed sheltering or perching) (Strauss, 1982; DeMartini 1996).

Results

Field Data

Table 1: Chi square analysis of Slim's Reef Data; 10/10,10/11, 10/19/97

	W.S.	MEL
Pocillopora meandrina	46	2
Pocillopora eydouxi	44	37
Porites lobata	18	1
Porites rus	1	0
Dead Coral	5	2
P value	1.89001E-06	

Table 2. Chi square analysis of Motu Ahi data, 11/6/97

	W.S.	MEL
Pocillopora meandrina	12	1
Pocillopora eydouxi	7	7
Porites rus	1	0
Porites sp. (purple)	3	0
dead coral	4	0
P value	0.04187676	

Table 3. Chi square analysis of medians of combined Plage de Temae data; 10/13, 10/20,11/14/97

	W.S.	MEL
Pocillopora meandrina	4	2
Pocillopora eydouxi	2	10
Pocillopora verrucosa	1	0
Porites lobata	1	0
Acropora sp.	1	1
Dead Coral	1	0
P value	0.119128117	

The chi-square test of Slim's Reef data (Table 1), based on three separate days and 156 surveyed fish, 114 W.S. and 42 MEL, showed a significant difference of perch use between W.S. and MEL morphs, P = 1.89 E-6. Motu Ahi data, based on two surveys on one day, and 35 sampled fish, 27 W.S. and 8 MEL, was also statistically significant, P = 0.04187 (Table 2.) The chi-square tests of Plage de Temae data, based on the median of three separate days and 87 surveyed fish, 49 W.S. and 38 MEL, was not significant, P = 0.119 (Table 3).

Average sizes of MEL individuals were higher at all three sites. MEL individuals averaged 1.67 cm. longer in T.L. than WS individuals at Slim's reef, with a significant t-test P value of 2.02 E-07 (Figure 1). MEL individuals averaged 1.46 cm. longer than W.S. at Motu Ahi, P = 0.00962 (Figure 2). The median of MEL T.L. averages was 1.96 cm. longer than the median of W.S. T.L. (Figure 3). P values for t-tests were: P= 5.45 E-05, 10/13/97; P=0.00348, 10/20/97; P=0.00281, 11/14/97.

Figure 1. Average Sizes of White Striped and Melanistic Individuals at Slim's Reef. Bars represent standard error.

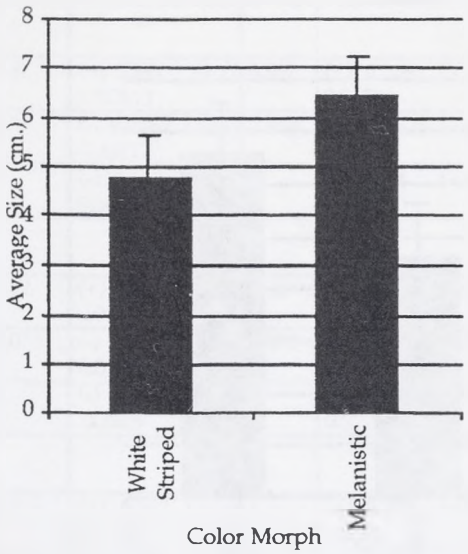
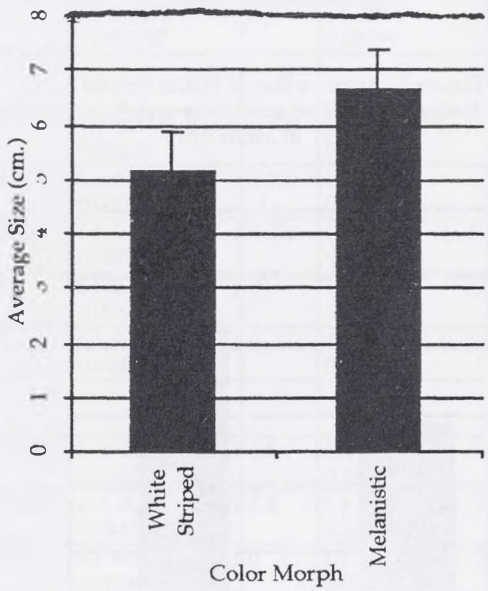


Figure 2. Average Sizes of White Striped and Melanistic Individuals at Motu Ahi.



Average sizes of W.S. individuals observed on *Poc. eydouxi* were higher than average sizes of W.S. individuals observed on *Poc. meandrina* at all three sites. At Slim's reef the individuals on *Poc. eydouxi* averaged 0.55 cm. longer T.L. than individuals found on *Poc. meandrina* (Figure 4), but the t-test of sizes from each group was not statistically significant, P = 0.0731. W.S. individuals found on *Poc. eydouxi* at Motu Ahi.

Figure 3. Medians of Three Size Averages of White Striped and Melanistic Individuals at Plage de Temae.

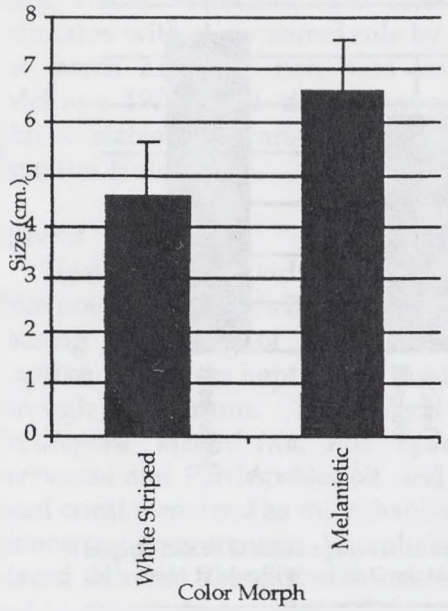


Figure 4. Average Size of White Striped Individuals Occurring on *Poc. meandrina* and *Poc. eydouxi* at Slim's Reef

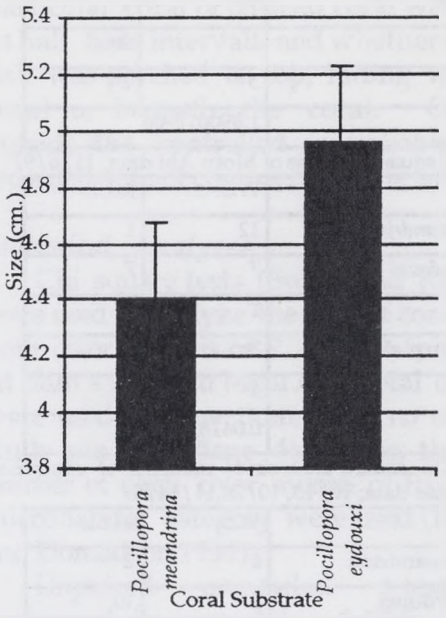


Figure 5. Average Size of White Striped Individuals on *Poc. meandrina* and *Poc. eydouxi* at Motu Ahi

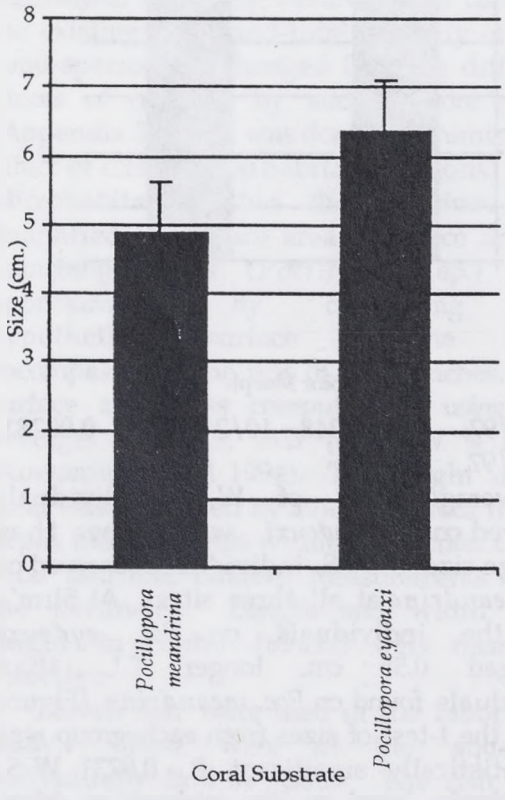


Figure 6. Median of Average Sizes of W.S. Individuals on *Poc. meandrina* and *Poc. eydouxi* at Plage de Temae

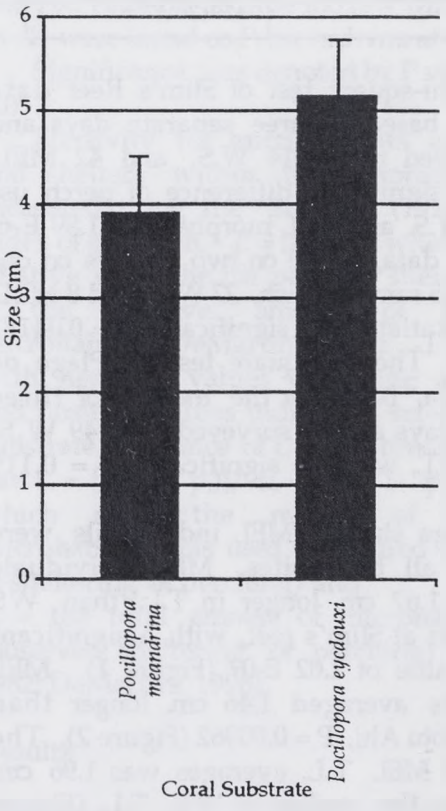


Table 4. Summary statistics for Strauss' (1979, 1982) electivity indices of substrate use for perching (DeMartini 1996) and sheltering.

Substrate Utilization: Total Utilization : Shelter Utilization : Perch Utilization

Dates	# fish	Substratum	Pi	ri	L (+/-) SE	ri	L (+/-) SE	ri	L (+/-) SE
10/23-29/97	3								
		Poc. eydouxi	0.489	0.857	**(+) 0.178** (+/-) 0.254	0.87	**(+) 0.381** (+/-) 0.0111	0.667	**(+) 0.368** (+/-) 0.0155
		Poc. meandrina	0.147	0.143	**(+) 0.186** (+/-) 0.325	0.13	**(-) 0.0167** (+/-) 0.00212	0.333	**(-) 0.00423** (+/-) 0.1089
		Por. lobata	0.364	0	**(-) 0.364** (+/-) 0.00771	0	**(-) 0.449** (+/-) 0.00503	0	**(-) 0.364** (+/-) 0.00472
10/30-11/5	3								
		Poc. eydouxi	0.3938	0.939	**(+) 0.545** (+/-) 0.0344	0.92	**(+) 0.526** (+/-) 0.0129	0.92	**(+) 0.526** (+/-) 0.0266
		Poc. meandrina	0.313	0.092	**(-) 0.231** (+/-) 0.00561	0.078	**(-) 0.235** (+/-) 0.0238	0.091	**(-) 0.222** (+/-) 0.0752
		Por. lobata	0.293	0	**(-) 0.293** (+/-) 0.00423	0	**(-) 0.239** (+/-) .00545	0	**(-) 0.293** (+/-) 0.0173
11/7-11/97	2								
		Poc. eydouxi	0.201	0.797	**(+) 0.596** (+/-) 0.00101	0.702	**(+) 0.501** (+/-) 0.0148	1	**(+) 0.799** (+/-) 0.0363
		Poc. meandrina	0.552	0.203	**(-) 0.349** (+/-) 0.0141	0.298	**(-) 0.254** (+/-) 0.0141	0	**(-) 0.552** (+/-) 0.00578
		Por. lobata	0.15	0	**(-) 0.150** (+/-) 0.00184	0	**(-) 0.150** (+/-) 0.0271	0	**(-) 0.150** (+/-) 0.00578
		Dead Coral	0.0973	0	**(-) 0.0973** (+/-) 0.00127	0	**(-) 0.0973** (+/-) 0.00187	0	**(-) .0973** (+/-) 0.00399
11/12-15/97	3								
		Poc. eydouxi	0.141	0.568	**(+) 0.427** (+/-) 0.0265	0.556	**(+) 0.415** (+/-) 0.05445	0.579	**(+) 0.438** (+/-) 0.0515
		Poc. meandrina	0.526	0.243	**(-) 0.283** (+/-) 0.00311	0.389	**(-) 0.137** (+/-) 0.0401	0.105	**(-) 0.357** (+/-) 0.00380
		Poc. verrucosa	0.097	0.027	**(-) 0.0700** (+/-) 0.0268	0.056	**(-) 0.292** (+/-) 0.0551	0.316	**(-) 0.219** (+/-) 0.00521
		Por. lobata	0.143	0	**(-) 0.143** (+/-) 0.00332	0	**(-) 0.0414** (+/-) 0.00681	0	**(-) 0.143** (+/-) 0.00645
		Dead Coral	0.928	0.162	**(-) 0.0928** (+/-) 0.00228	0	**(-) 0.0928** (+/-) 0.00468	0	**(-) 0.0928** (+/-) 0.00443
11/17-20/97	5								
		Poc. eydouxi	0.196	0.333	**(+) 0.137** (+/-) 0.0458	0.294	**(+) 0.981** (+/-) 0.0620	0.5	**(+) 0.304** (+/-) 0.111
		Poc. meandrina	0.493	0.619	**(+) 0.126** (+/-) 0.0360	0.647	**(+) 0.154** (+/-) 0.0445	0.5	**(-) 0.007** (+/-) 0.240
		Poc. verrucosa	0.0909	0.048	**(-) 0.0400** (+/-) 0.00472	0.059	**(-) 0.0320** (+/-) 0.00583	0	**(-) 0.0909** (+/-) 0.00206
		Por. lobata	0.1335	0	**(-) 0.134** (+/-) 0.00551	0	**(-) 0.134** (+/-) 0.00680	0	**(-) 0.134** (+/-) 0.0289
		Dead Coral	0.0868	0	**(-) 0.868** (+/-) 0.00377	0	**(-) 0.0868** (+/-) 0.00466	0	**(-) 0.0868** (+/-) 0.0198

Ahi averaged 1.48 cm. longer T.L. than individuals found on *Poc. meandrina* (Figure 5), the t-test of sizes of each group was statistically significant, $P = 0.00894$. The median of average T.L. of W.S. individuals found on *Poc. eydouxi* at Plage de Temae was 1.25 cm. longer than the T.L. of individuals found on *Poc. meandrina* (Figure 6). The t-tests of sizes of each group were not significant for data obtained 10/13/97 and 11/14/97, $P = 0.187$ and $P = 0.0574$ respectively, but was significant for data obtained 10/20/97, $P = 0.0464$.

Laboratory Data

Strauss indices of *Pocillopora eydouxi* were positive (L) for total substrate utilization by *P. arcatus* (use as both a

perch and shelter), use as a shelter, and use as a perch (Table 4) suggesting selection by *P. arcatus* for a microhabitat for perching and shelter. Indices for *Poc. meandrina* were negative except from 11/17-11/20/97 for total substrate utilization and for use as a shelter (Table 4.) All *Poc. meandrina* indices for perch utilization were negative, suggesting avoidance by *P. arcatus*.. All indices for *Poc. verrucosa* , *Porites lobata*, and dead coral were negative, suggesting avoidance by *P. arcatus* (Table 4).

Microhabitat And Color Morph

Discussion

MEL morphs of *P. arcatus* use *Pocillopora eydouxi* proportionately more often than W.S. morphs do. A possible benefit of using *Poc. eydouxi* may be that the MEL morphs appear more cryptic by hiding in *Poc. eydouxi*, which on Moorea is often a darker shade than *Poc. meandrina* . Although the bright white stripe of the W.S. morph may be conspicuous (DeMartini and Donaldson 1996), the lighter tone of body coloration of the W.S. morph may be more cryptic than the MEL morph when *Poc. meandrina* is used as a perch/shelter. This howerver, contradicts the findings by DeMartini and Donaldson (1996) that W.S. are more common in shallow waters when *Poc. meandrina* is scarce. This may be because when branching corals, such as *Pocillopora* sp., and fish densities are low, the W.S. morph may have an advantage of being more conspicuous for signalling conspecifics (DeMartini and Donaldson 1996).

Microhabitat And Size

MEL morphs are larger on average within the lagoon at Moorea. This pattern is not seen in Hawaii (DeMartini and Donaldson 1996). Because this difference in mean size of both color morphs is not universal across Oceania, there may be selection pressures, or predatory effects acting upon MEL morphs that would affect mean population sizes. Small individuals of MEL morphs are rare and MEL morphs use*Poc. eydouxi* almost exclusively. Predation may be higher for MEL morphs that are found on *Poc. meandrina* because the dark body may be more conspicuous on a lighter color coral. Larger MEL morphs may be more likely to obtain and defend *Poc. eydouxi* as a perch and shelter, and thus be more common than smaller individuals. If this is true, one would expect W.S. morphs that use *Poc. eydouxi* to be larger on average than W.S. morphs found on *Poc. meandrina* and this trend is observed and was sometimes statistically significant.

Microhabitat Preference

Poc. eydouxi appears to be the preferred microhabitat over *Poc. meandrina*, and *Poc. verrucosa*. *Por.lobata* and dead coral appear to be avoided as found in the field by DeMartini (1996).

W.S. morphs in the laboratory were utilizing *Poc. eydouxi* with greater frequency then the other Pocilloporid corals, suggesting that *Poc. eydouxi* is preferred when available, in each morph. Perhaps size limits the availability of *Poc. eydouxi* as a microhabitat and intraspecific factors determine microhabitat partitioning in the field. Some territoriality has been observedin *P. arcatus* (DeMartini 1996).

Acknowledgements

I would like to thank Professors: Tracy Benning, Carole Hickman, Jere Lipps, and David Stoddart. Many thanks to David Borslien, Lauren Gershman, Jung Lee, and John Lee for help and moral support. Special thanks to Vince Resh and Steve Strand for use of the facilities at the Richard B. Gump Biological Station, Moorea, French Polynesia.

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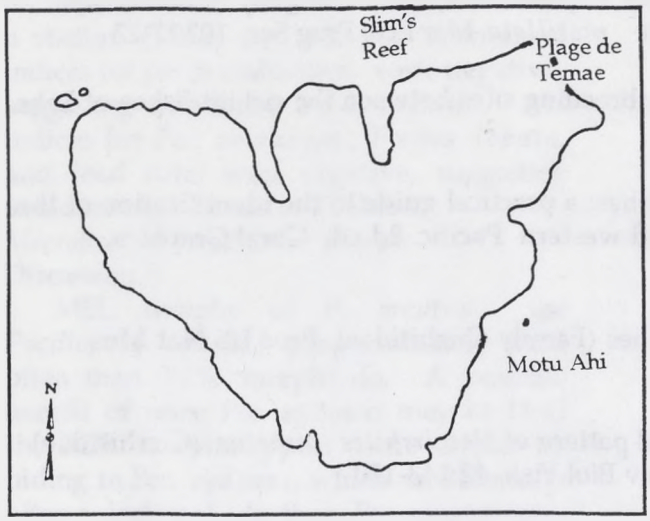
Appendix 1.
Map of Study Sites on Moorea French Polynesia



Appendix 2.

Dates Used	Corals Used In Order Of Relative Position (clockwise)
10/23/97	*Poc. eydouxi* (A), *Poc. meandrina* (A), *Por. lobata*
10/24 to 10/27/97	*Poc. meandrina* (A), *Por. lobata*, *Poc. eydouxi* (A)
10/28 to 10/29/97	*Poc. eydouxi* (A), *Por. lobata*, *Poc. eydouxi* (A)
10/30 to 11/1/97	*Poc. eydouxi* (A), *Poc. meandrina* (A + a1 and a2), *Por. lobata*
11/1 to 11/5/1997	*Poc. meandrina* (A + a1 and a2), *Por. lobata*, *Poc. eydouxi* (A)
11/7 to 11/11/97	*Poc. meandrina* (A + a1 + a2 and a3), *Poc. meandrina* (B + dead coral), *Poc. meandrina* (C), *Por. lobata*, *Poc. eydouxi* (A)
11/12 to 11/16/97	*Poc. meandrina* (A + a1 + a2 and a3), *Poc. meandrina* (B + dead coral), *Poc. verrucosa*, *Poc. meandrina* (C), *Por. lobata*, *Poc. eydouxi* (B)
11/17 to 11/20/97	*Poc. meandrina* (A + a1 + a2 and a3), *Poc. meandrina* (B + dead coral), *Poc. verrucosa*, *Poc. meandrina* (C), *Poc. eydouxi* (C), *Por. lobata*

Appendix 3.
Summary of fish used in the laboratory

Morph	Size T.L. (cm.)	Dates Kept In TheLaboratory
W.S.	3.5	10/23 to 10/24/97
W.S.	8	10/23 to 10/24/97
W.S.	6	10/27 to 11/3/97
W.S.	10	10/31 to 11/3/97
W.S.	6	11/5 to 11/11/97
MEL	11	11/7 to 11/13/97
W.S.	6.5	11/13 to 11/17/97
W.S.	5	11/14 to 11/17/97
W.S.	5.5	11/17 to 11/20/97
W.S.	6.5	11/19 to 11/20/97
W.S.	5	11/20/97

Tradeoffs of Recruiting Inside Adult Colonies in the Damselfish *Stegastes nigricans*

Jonathan S.F. Lee
Department of Integrative Biology
University of California at Berkeley
Berkeley, CA 94720

ABSTRACT. Juveniles of *Stegastes nigricans* occur 1) in adult colonies, 2) in juvenile colonies, and 3) solitarily. We I) examined the costs and benefits of different settlement strategies, II) quantified the territory requirements of adults, and III) investigated mechanisms by which juveniles make the transition to adults holding adult territories. I) Compared with solitary juveniles, juveniles <4 cm TL in adult colonies benefit from reduced heterospecific competition for food; all juveniles in adult colonies benefit from a greater food density. A cost of recruiting in an adult colony is increased agonistic interactions with conspecific adults. II) Adult territories must 1) correspond in area to total length of fish, 2) contain tunnel entrances of a suitable size for the fish, and 3) be near other adult territories. III) Juveniles originally settling in adult colonies do so by 1) taking refuge from the aggression of adults in small holes inaccessible to adults and 2) reducing attacks by adults by settling between the territories of multiple adults in "halos" of undefended space. As juveniles in adult colonies grow, chases by adults on the juveniles decrease, while chases by juveniles on conspecific adults and heterospecifics increase. Territory size correlates with fish size in adult colonies; as the fish grows, it probably expands its territory at the expense of neighboring adults, and eventually obtains a territory suitable for an adult. Settling in adult colonies and eventually obtaining space required by adults may be easiest for juveniles that originally settle in adult colonies. Juveniles that originally settle solitarily or in juvenile colonies may later attempt to enter adult colonies, but, because they do so as larger juveniles, probably cannot utilize the two settlement strategies seen in juveniles which originally settle in adult colonies.

Key words. *Stegastes nigricans*, recruitment, Moorea, colony, territory, hierarchy of territoriality, settlement strategies, Pomacentrid

Introduction

Survival to adulthood has traditionally been considered limited by the survival of planktonic larvae (Doherty 1982; Victor 1986; Williams et al. 1994). Recent studies, however, demonstrate the importance of the post-settlement juvenile stage (Jones 1991; Tupper and Boutilier 1995).

Recruitment success has been shown to vary with the distribution of habitats (Levin 1993, 1994), habitat complexity and the availability of food (Tupper and Boutilier 1995), and predator and shelter abundance (Shulman 1985; Miranda and Hubbard 1994).

Sale (1980) documented three settlement strategies by which *Pomacentrus wardi* gain space: 1) "the flank attack," in which recruits settle on the borders of adult territories, 2) "topological deception," in which juveniles settle in adult territories, avoiding adult aggression by taking cover in the topology of the substratum, and 3) the "I'll take almost anything strategy," in which recruits settle in areas previously and currently unoccupied by adults. Assuming that adults occupied "good" sites and defended their sites from juveniles, Sale (1980) argued that the first two strategies allowed juveniles to access "good" space. Sale (1974) reported these first two strategies in juvenile *Abedefduf lachrymatus*,

Pomacentrus apicalis, *P. flavicauda*, and *P. wardi*, and documented their capabilities of then expanding their territories at the expense of neighboring adults. Juvenile *P. wardi* utilizing the third strategy settled for inferior sites, probably waiting for vacancies in "good" space (Sale 1980).

This study I) examined the costs and benefits of different settlement strategies, II) quantified the territory requirements of adults, and III) investigated mechanisms by which juveniles utilizing different settlement strategies make the transition to adults holding these territories in juveniles of the pomacentrid, *Stegastes nigricans*.

Stegastes nigricans is found in the Indian-Pacific Ocean (Allen 1975). Adults defend individual territories that provide food and sites for reproduction and shelter. These territories are clustered, forming colonies.

Preliminary observations found juveniles to occur 1) in adult colonies, 2) in juvenile colonies, and 3) solitarily.

Costs and benefits

The differences between these three strategies can be broken into two primary components: 1) degree of aggregation and 2) size of neighboring fish. Fish in adult colonies are 1) aggregated and 2) surrounded by large neighbors. Fish in juvenile colonies are also 1) aggregated, but are 2) surrounded by small neighbors. Fish that settle solitarily are 2) not aggregated, and have 2) no neighbors.

Costs and benefits may be associated with each of the two components (Figure 1).

Degree of aggregation. Chases against heterospecifics decreased and chases against conspecifics increased with increasing distance from the colony edge in *Stegastes planifrons* (Meadows 1995). Surrounding territories buffered fish near the center from heterospecifics, but also exposed them to more conspecifics. Extending this to juveniles settled solitarily and juveniles settled in colonies should reveal a tradeoff: compared to settling solitarily, settling in a colony should lead to fewer heterospecific chases (benefit) (Figure 1, 2), but more conspecific chases (cost) (Figure 1, 2).

Size of neighboring fish. Defensive actions, effectiveness of the attempts, and algal biomass in territories increased with fish size in *Stegastes dorsopunicans* (Foster 1985). If this is true for *S. nigricans* (Figure 1), a fish with larger neighbors should be more buffered from heterospecifics and consequently should have access to a greater amount of algae (benefit) (Figure 2). Because *S. nigricans* are territorial against both heterospecifics and conspecifics, larger neighbors should also better defend against conspecifics. Therefore, it should be more difficult for juveniles settling near larger neighbors to obtain space (cost) (Figure 2).

We test this model for two different recruitment strategies: recruiting in an adult colony and recruiting solitarily away from conspecifics. Juveniles in juvenile colonies were too rare to be studied. Unfortunately, this limits

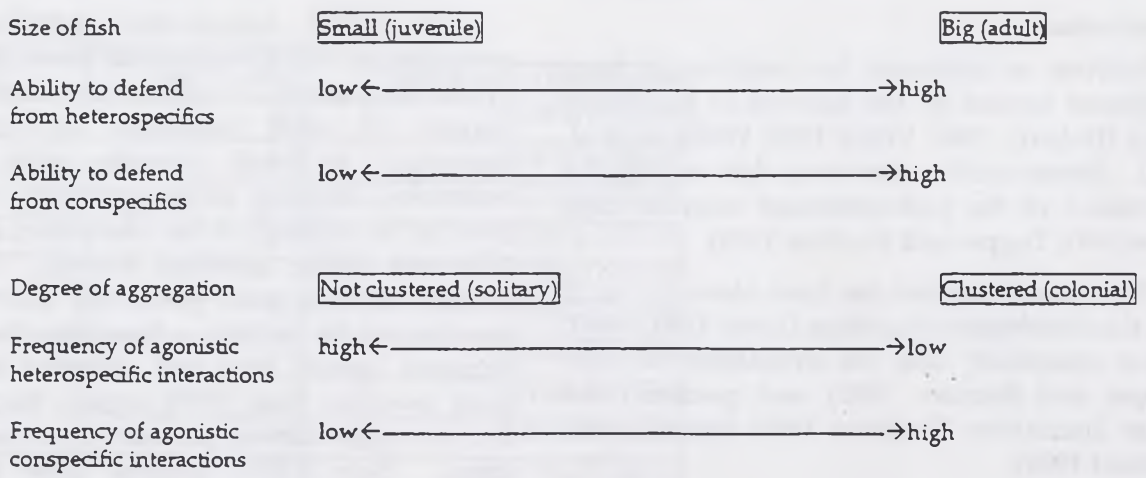


Figure 1. Abilities of individual fish of different sizes and degrees of aggregation

	Solitary Juvenile	Juvenile in Juvenile Colony	Juvenile in Adult Colony
Size of neighboring fish	none	small	big
Degree of aggregation	not clustered	clustered	clustered
Cost of defense of algae from heterospecifics	high (cost) ←		→ low (benefit)
Amount of algae available	low (cost) ←		→ high (benefit)
Cost of defense of algae from conspecifics	low (benefit) ←		→ high (cost)
Difficulty of obtaining space	low (benefit) ←		→ high (cost)

Figure 2. Costs and benefits of individual juveniles settled in different habitats

us to only a coarse test of this model.

Benefits–Food: Juveniles in adult colonies should benefit from joint defense of the territories and larger neighbors. 1) Juveniles in adult colonies should less frequently chase heterospecific intruders than do solitary juveniles. 2) As a result, juveniles in adult colonies should have access to more food.

Costs–Agonistic interactions with conspecifics: 3) Compared to solitary juveniles, juveniles in adult colonies should have more agonistic interactions with conspecific adults.

Suitable space

We attempt to quantify the territory requirements for adult *S. nigricans* and to determine its availability. 4) Fish of different sizes may utilize shelter resources. Fish TL should be directly proportional to tunnel entrance size. 5) Adult space may be limited.

Obtaining suitable adult space

We also investigate trends in the aforementioned data and conduct preliminary model-bottle tests to learn about juvenile strategies for making the transition to adults holding adult territories.

Methods and materials

Site

Data were collected via snorkeling and free diving from October to November 1997 at Gump Reef in front of the UC Berkeley Gump Biological Research Station on the west side of PaoPao Bay in Moorea, French Polynesia (Figure 3). Visibility ranged from one to five meters, depending on weather. The reef averages a depth of 0.5-3 meters before it drops off to 30 meters. The fish observed in this study inhabited stands of dead *Acropora* at depths between 0.5 and 3 meters; other *Stegastes nigricans* were seen elsewhere to inhabit partially live *Porites*.

Fish total length was estimated by observing

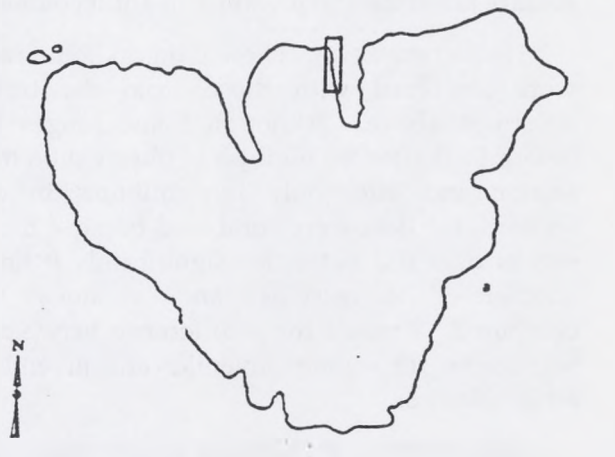


Figure 3. The island of Moorea. Study site is boxed.

the fish until it swam in front of a reference object, which was then measured. Fish smaller than six cm total length (TL) are referred to as juveniles.

Distribution

A transect was run along the bottom of the reef and every fish along and within a meter of the line was observed for five minutes. I recorded home range size and location, within home-range tunnel entrance sizes, social situation (in a colony or solitary) and fish total length. Home range was defined as the space occupied by the fish; the length and breadth of this space was measured with a ruler and used to calculate its total area. Tunnel entrances in the substrate were measured along its longest axis and along the axis normal to that line. Tunnel entrance depth was sounded by placing a ruler into the hole until the rear wall was hit. Tunnels were typically extensive networks; fish were often observed entering from one opening and exiting from another.

Costs and benefits--Food

Each of 21 juveniles in adult colonies and 21 solitary juveniles was observed once for ten minutes. Access to food was estimated by counting bites at algae, measuring home-range size, and quantifying algal density.

Bites at algae. Bite data were converted to bite per minute ratios and plotted against fish TL. Regressions and r-values were computed. I tested for a difference between the regressions for solitary juveniles and juveniles in adult colonies.

Home range size. These data on home ranges were combined with those from the transect described above. Although home ranges were determined after ten minutes of observation in this section and after only five minutes in other sections, the data were combined because the two sets of data did not differ significantly from one another. Regressions and r-values were computed. I tested for a difference between the regressions for solitary juveniles and juveniles in adult colonies.

Algal density. Preliminary observations found a visually obvious difference in algal tuft densities and lengths between areas in colonies and areas outside of colonies. Algal density was estimated for ten juveniles in adult colonies by using chisel and hammer to remove a portion of the dead coral from three categories of space: 1) inside the juvenile's territory, 2) inside an adjacent adult's territory, and 3) outside the colony. Algal density was also estimated for ten juveniles outside of adult colonies by sampling in the same manner from two categories of space: 4) inside the juvenile's territory and 5) outside the juvenile's territory. Because algal cover varied little within each category of space, each sample is considered representative of the entire area. The coral was then dried for 24 hours in a standard plant drier. After drying, all algae was removed from a square cm of surface area under a dissecting microscope and weighed to the nearest ten-thousandth of a gram. Differences in algal biomass per square cm between categories of space were examined with a Kruskal-Wallis One Way ANOVA on Ranks and the Student-Newman-Keuls Method.

Costs associated with defending food were estimated by counting chases against heterospecific herbivorous intruders. Chase frequency differences between solitary and colonial juveniles were determined with the Mann-Whitney Rank Sum Test using the statistical program SigmaStat (Jandel Scientific 1994). The correlation coefficient relating fish TL and chases was determined and I tested the slopes of the lines against a slope of zero.

Costs and benefits--Interactions with conspecifics

Chases by and against adults were counted during the same ten-minute periods described above. Adults did not always respond to chases by juveniles, so chases against adults are better described as agonistic interactions directed toward adults by juveniles. Differences in chases between solitary juveniles and juveniles in adult colonies were determined with the Mann-Whitney Rank Sum Test using the statistical program SigmaStat (Jandel Scientific 1994).

Suitable space

To determine the size of the fish that could fit into tunnel entrances, 112 specimens of *Stegastes nigricans* from the California Academy of Sciences were measured for total length (TL), greatest body depth, and greatest body width. Growth curves for these measurements were then constructed.

The largest fish that could physically fit into the entrance was determined, using the growth curves and plotted against the size of the fish occupying the home range that contained the tunnel entrance. The fish sizes computed were those that could physically fit into the entrances. However, a fish might choose a slightly bigger tunnel entrance. Another graph was constructed by plotting the depth of tunnel entrances possessing an opening with a greatest axis of at least 5 cm against fish total length. Correlations were computed and regressions were tested against slopes of zero for both sets of data.

Saturation of habitats and the distribution of the different sized tunnel entrances in the field were determined using a 200-meter transect line across the reef. At each meter, fish within a half meter of the transect line were observed for five minutes. Home-range size, the number and size of tunnel entrances within the home range, size and social situation (in a colony or solitary), and terrain (sand or dead coral) were recorded using the methods previously described. If no fish were present, only terrain and tunnel entrance sizes were recorded for the area within a half meter of the transect.

Adult colonies were always situated on relatively tall patches of dead coral. These coral patches provided the large tunnel entrances required by adults. The relationship between the coral-patch area and number of fish in the colony was assessed by measuring the size of the area occupied by the dead coral patch and counting the number of fish in the colony. The length and breadth of the coral patch was measured with transect tape and used to calculate its total area. The number of fish was estimated by counting the number visible in a two-minute period, using a hand counter. This was done three times, and the mean value was used. Because the fish seldom remained out of view more than half a minute, a two-minute observation provided the best chance of counting all fish in the colony. Regressions were computed, r-values were determined, and regressions were tested against slopes of zero.

Obtaining suitable adult space

Preliminary model-bottle tests (Myrberg and Thresher 1974) were performed to determine the effect of intruder size on the aggression of the territorial fish. A 3.4 cm. juvenile was captured with hand nets and put in a clear glass jar. The jar was placed in the territories of fish 1.9, 1.9, 3.2, 4.3, 4.7, 4.9, 6.2, and 10.6 cm TL for five minutes, during which their reactions were recorded. Aggressive behavior was divided into five categories.

Bite: a forward motion of less than one body length toward the model-bottle fish, ending with the attacking juvenile contacting the bottle with its mouth.

Charge and bite: same as "bite," except the forward motion is an accelerating swim of more than one body length.

Charge without bite: an accelerating forward motion of more than one body length toward the model bottle, but ending with braking and no contact between the attacking juvenile and the model bottle.

Display: the attacking juvenile presents one side to the facing model-bottle fish while extending its median fins. The attacking fish then often rotated its body so that its dorsal spines were pointed at the model-bottle fish.

Tail beat: the attacking juvenile presents one side to the facing model bottle fish and beats its tail toward the model-bottle fish.

Results

Distribution

Juveniles settle in adult colonies, juvenile colonies, and solitarily. Juveniles in adult colonies always occurred at the boundaries of adult territories and often at the junction of several adult territories. Juvenile colonies were situated outside of adult colonies and consisted of two to ten juveniles in contiguous territories. These territories were defended against both heterospecifics and conspecifics. Adults occurred exclusively in colonies. No fish greater than six cm total length were found solitarily or in juvenile colonies. The second transect (200m) resulted in similar results.

Costs and benefits--Food

No significant differences were observed in bites taken between solitary juveniles and

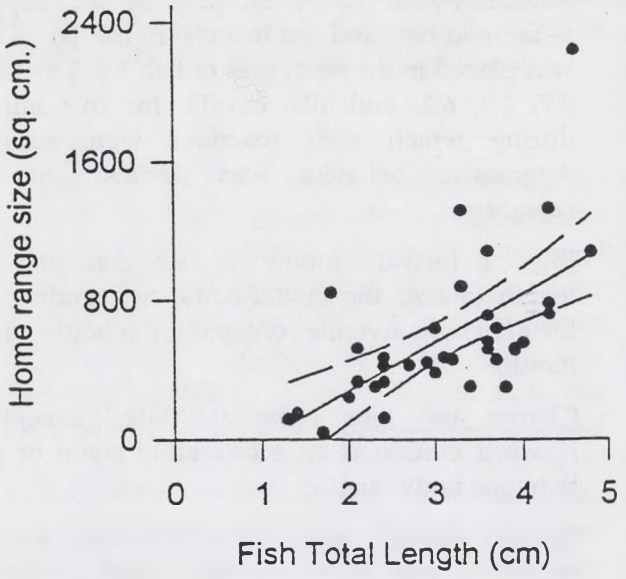


Figure 4. Home range size of solitary juveniles. Solid line represents regression line; dashed line represents 95 per cent confidence interval. (N=36)

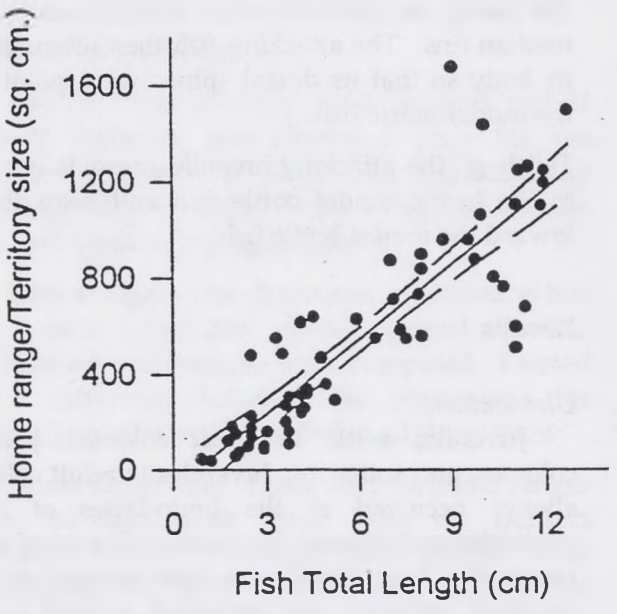


Figure 5. Home range/territory size of fish in adult colonies. Solid line represents regression line; dashed line represents 95 per cent confidence interval. (N=63)

juveniles in adult territories (P>0.05). When home-range size was plotted separately for solitary juveniles and juveniles and adults in adult colonies, home range size was positively correlated with fish size for both solitary juveniles and juveniles in adult colonies (r=0.62, Figure 4; r=0.87, Figure 5, respectively). Those juveniles settled in adult colonies had smaller home ranges than solitary juveniles (P<0.01; Figure 6).

No statistical difference in algal density per square cm existed between the territories of adults and the home ranges of juveniles in adult colonies (P>0.05; Figure 7), nor between the home ranges of solitary juveniles, the area outside of adult colonies, and the area outside of solitary juvenile home ranges (P>0.05; Figure 7). Both the

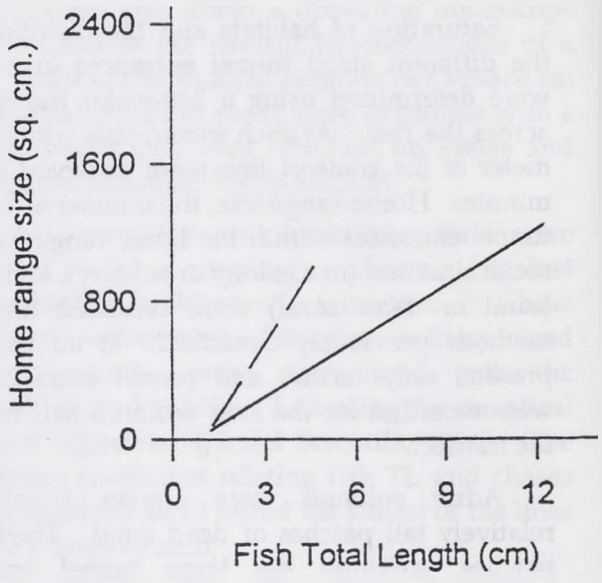


Figure 6. Dashed line represents the regression for solitary juveniles; solid line represents the regression for fish in adult colonies.

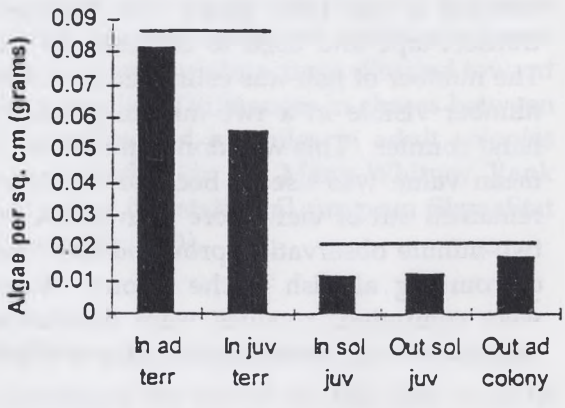


Figure 7. Means connected by horizontal lines do not differ significantly by the Kruskal-Wallis One Way ANOVA on Ranks and the Student-Newman-Keuls Method (P>0.05)

territories of adults and the home ranges of juveniles in adult colonies contained a higher density of algae per square cm than the home ranges of solitary juveniles, the area outside of adult colonies, and the area outside the home ranges of solitary juveniles ($P<0.05$; Figure 7).

Juveniles <4 cm TL in adult colonies conducted fewer chases against heterospecific intruders than did solitary juveniles ($P<0.05$);

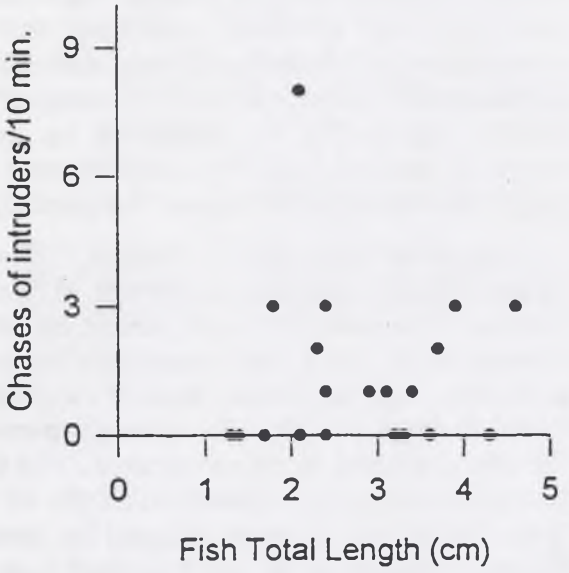


Figure 8. Solitary juveniles: chases against heterospecific intruders. (N=21)

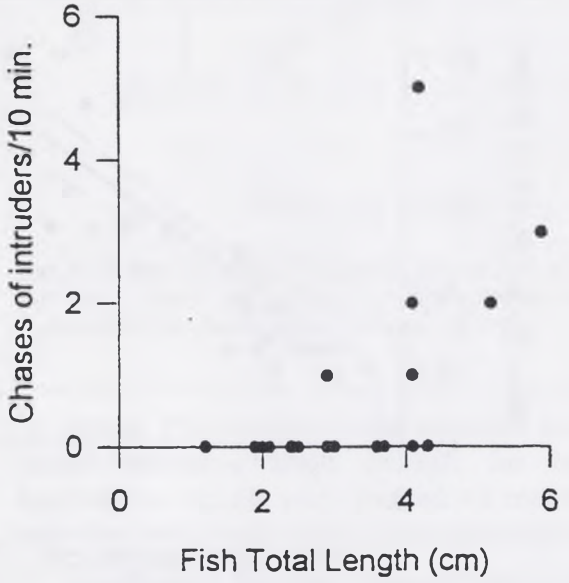


Figure 9. Juveniles in adult colonies: chases against heterospecific intruders. The number of chases by juveniles under four cm TL is statistically different from the number of chases by juveniles greater than four cm TL. (N=21; $P<0.01$)

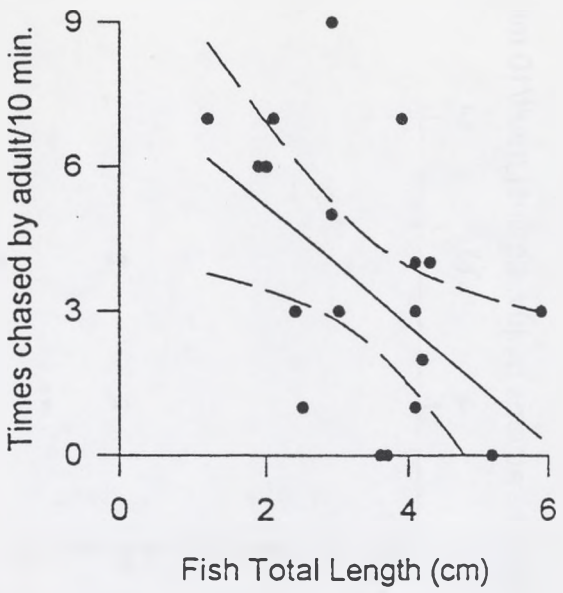


Figure 10. Chases directed by adults at juveniles in adult colonies are negatively correlated with size. Solid line represents regression line; dashed line represents 95 per cent confidence interval. (N=21)

juveniles >4 cm TL did not demonstrate a statistically different frequency of chases against heterospecific intruders ($P>0.05$) (Figure 8, Figure 9).

Costs and benefits--Interactions with conspecifics

The larger the juvenile in the colony, the less the adults chased it ($r=-0.52$, $p<0.05$; Figure 10). The locations of the chases also differed between younger and older juveniles. Younger juveniles were chased regardless of their location in their home ranges, whereas older juveniles were chased only at the edges of their home ranges, and often only after they had taken bites of algae from inside the neighboring adult's territory. Solitary juveniles never encountered adults and consequently were never chased by adults.

Juveniles less than four cm in adult colonies never initiated agonistic interactions with adults (Figure 11), although adults did intrude upon these juveniles' home ranges. Six out of seven juveniles over four cm in adult colonies initiated such interactions (Figure 11). Solitary juveniles never encountered adults and consequently never initiated agonistic interactions with adults. Thus, juveniles >4 cm TL in adult colonies had more

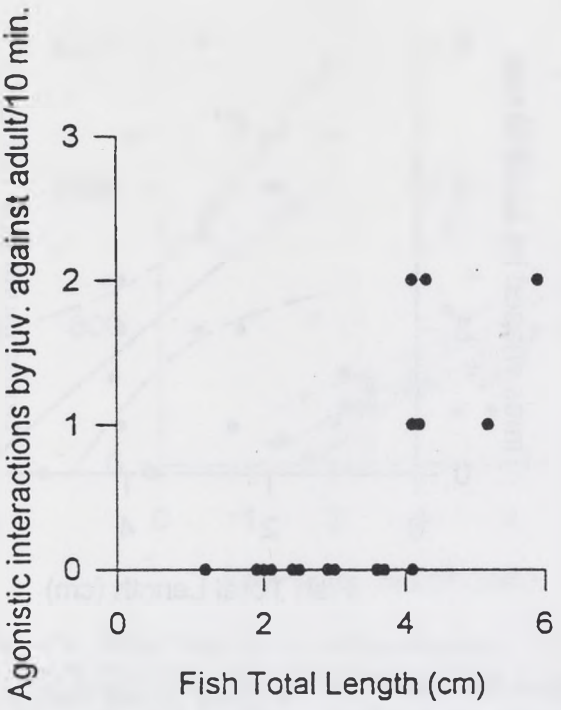


Figure 11. Juveniles in adult colonies: Agonistic interactions initiated by juveniles against adults. The number of initiations by juveniles under four cm TL is statistically different from the number of initiations by juveniles larger than four cm TL. (N=21; P<0.01)

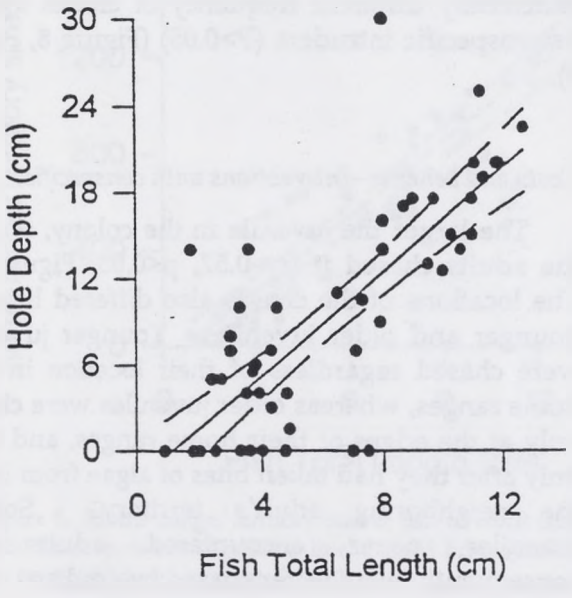


Figure 12. Depth of holes with openings greater than five cm vs TL of fish occupying the area containing the holes. Solid line represents regression line; dashed line represents 95 per cent confidence interval. (N=35)

agonistic interactions with adults than did solitary juveniles and juveniles <4 cm TL in adult colonies (P<0.01).

Suitable space

The depth of tunnel entrances having an opening with a greatest axis of at least 5 cm was positively correlated with the total length of the fish holding the home range containing the tunnel entrance (r=0.79; P<0.01; Figure 12). Fish of a size greater than eight cm TL always held territories that contained at least one and often more than one tunnel entrance measuring more than five cm along its greatest axis and deeper than ten cm. Fish size was positively correlated with the maximum-size fish that could take shelter in the largest tunnel entrance of the home range (r=0.81; P<0.01; Figure 13), as determined by growth curves of greatest body depth and greatest body width and the TL of fish (Figure 14, Figure 15).

Degree of saturation of habitats. The 200 meter transect included 50 percent of the reef covered with sand and eight percent of the reef covered with dead coral containing no tunnel entrances. No *Stegastes nigricans* of any size was found in these habitats. Twenty-eight percent of the reef contained tunnel entrances of a size which juveniles were seen to inhabit in nature; of these holes, thirty percent were occupied by juveniles. Fourteen percent of the reef contained holes of a size which adults were seen to inhabit in nature; of those tunnel entrances, 93 percent were occupied

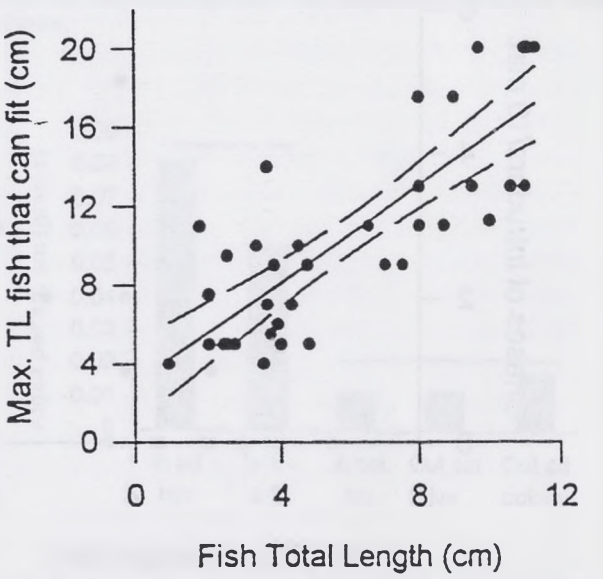


Figure 13. Maximum size of fish that can fit into the largest hole vs size of fish occupying the area containing the holes. Solid line represents regression line; dashed line represents 95 per cent confidence interval. (N=35)

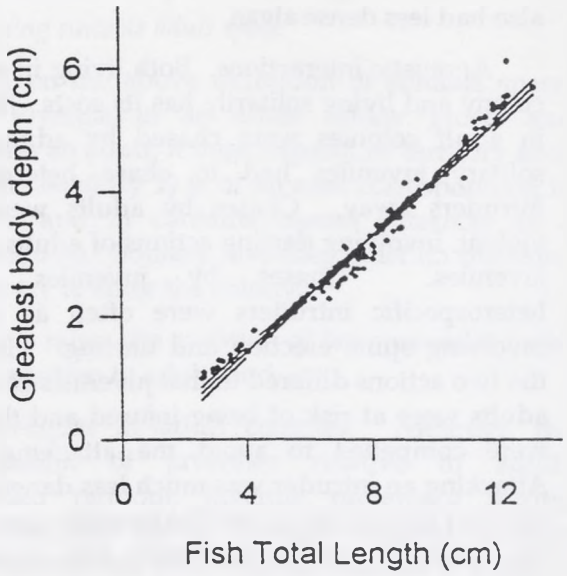


Figure 14. Growth curve of greatest body depth in *Stegastes nigricans*. Solid line represents regression; dashed line represents 99 per cent confidence interval. (N=112)

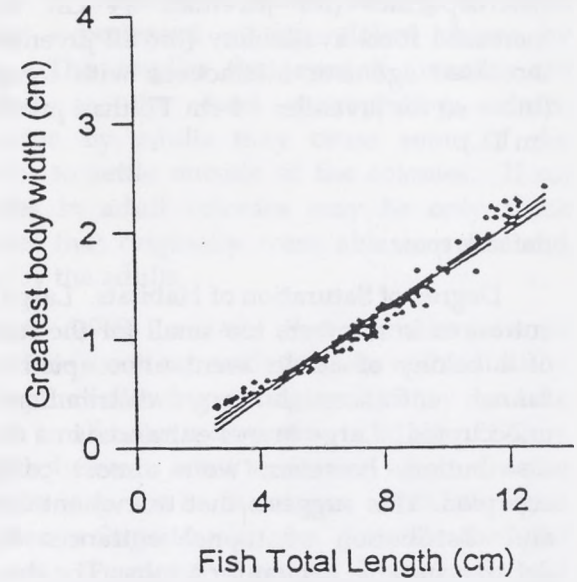


Figure 15. Growth curve of greatest body width in *Stegastes nigricans*. Solid line represents regression; dashed line represents 99 per cent confidence interval. (N=112)

by adults. The portions of the reef that contained tunnel entrances large enough for but not inhabited by adults were located >5 meters from any other tunnel entrances of an equivalent size.

Relationship Between Sizes of Coral Patch and Fish Colony. Not surprisingly, the number of fish in a colony increased with increasing size of the coral patch (r=0.94; P<0.01; Figure 16).

Obtaining suitable adult space

Model Bottle. Aggressive behavior toward the model-bottle fish was seen from all fish larger than 1.9 cm TL. The types of behavior consisted mainly of bites and charge and bites, although the number of times these aggressive acts were performed varied. The two smallest juveniles (both 1.9cm) exhibited a behavior which consisted of floating slowly upward or laterally with the head higher than the rest of the body and the body perpendicular to the ground. Their coloration was lighter than normal, becoming light tan, while the forehead became darker. On a few occasions during casual observations of natural interactions, juveniles under 1.9 cm TL (as low as 0.9 cm) were seen to direct aggressive behavior towards other juveniles, but never against other juveniles significantly larger (more than 1 cm larger) than themselves.

Discussion

Costs and benefits

Food. Three factors were studied to determine how the intake of food is affected by social situation: bites, algal density, and territory size.

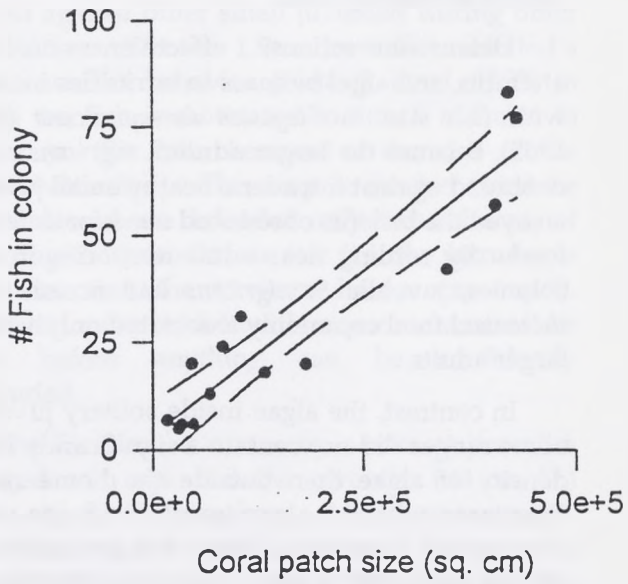


Figure 16. Coral patch size vs fish colony size. (N=14)

Although the number of bites taken by solitary juveniles did not differ from those by juveniles in adult colonies, the quality or amount of food ingested in each bite may have differed. Juveniles in adult colonies had on average four times as much algae by density per square cm in their territories as did solitary juveniles. But solitary juveniles had larger home ranges than juveniles in adult colonies, and thus had access to a wider area for food. If the amount of algae per square cm in each territory is adjusted to the total amount of algae in each territory by multiplying home range size by amount of algae per square cm, the juveniles in adult colonies had access to the greatest amount of algae. It should follow that they consume either food of higher quality, or a greater amount of food, with each bite.

Juveniles under four cm TL in adult colonies rarely needed to defend against intruders because intruders were usually driven off by nearby adults. Home ranges of these juveniles were small, and approach by intruders usually meant a close approach to a nearby adult territory holder. Thus, an attack by a heterospecific on the juvenile's home range may have been interpreted by the adult as an attack on the adult's territory and consequently defended against by the adult. Larger juveniles, however, defended their own larger territories against adults and consequently had to defend more against heterospecific intruders. Thus, juveniles less than four cm TL in adult colonies experienced the benefit of decreased cost of defending food.

Defensive actions, effectiveness of the attempts, and algal biomass in territories increased with fish size in *Stegastes dorsopunicans* (Foster 1985). Because the larger adult *S. nigricans* readily defended against intruders, nearby small juveniles enjoyed the benefits of reduced need for defense of food. By settling near adult territories in adult colonies, juvenile *S. nigricans* had access to the increased food commonly associated only with the larger adults.

In contrast, the algae inside solitary juveniles' home ranges did not contain a significantly higher density of algae than outside the home ranges. Compared with the algae inside the home ranges of juveniles in adult colonies, the amount in the solitary juveniles' home ranges was significantly lower. Thus, solitary juveniles not only had to defend more against heterospecific intruders, but also had less dense algae.

Agonistic interactions. Both living in an adult colony and living solitarily has its costs. Juveniles in adult colonies were chased by adults while solitary juveniles had to chase heterospecific intruders away. Chases by adults were often violent, involving darting actions of adults toward juveniles. Chases by juveniles against heterospecific intruders were often as intense, involving spine erection and darting. However, the two actions differed in that juveniles chased by adults were at risk of being injured and therefore were compelled to avoid the attacking adult. Attacking an intruder was much less dangerous in terms of risk of injury, and the juvenile always had the option to, and occasionally did, ignore the intruder.

Thus, the tradeoff for juveniles in adult colonies is a decreased need for defense against heterospecifics (for juveniles <4 cm TL) and increased food availability (for all juveniles), but increased agonistic interactions with conspecifics (more so for juveniles <4 cm TL than juveniles >4 cm TL).

Suitable space

Degree of Saturation of Habitats. Large tunnel entrances in numbers too small for the formation of a colony of adults went unoccupied. Small tunnel entrances in any distribution went unoccupied. Large tunnel entrances in a clumped distribution, however, were almost completely occupied. This suggests that tunnel entrance size and distribution of tunnel entrances together define a suitable habitat for adults. The data show that territories held by adults 1) correspond in area to total length of fish, 2) contain holes of a suitable size for adults as determined by the growth curves, and 3) are near other adult territories. Taking this definition of "suitable" space into consideration, all suitable adult habitats were occupied. This further suggests that competition for entry into adult colonies is intense.

Relationship Between Coral-Colony Size and Fish-Colony Size. The tight correlation between coral-patch size and fish-colony size indicates that space is limiting (Sale 1972). Adults, therefore, probably compete for space.

Obtaining suitable adult space

Given the above definition of suitable space, as a juvenile in an adult colony grows and becomes an adult, it must expand its territory such that the territory 1) is of an area corresponding to its TL, and 2) contains tunnel entrances of a suitable size. Solitary juveniles must do the same if they try to enter the colony.

This raises the question of how juveniles make this transition to adulthood.

Juveniles in adult colonies. Although the distribution of juveniles relative to adults appeared random, juvenile preference during settlement may not be. Juvenile *Stegastes nigricans* may be attracted to the greater amount of algae in adult colonies. Adult *Stegastes nigricans* are territorial over food; any conspecific that locates within its space is immediately a competitor. New recruits of *Stegastes nigricans* settling in adult colonies experienced intense violent chases by adults. This implies that even if juveniles are attracted to the food surrounding adults, aggression by adults may cause some of the juveniles to settle outside of the colonies. If so, juveniles in adult colonies may be only those juveniles that originally were able to withstand chases by the adults.

Sale (1980) noted that small juvenile *Pomacentrus wardi* can settle in areas with adults by utilizing the following strategies. 1) They can take cover in small holes inaccessible to adults. 2) They can settle between adult territories, where defense by adults may not be as intense. Both strategies were seen in *Stegastes nigricans*. Juvenile *Abedefduf lachrymatus, Pomacentrus apicalis, P. flavicauda,* and *P. wardi,* which also exhibit these two strategies, may then expand their territories at the expense of neighboring adults (Sale 1974). If this is true for *S. nigricans,* selection for fish that will eventually obtain adult space in adult colonies may begin at the moment a juvenile is able to stay in an adult colony despite the presence of adults.

Sale (1980) reasoned that adults eventually habituate to the juveniles. If the juvenile can persist long enough by taking cover in small holes or by settling at the boundaries of adult territories, the adult may eventually habituate to the juvenile and reduce aggression towards the juvenile. This hypothesis is supported in this study by the negative correlation between fish TL and chases by adults. However, this negative correlation could also support an alternative hypothesis, that adults are simply responding to the greater risk presented by the larger juvenile. Regardless of the cause, the important idea is that these juveniles, if they can initially survive despite the pressure by adults, experience increasingly reduced pressure by adults.

Hierarchy of territoriality. The term "home range" has been used liberally up to this point because territoriality by definition requires defense of the area used. Defense against both conspecific and heterospecific intruders of all sizes was only seen in colonial fish greater than four cm TL. Thus the term territorial could be applied to those fish. Colonial fish smaller than four cm TL were seen consistently to defend their territories against other juveniles but not against adults, indicating a hierarchy of territoriality: fish selectively defended against only those intruders they could successfully deter.

Although preliminary and few in numbers, model-bottle tests supported the idea of selective defense. The model-bottle fish was 3.4 cm TL, and fish smaller than that defended their territories against the fish, suggesting that a fish will defend against a larger fish. But how much larger the intruder can be is limited. Both 1.9 cm juveniles did not exhibit overt aggressive behavior towards the 3.4 cm model bottle intruder, although fish smaller than 1.9 cm were seen a few times to defend against other small juveniles during other observations. The two 1.9 cm juveniles exhibited a classic conflict behavior (Bastock et al. 1953) in which the fish is motivated to attack but also to retreat (in this case, because of the size of the model-bottle fish). This may be further evidence that territories are defended only if the chances of deterring the intruder are fair (i.e. the intruder is of a size that the territory holder can repel). However, more model-bottle experiments must be done before anything can be confidently concluded.

The location of chases by adults at juveniles changed with age. Smaller juveniles (<4 cm TL) were attacked throughout their home ranges. However, larger juveniles (>4 cm TL) were not attacked if they stayed in the center of their home ranges. This suggests that adults respected the larger juveniles' home ranges as territories.

Aggressive encounters occurred exclusively at the edges of the larger juveniles' territories, and usually only when the juveniles ventured outside of their territories and into a neighboring adult's territory to feed. That adult chases of juveniles occurred, and occurred at the edges of the juveniles' territories, usually when the juvenile ventured into the adult's territory to feed, suggests that the juveniles were expanding their territories. Further evidence of this expansion is provided by the correlation between fish size and territory size of juveniles in adult colonies.

Continued growth by the juvenile and the concordant increase in competitive abilities leads to a continued expansion of its territory. This may be how *S. nigricans* juveniles that originally settle in adult colonies make the transition to adulthood in adult colonies. Obtaining suitable adult space may thus be a long process, requiring initial settlement in the colony as a small juvenile.

Solitary juveniles. No solitary juveniles greater than six cm total length were seen. Therefore, by the time solitary juveniles reach six cm. total length, they must 1) enter adult colonies, 2) enter floater populations, or 3) suffer from predation.

1) Sale (1980) documented a similar situation in *P. wardi*, which he called the "I'll take almost anything" strategy. These juveniles occupied sub-optimal sites. Sale hypothesized that if a juvenile could survive initially, it could later take the space vacated following an adult mortality. These juveniles using the "I'll take almost anything" strategy were similar to the solitary juveniles encountered in this study.

Entrance into adult colonies at six cm should be difficult. Juveniles of this size would immediately have to establish territories of approximately five hundred square cm (Figure 5) in the presence of extremely territorial adults. Juveniles that settle as new recruits in colonies, on the other hand, can take cover in small holes and between adult territories and only need to maintain small home ranges. These juveniles in adult colonies can then gradually expand their territories.

2) Williams (1978) removed individuals from colonies of the damselfish *Stegastes planifrons*, a fish similar to *S. nigricans* in ecology and evolutionary history. New inhabitants of the vacated spaces came from "floater" populations of non-territory-holding, non-reproductive *S. planifrons*. Juveniles were outcompeted by these larger floaters. If floater populations exist in *S. nigricans*, some juveniles may at some time become members of these populations and eventually take a vacated space in an adult colony. However, if natural adult mortality in *S. nigricans* is low, then removal experiments are misleading, since vacant spaces rarely appear in nature and members of floater populations consequently rarely enter adult colonies.

3) If a juvenile is unable to find a larger tunnel entrance in a colony, mortality may follow.

Conclusion

Small juveniles cannot effectively defend their algal patches from heterospecific herbivorous intruders while adults can effectively defend against herbivorous intruders and consequently hold larger and thicker algal patches. Ability to defend against herbivorous intruders should increase with body size. Small juveniles can "cheat" the curve of body size vs. ability to defend/density of algal patch by settling near an adult territory in an adult colony. A cost, however, is increased chases by conspecific adults on the juveniles.

Reproductive success, requiring the obtainment of a territory which 1) corresponds in area to total length of fish, 2) contains holes of a suitable size for the fish, and 3) is near other adult territories, may be restricted to those juveniles who, upon settlement, can withstand attacks by adult conspecifics. Adults normally chase all herbivorous intruders, both heterospecific and conspecific. However, juveniles are able to remain near adult territories by 1) taking cover from attacks/retreating to small holes inaccessible to the larger adults and 2) reducing attacks by adults by settling between the territories of adults, in "halos" of non-defended space.

As the juvenile grows, pressure from adults on the juveniles in the form of chases decreases while pressure from the juveniles on neighboring adults increases. An increase in the juvenile's body size leads to an increase in its abilities to defend against both heterospecifics and conspecifics. It consequently expands its home range and defends it as a territory. Continued expansion leads to the obtaining of adult space in an adult colony.

Those juveniles who cannot initially withstand adult attacks settle solitarily and may never reach adulthood.

These hypotheses concerning the obtainment of adult space need to be tested by marking juveniles at the time of settlement and following them throughout recruitment.

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The Feasibility of Using Butterflyfishes (Family Chaetodontidae) as Bioindicators of Coral Reef Health

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

ABSTRACT. A study was conducted on the island of Moorea to assess the feasibility of using butterflyfishes of the family Chaetodontidae as bioindicators of coral reef health. Obligate corallivore Chaetodontids sould be good candidates for bioindicator species since they coevolved with scleractinian corals and feed directly on them. Results showed a weak correlation for both obligate corallivores as well as all Chaetodontids with live coral cover. However feeding data showed significant differences in the feeding behaviors of the two Chaetodontids studied, *Chaetodon trifasciatus* and *Chaetodon citrinellus*, in areas of high coral cover versus low coral cover. This suggests that both species of Chaetodontids show promise of becoming bioindicator species; however more work must be done in order to determine exactly when butterflyfishes first begin to show signs of stress on a reef.

Keywords : bioindicator, butterflyfishes, Chaetodontidae, coral reefs, Moorea, indicator species

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Introduction

Coral reef ecosystems are one of the most diverse on the planet. Because coral reefs are linked to a wealth of biodiversity in the ocean, the deterioration of coral reefs may have devastating effects on the ocean ecosystem and the world. For this reason many protocols have been proposed to detect stress on a reef before it is too late to stop their deterioration. Many species of butterflyfishes (family Chaetodonidae) are known to be obligate corallivores which feed directly on the live tissues of corals (Reese 1977, 1981,1994; Harmelin-Vivien 1983; Bell et al. 1985; Hourigan et al. 1988; Crosby and Reese 1996). For this reason butterflyfishes have been proposed as possible bioindicator species for the conservation and management of coral reef ecosystems (Reese 1977, 1981,1994; Hourigan et al. 1988; Crosby and Reese 1996)

The Bioindicator Species Concept

The concept of a bioindicator species has been proposed to detect chronic sublethal environmental changes which are otherwise hard to detect by conventional means (Crosby and Reese 1996). Good indicator species are organisms that exhibit certain characteristics which enable the organism to detect sublethal stress on an ecosystem (Jones and Kaly 1988; Crosby and Reese 1996) . There are several essential qualities an organism must exhibit in order to make it a good candidate for a bioindicator species. A good indicator species must show sign of stress on an ecosystem before it is too late to do something about it (Jones and Kaly 1988; Crosby and Reese 1996). Clearly bioindicator species are not needed in catastrophes such as oil spills where the stress on the ecosystem is blatantly obvious (Crosby and Reese 1996, Erdmann 1997). Bioindicator species also must be specific to what it is monitoring (Jones and Kaly 1988, Erdmann 1997) in that bioindicators should not sound off any "false alarms" due to natural temporal variations within the ecosystem (Erdmann 1997).

Butterflyfishes as Bioindicators

Butterflyfishes are coevolved with scleractinian corals (Reese 1977, 1981, 1994; Hourigan et al. 1988; Crosby and Reese 1996). They are also brightly colored, diurnal, and form monogamous pairs making them remarkably easy to census and identify. Because many species of butterflyfish are obligate corallivores Reese (1977) first proposed that they may be used as possible bioindicator species because they feed directly on the live tissue of coral (Reese 1977, 1981, 1994; Hourigan et al. 1988; Crosby and Reese 1996). It has been hypothsized that butterflyfishes will react to the stress on a reef in due to the fact that as a reef becomes progressively stressed, the coral is forced to

respire more and to lower its production of energy storage products such as glycogen and lipids (Reese 1994; Crosby and Reese 1996). This leads to a reduction in the nutritional value of the coral which the butterflyfishes can detect (Reese 1994; Crosby and Reese 1996). The coral are sessile and are forced to stay in place, however the butterflyfishes are not. It has been suggested that butterflyfishes will respond to the change in nutritional value of the coral, due to the stress on the reef, in several ways . These include 1) expansion of a territory or home range, 2) an increase in agonistic encounters as mated pairs try to expand their territory into the territories of neighboring fish, 3) the eventual emigration to a "healthier" site as the levels of stress on the reef increase, 4) an increase in feeding rates at first as mated pairs try to maintain their nutrient uptake, and 5) the eventual decrease in feeding rates as more time is spent by the fish foraging for food and defending its territory (Reese 1981, 1994; Hourigan et al. 1988; Crosby and Reese 1996).

The protocol for monitoring coral reef health with butterflyfishes is inexpensive, "low-tech", and unobtrusive. Developing countries, where many coral reefs lie, will find this method especially attractive since they lack funds and equipment for costly extensive monitoring programs. The purpose of this study was to determine whether or not butterflyfishes of the family Chaetodontidae could be used as bioindicators of coral reef health on the island of Moorea, French Polynesia. It was hypothesized that obligate corallivore Chaetodontids would make promising candidates for bioindicator organisms. If butterflyfishes could be used to successfully monitor the coral reef ecosystem of Moorea, this protocol may be used throughout the world as a model for the conservation and management of the coral reefs ecosystem.

Materials and Methods

This study was conducted on the island of Moorea (Society Islands), French Polynesia (17 30' south, 149 50' west) . Three sites of varying coral cover were chosen on the coral reef (figure 1). Site 1 is located on the fringing reef in front of the Richard B. Gump Biological Station which is situated on the northwest corner of Pao Pao Bay. Site 2, which is located on the barrier reef flat on the northeast corner of Pao Pao Bay, was renamed Slim's Reef for the purposes of this study. Site 3 is located on the barrier reef flat at Temae. The site with the highest average live coral cover was the barrier reef flat at Temae whereas the site with the lowest average live coral cover was the fringing reef off of Gump Station (figure 2).

Thirteen 50 meter transects were laid out parallel to the algal ridge at each site. Since this study was concerned with the relationship between Chaetodontids and scleractinian corals, the transects were purposely laid out in areas of high coral cover relative to the area. The distance from the algal ridge varied between 10 meters and 50 meters. The abundance of all Chaetodontid species was censused as well as the percent live coral cover and coral composition of each transect. All Chaetodontids within 5 meters of each side of the transect were counted and recorded, yielding the total abundance of Chaetodontids within a 500 square meter area. Percent live coral cover was calculated using the Line and Point Intercept Transect method (Ohlhorst et al. 1988; Crosby and Reese 1996) where the genus of coral was identified and recorded at every meter interval within the transect. This yielded in a total of 50 data points for the 50 meter transect. These data points were then simply multiplied by two to estimate the total percent live coral cover and the percent coral composition at each particular site.

The study of the feeding behavior of Chaetodontids focused on using two species of butterflyfish. Feeding rates were recorded for *Chaetodon trifasciatus,* an obligate corallivore, and *Chaetodon citrinellus,* a facultative corallivore as our control (Harmelin-Vivien and Bouchon-Navaro 1983). Data were recorded at the site with the highest live coral cover (Temae) and at the site with the lowest live coral cover (Gump Station). Feeding rates were taken for six individual fish of *Chaetodon trifasciatus* and *Chaetodon citrinellus* at each site. Three-five minute intervals were used for each individual fish for a total sampling time of fifteen minutes. The number of bites as well as the material being eaten was recorded for each fish.

Analysis of Variance tests were used to determine if there were significant differences between study sites in the amount of live coral cover, the number of total obligate corallivore

Chaetodontids, and the total number of all Chaetodontids present. Tukey-Kramer analyses were then used to determine between which study sites these differences occurred. Regression analyses were used for both total obligate corallivore Chaetodontids and total Chaetodontids versus percent live coral cover in order to determine if a correlation could be found between the number of Chaetodontids present and the percent live coral cover.

The feeding behaviors of both *Chaetodon trifasciatus* and *Chaetodon citrinellus* were analyzed using t-tests. A t-test was run in order to determine if there was a significant difference in the number of coral bites taken by *Chaetodon trifasciatus* at an area of high coral cover (Temae) versus an area of low coral cover (Gump Station). A t-test was also run for *Chaetodon citrinellus* to determine if there was a significant change in the number of coral bites taken at Temae versus Gump Station. In addition to the number of coral bites, the number of noncoral bites taken by *Chaetodon citrinellus* at Temae and Gump Station was also analyzed using a t-test.

Results

The reef at Gump Station was characterized by high levels of algal cover and composition, whereas Slim's Reef and the reef at Temae showed little or no algal cover. The turbidity of the water at Gump Station was also higher when compared to Slim's Reef and the reef at Temae. On average days with no precipitation the visibility at Gump Station would reach 7-9 meters whereas the visibility at Slim's Reef and Temae would routinely reach 15-20 meters.

Transect Data

Analysis of Variance and Tukey-Kramer tests showed that the percent live coral cover at Temae and Slim's Reef showed a significant difference when compared to the percent live coral cover at Gump Station (figure 2). However the Tukey-Kramer analysis revealed that Temae and Slim's Reef did not differ significantly in the amount of live coral cover. Analysis of Variance and Tukey-Kramer analyses also revealed that there were significant differences in the abundance of both total obligate corallivores and total number of Chaetodontids between all three sites.

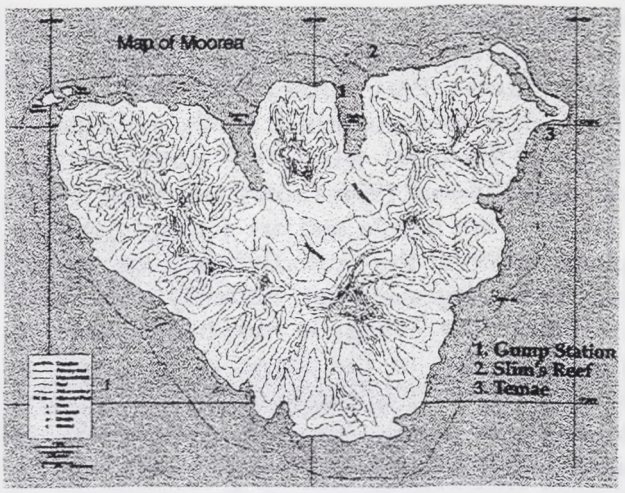

Figure 1. Map of Moorea showing the location of study sites with 1) depicting the reef at Gump Station, 2) depicting Slim's Reef,, and 3) depicting the reef at Temae.

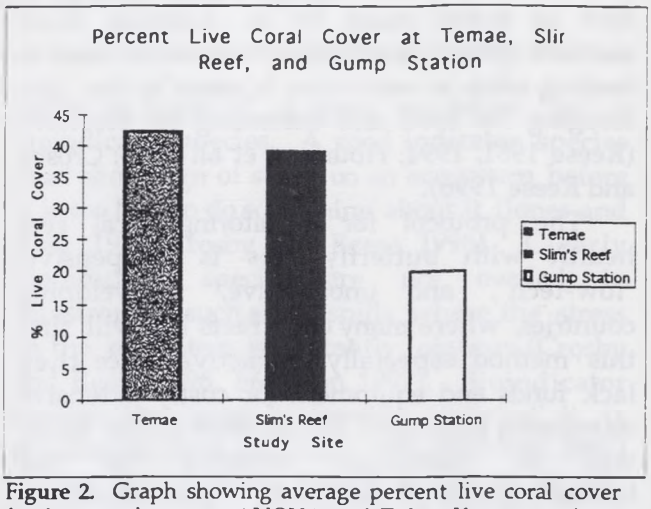

Figure 2. Graph showing average percent live coral cover for the sample areas. ANOVA and Tukey-Kramer analyses idicate that percent live coral coral cover is significantly different between Temae and Gump Staion as well as between Slim's Reef and Gump Station, but not significantly different between Temae and Slim's Reef ($p < 0.05$).

Regression analysis of total obligate corallivore Chaetodontids versus percent live coral cover revealed a R^2 value of 0.42 indicating a weak correlation between the abundance of obligate corallivore Chaetodontids and percent live coral cover (figure 3). However the same regression analysis for the total number of Chaetodontids versus percent live coral cover revealed a nearly identical R^2 value of 0.43 signifying that the total number of all Chaetodontids was also weakly correlated with percent live coral cover (figure 4). In fact the regression analyses revealed that the total number of all Chaetodontids was slightly better correlated with live coral cover than the number of total

obligate corallivores. The slopes of the linear regression lines for both obligate corallivores and total Chaetodontids were shown to be significantly different from zero ($p < 0.01$).

Feeding Rates

T-test analyses revealed that the number of coral bites taken by *Chaetodon trifasciatus* as well as by *Chaetodon citrinellus* at Temae was significantly different from the number of coral bites taken by the respective fishes at Gump Station (figure 5; figure 6). T-test analysis also revealed that the total number of noncoral bites taken by *Chaetodon citrinellus* at Temae was significantly different from the total number of noncoral bites taken at Gump Station (figure 6).

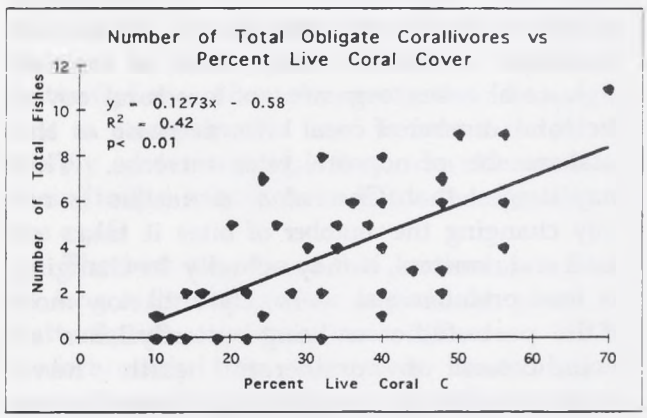

Figure 3. Regression analysis using number of total obligate corallivores vs. percent live coral cover. R^2 value of 0.42 idicates a weak correlation between total number of obligate corallivores vs. percent live coral cover. The slope of the linear regression line is highly significant when compared with a slope of zero ($p < 0.01$).

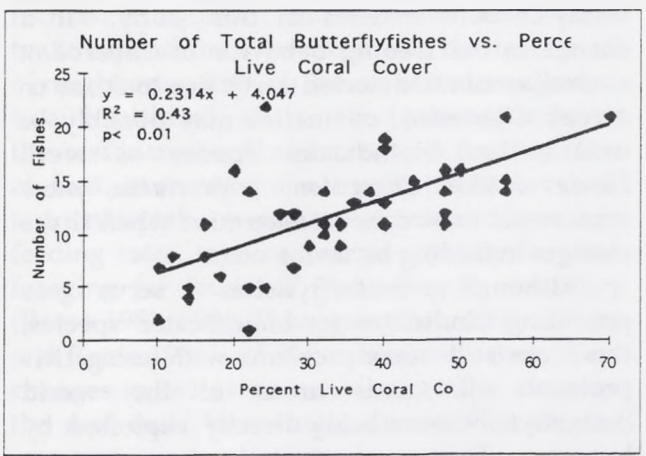

Figure 4. Regression analysis using number of total Chaetodontids vs. percent live coral cover. R^2 value of 0.43 indicates a weak correlation between total number of Chaetodontids and percent live coral cover. The slope of the regression line is highly significant when compared with zero ($p < 0.01$).

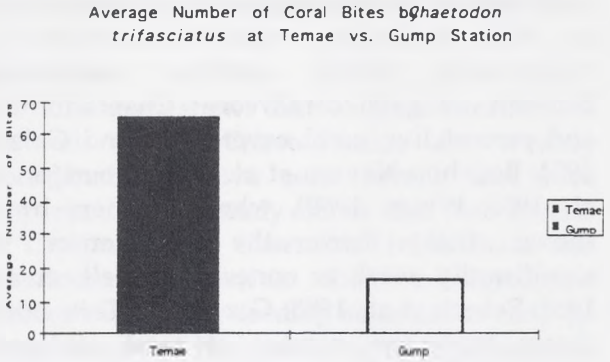

Figure 5. Graph showing the average number of coral bites by *Chaetodon trifasciatus* at Temae and Gump Station. T-test analysis shows that there is a significant difference in the number of coral bites between the two sites.

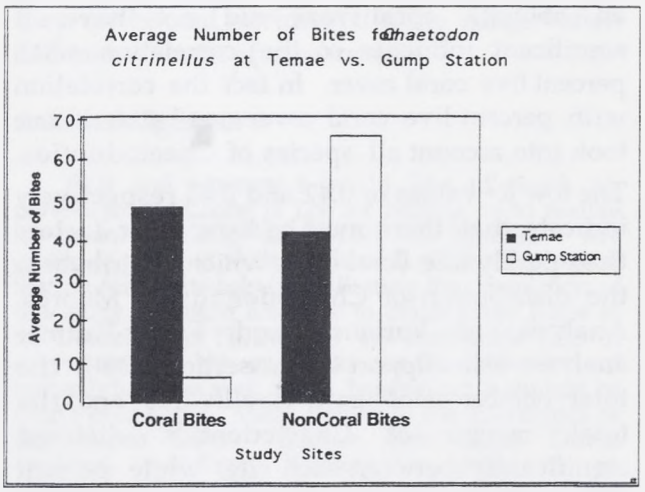

Figure 6. Graph showing the average number of coral and non coral bites by *Chaetodon citrinellus* at Temae and Gump Station. T-test analysis indicate a significant difference in the amount of coral bites as well as the number of noncoral bites between the two sites.

Discussion

Since we are interested in the relationship between Chaetodontids and scleractinian corals, transects were purposefully laid out in areas of relatively high coral cover for that particular site. We are not pretending to assess the percent live coral cover for each site, but for the purposes of our study it is viable to compare the data for the area sampled within each transect.

It was hypothesized that because obligate corallivore Chaetodontids feed directly on live coral tissue, there would be a strong positive correlation between the abundance of obligate corallivores and percent live coral cover.

However past studies on the subject have conflicted on how strong the correlation really is. Some studies have shown that there is a significantly strong positive correlation between obligate corallivore Chaetodontids and percent live coral cover (Bell and Galzin 1984; Bouchon-Navaro et al. 1985; Hourigan et al. 1988; White 1989), whereas others have shown that there the correlation is significantly weak or nonexistent (Bell et al. 1985; Roberts et al. 1988; Cox 1994). This study shows that the number of total obligate corallivore Chaetodontids is only weakly correlated with live coral cover (figure 3). When regression analysis was run on total number of Chaetodontids, it showed a slightly greater correlation than solely the obligate corallivores (figure 4). This suggests that being an obligate corallivore did not have a significant influence on the correlation with percent live coral cover. In fact the correlation with percent live coral cover was better if one took into account all species of Chaetodontids. The low R^2 values of 0.42 and 0.43 respectively indicate that there must be some other factors than purely live coral cover which contribute to the distribution of Chaetodontids in Moorea. Analysis of Variance and Tukey-Kramer analyses also support this assertion. Both the total number of obligate corallivores and the total number of Chaetodontids differed significantly between each site, while percent live coral cover only differed only between Temae and Gump Station and between Slim's Reef and Gump Station. The fact that a significant difference in the number of both total obligate corallivores and total Chaetodontids was seen between Temae and Slim's Reef, while no significant difference was observed in the percent live coral cover suggest that there must be other factors involved in the distribution of both obligate corallivores and all Chaetodontids than just live coral cover.

The significant difference in the feeding behavior of *Chaetodon trifasciatus* between areas of high coral cover and low coral cover indicates that the obligate corallivore *Chaetodon trifasciatus* is a promising candidate for a bioindicator species. This is due to the fact that *Chaetodon trifasciatus* changes its feeding behavior as it goes from an area of high coral cover to an area of low coral cover. However more work must be done to determine when *Chaetodon trifasciatus* begins to show signs of change in its feeding behavior. If *Chaetodon trifasciatus* can show signs of change in its feeding behavior due to stress on the reef before any visible signs of stress could be seen on the reef itself, *Chaetodon trifasciatus* may be used as an indicator species.

The significant changes in the feeding behavior of *Chaetodon citrinellus* make it a promising candidate for a bioindicator species as well. *Chaetodon citrinellus* exhibited a significant difference in the amount of coral bites taken as well as noncoral bites taken at an area of high coral cover versus an area of low coral cover. This difference in feeding behavior indicates that *Chaetodon citrinellus* as well as *Chaetodon trifasciatus* serve as promising candidates for bioindicator species. In fact as *Chaetodon citrinellus* moves from an area of high coral cover to an area of low coral cover, the total number of coral bites decrease as the total number of noncoral bites increase. This may suggest that *Chaetodon citrinellus* is not only changing the number of bites it takes on coral and noncoral, it may actually be changing its food preference as well. Up until now most of the past studies on using butterflyfishes as bioindicators of coral reef health have concentrated on the use of obligate corallivores (Reese 1977, 1981, 1994; Hourigan et al. 1988; Crosby and Reese 1996; Jones and Kaly 1996). Perhaps facultative corallivores like *Chaetodon citrinellus* can also be used to detect stress on a reef. *Chaetodon citrinellus* exhibited a significant change in feeding behavior between sites in this study. If a change in the feeding behavior of *Chaetodon citrinellus* can be detected early due to stress on a reef, *Chaetodon citrinellus* may possibly be used as a bioindicator species as well. However like *Chaetodon trifasciatus*, more work needs to be done to determine when these changes in feeding behavior occur.

Although butterflyfishes serve as promising candidates for bioindicator species, there are still some problems with using this protocol. In some areas of the world butterflyfishes are being directly exploited by humans. This is particularly important in areas like the Western Pacific where butterflyfishes are exploited by humans for the aquarium trade as well as for food (Erdmann 1997). Clearly the protocol for using butterfly-

fishes as bioindicators of coral reef health will be severely hampered when assessing these areas. However the real question with using this method lies in the timing of the early warning signal. Remember a good indicator species will signal an early warning of stress on a reef before it is too late to stop the deterioration of a reef. Also a good indicator species will signal stress on a reef when no other signs are visible. If one can get a better assessment of the level of stress by visually looking at the coral, there would be no need for bioindicator species. Indicator species must signal an alarm when chronic sublethal stress is being applied to the reef and when the only other method of assessing the stress on the reef is often expensive and high tech. More work needs to be done to determine when exactly the changes in butterflyfish behavior begin. If butterflyfishes show changes in their behavior due to stress on the reef before the reef is visibly deteriorating, they can be used as bioindicator species to monitor the health of the reef.

The best way to use this method is to look at long term changes in individual pairs of butterflyfish over time (Reese 1997). Unfortunately this study was limited to a spatial study due to time constraints. More work needs to be done working with individual pairs of butterflyfish in order to determine when butterflyfish begin to show signs of change in their behavior due to stress on the reef. These changes in behavior include 1) expansion of a territory or home range, 2) as increase in agonistic encounters as mated pairs try to expand their territory into the territories of neighboring fish, 3) the eventual emigration to a "healthier" site as the levels of stress on the reef increase, 4) an increase in feeding rates at first as mated pairs try to maintain their nutrient uptake, and 5) the eventual decrease in feeding rates as more time is spent by the fish foraging for food and defending its territory (Reese 1981, 1994; Hourigan et al. 1988; Crosby and Reese 1996). If it can be shown that these changes in behavior occur before the stress on the reef could be visually assessed looking at the coral, butterflyfishes may hold an answer for monitoring coral reef health in the future.

Conclusion

This study shows that obligate corallivores as well as all Chaetodontids are weakly correlated with live coral cover. But more importantly this study shows that two species of Chaetodontids, *Chaetodon trifasciatus* and *Chaetodon citrinellus*, show a significant differences in their feeding behavior as they go from an area of high coral cover to an area of low coral cover. More work needs to be done to determine exactly when these fishes show a change in their behavior before this protocol could be used to monitor the health of the coral reef ecosystems of the world. If butterflyfish show early signals of stress on a reef, perhaps they can be used worldwide in the conservation and management of coral reefs.

Acknowledgments

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Effect of the introduced mangrove, *Rhizophora stylosa*, on the diversity and abundance of intertidal gastropods on Moorea, French Polynesia

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

ABSTRACT. Abundance and diversity of gastropods living in stands of the introduced mangrove *Rhizophora stylosa* were studied, and compared to rocky intertidal sites and salt marsh sites inhabited by the grass *Paspalum vaginatum*. There was a significant difference in diversity between all three habitat types, with five species of gastropod found exclusively in areas dominated by mangroves. Abundance of the gastropod *Littoraria intermedia*, a species commonly found in mangroves throughout the Indo-Pacific, was considerably higher in the mangroves than in the other two sites, while densities of *Clithon chlorostoma* in the mangroves have severely declined. This suggests that the introduction of a habitat that is dramatically different from the original has both limited as well as aided in the expansion of gastropod populations on Moorea.

Key words. *Rhizophora stylosa*, *Littoraria intermedia*, *Paspalum vaginatum*, *Clithon chlorostoma*, mangroves, intertidal, gastropods, Moorea, French Polynesia, introduced species

Introduction

Introduced species can have drastic effects on a habitat, ranging from changes in the topography and substrate, to increased sedimentation, which can alter the biota (Simberloff 1995). The mangrove *Rhizophora stylosa* was introduced to Moorea in the 1930s for oyster cultivation, and since then has spread to other sites along the shore that are conducive to its establishment. This species offers a new resource that changes the shoreline enough to greatly alter the original habitat (Ross and Underwood 1997), hence potentially changing the composition of fauna in the immediate area.

Mangroves are rich habitats with important commercial value. They provide forest resources such as wood and tannins, and through a detritus chain, provide nutrition to the surrounding marine environment (Tomlinson 1994). This creates a favorable habitat that can serve as spawning and settling ground for many commercially exploited marine animals such as fish, oysters, and other shellfish.

R. stylosa can grow in a wide variety of habitats, ranging from salt marsh areas to coral/rock sand and rock substrates (Duke and Bunt 1979). The two types of habitats that *R. stylosa* has invaded are: 1) wide, flat salt marsh areas dominated by the grass *Paspalum vaginatum* and bordered by a fringe of *Hibiscus tiliaceus* on the inland edge, and 2) narrow, rocky intertidal habitats shaded by a canopy of *H. tiliaceus*.

The most obvious effect of the mangroves is a change in the physical environment. The firm substratum of *R. stylosa* is quite different than that of a sandy sediment surface with grass, or that of a rocky shoreline in that it has stilt roots, which branch out from the trunk and other established roots (Tomlinson 1994) and which grow in an intertwined network (personal observation).

The purpose of this study was to investigate whether or not the presence of *R. stylosa* has affected the abundance and diversity of gastropods in the intertidal zone. This may provide the basis for further analyses of ecological changes that have occurred as a result of this introduction.

Materials and Methods

Study areas

Field data were collected during October and November, 1997 on Moorea, French

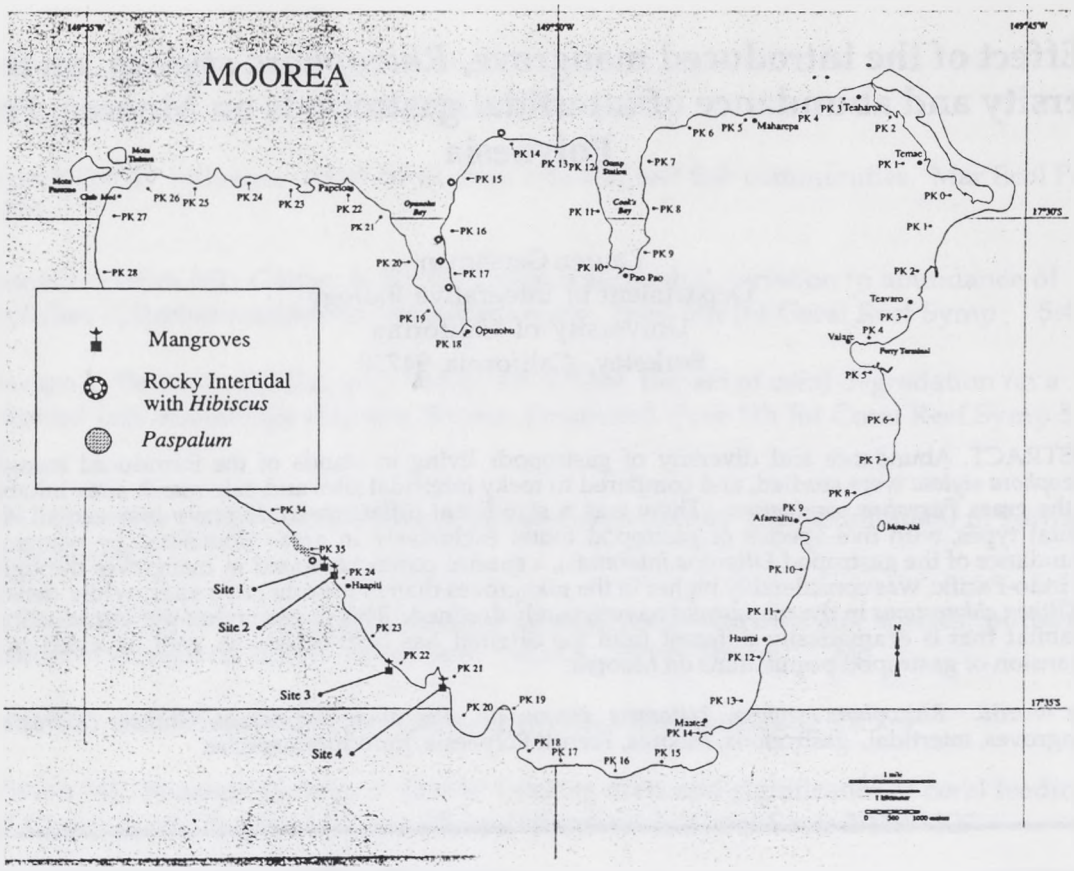

Figure 1. Map of sampling sites.

Polynesia (17 30' S, 149 50' W). Mangrove sites (Figure 1) are located at PK 35, 24, 22 and 21 near Haapiti on the South-west side of the island, which has extensive stands of *Rhizophora stylosa*.

Site 1 is a newly establishing stand of mangroves that consists of seedlings, saplings, juvenile, and mature trees that line the shore and do not extend any further than five meters into the water. One area of the site is very dense with trees, and the other area has many young trees with 1-5 meter separation between individuals. Site 2 is an older site, that consists of very dense mature trees with seedlings growing among the roots of the mature individuals. The trees at this site extend up to 45 meters away from shore. Site three consists of four nuclear trees with 10-15 meter separation between individuals. They are 1-7 meters away from shore. Site 4 consists of a dense stand of mature trees with seedlings growing among the roots. The stand extends up to 25 meters into the water. At the northern side of the stand, trees line the shore of a stream mouth, and are in brackish water.

Various rocky intertidal sites were chosen around the island from PK 14 to PK 35 (Opunohu to Haapiti) according to the following criteria: the presence of basalt rocks and boulders with a canopy of *Hibiscus*. *Paspalum* sites were chosen near PK 35 where it grew more than 10 meters continuously along the shore, and was undisturbed by mangroves or other flora.

Sampling

Densities of gastropods were counted within transects that were 10 meters parallel to the shore. Only the first three meters into the stand were surveyed for gastropods because on preliminary observations they were not observed any deeper. Snails of the genus *Littoraria* occur only on the outer edge of mangrove stands (D Reid, pers. comm.), and sampling of other species of gastropods was limited to the outer edge of the stand due to the inability to reach deeper into the stand. In transects where the stand was less than three meters thick, the width of the stand was also measured, in order to calculate the entire area sampled. Snails were marked

with nail polish or white correction fluid or were removed from roots when some form of marking was unavailable, so that individuals would not be counted more than once.

Sampling within 10 meter transects was also performed in habitats with the following zonation: *Paspalum* growing along the shore, and rocky intertidal habitats which had *Hibiscus* growing beyond the rocks, hanging over the water. These habitats were used as a control because they are the two types of habitat that have been invaded by mangroves.

Data Analysis

A t-test and analysis of variance were used to look at the differences in absolute densities between mangrove and non-mangrove sites. A Shannon-Weiner diversity index was calculated to compare diversity between mangrove and non-mangrove habitats, and the results were compared using analysis of variance.

Results

Diversity

A total of 15 species were sampled in all

Table 1. List of all species of gastropods collected and the habitats in which they were found.

Species	Mangroves	Rocky Intertidal	*Paspalum*
Clithon chlorostoma	x	x	x
Ceritheum alveolus	x		
Neritina zigzag	x		
Puperita reticulata	x		
Nerita sp.	x		
Cypraea serrulifera	x		
Littoraria intermedia	x	x	
Littorina coccinea	x	x	
Erosaria obvelata	x	x	
Nerita plicata		x	
Morula uva		x	
Mitra cf. paupercula		x	
Thais aculeata		x	
Oliva sp.		x	
Nerita argus		x	

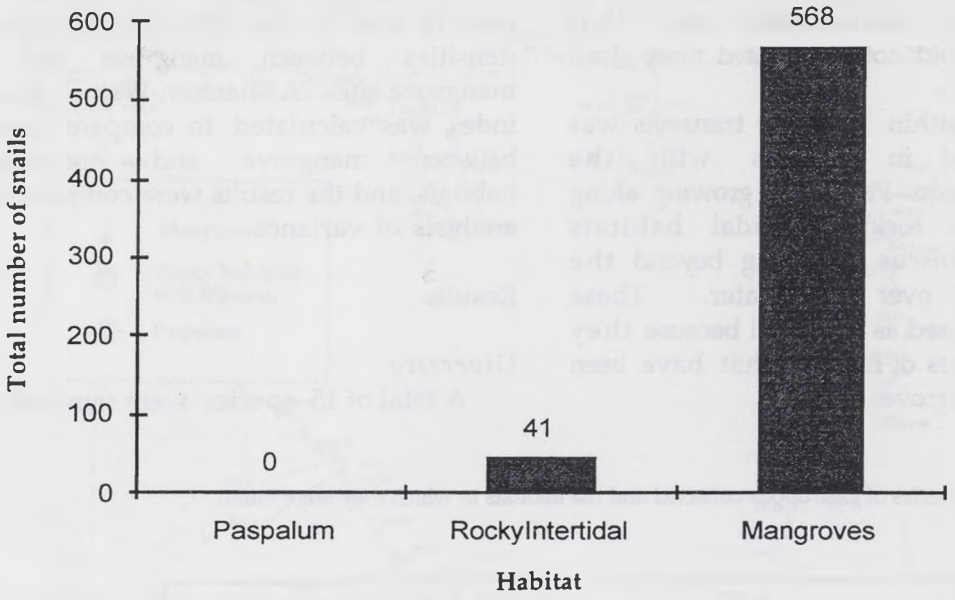

Figure 2. Absolute population size of *L intermedia*, based on an equal number of 10 m transects in each habitat.

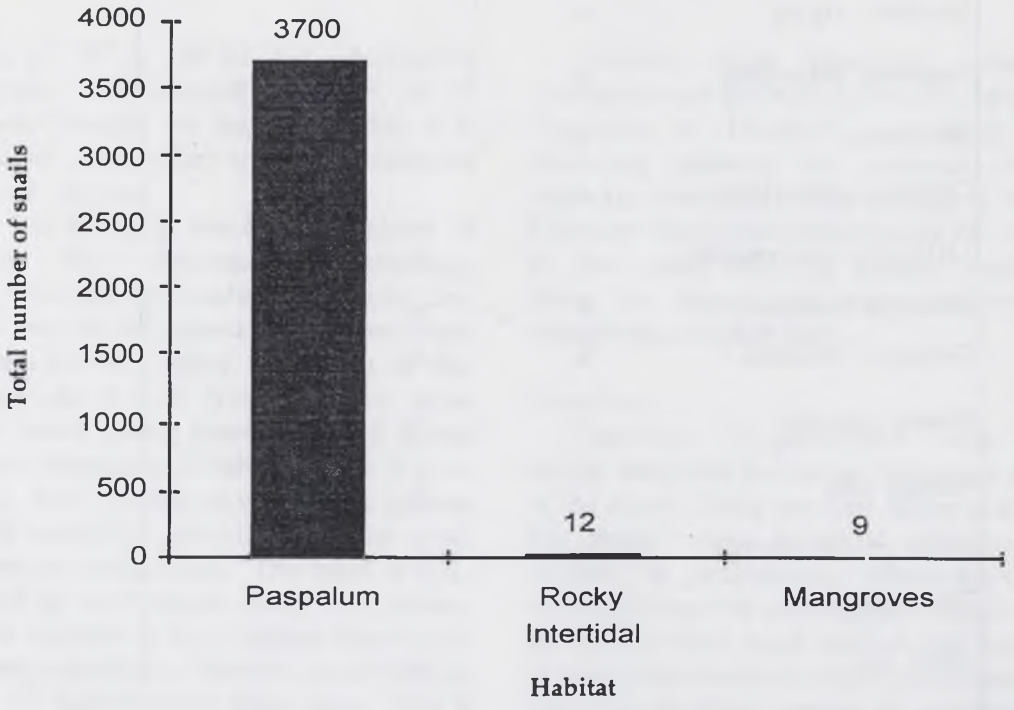

Figure 3. Absolute population size of *Clithon chlorostoma*, based on an equal number of transects in each habitat.

three habitats (mangrove, rocky intertidal, and *Paspalum*) (Table 1). Analysis of variance showed that the species diversity between the three habitat types was significantly different ($F_{[3,171]} = 10.836$, $P < 0.001$). Nine gastropod species were found in mangroves, five of which were exclusive to the mangroves. Nine species were found in the rocky intertidal habitat, with six species found exclusively in this habitat. Three species of snails were found in both the mangroves and rocky intertidal habitats, and one gastropod species was found in all three habitat types. Only one gastropod species, *Clithon chlorostoma*, was found in *Paspalum* (Table 1).

Abundance

There was a significant difference ($t = 2.048$, $df = 28$, $P < 0.005$) in abundance of the gastropod *Littoraria intermedia*, which was almost 14 times more abundant in the mangroves than in the rocky intertidal habitat, and which does not occur at all in *Paspalum* (Figure 2). The other two species that occurred in both the mangroves and rocky intertidal, *Littorina coccinea* and *Erosaria obvelata*, were not significantly abundant to allow for statistical comparison.

Clithon chlorostoma, was the only gastropod species to occur in all three habitat types, but had the highest population density in *Paspalum* (Figure 3). It was found in significantly lower numbers in the mangroves than in *Paspalum* ($t = 1.796$, $df = 11$, $P < .05$).

Discussion

Diversity

Rhizophora stylosa has severely altered the habitats that it has invaded. This tree provides a large amount of introduced surface area, as well as a substratum that is different from both *Paspalum* habitats and rocky intertidal habitats. In areas that are dominated by *Paspalum*, gastropods are not diverse due to limitation of substrate. For example, the sandy sediment and small size of the blade and the base of the tuft of grass are not large enough or strong enough to support gastropods much larger than a few millimeters in length. Hence the only gastropod found in *Paspalum* was *Clithon chlorostoma*, which is very small. Furthermore, these substrates would not support a gastropod such as a littorinid, whose form of locomotion is adapted to movement on a firm substratum like that of mangrove prop roots (Miller 1974).

The change from a somewhat spherical-shaped basalt rock habitat to the intertwined prop roots of mangroves is also quite dramatic. First of all, movement along the surface of mangroves is limited to a vertical, rather than multidirectional migration. The shape of the surface also discriminates against some gastropod species, like *Nerita plicata*, which seem to prefer a rock surface with grooves and indentations that they can embed themselves in (personal observation).

The question of whether or not the gastropod species found in the mangroves are introduced is difficult to answer due to the lack of sufficient information. Of all the species, *Neritina zigzag* is not native to Moorea, but does occur in mangroves in its natural habitat (S Boyer, pers. comm.). It is unknown however, whether or not it was introduced with *R. stylosa*. It was found in very low numbers which suggests that it may not have been introduced with the mangroves. It is yet undetertimed whether *Nerita sp.* was introduced to Moorea. All other gastropods recorded from the mangroves have been identified as occurring in French Polynesia, but it is not stated if the occurrence is a result of an introduction (Salvat and Rives 1983).

Abundance

Two species' abundances have been affected significantly by the introduction of the mangroves: *C. chlorostoma*, which has suffered a decrease in population, and *Littoraria intermedia*, which has shown an increase in population size. *C. chlorostoma* is found along the shoreline in an area that experiences very shallow inundation at high tide, and even at this time is not continually covered by water. *R. stylosa* grows out into the water and eliminates the *Paspalum* in the immediate vicinity. This effectively forms a barrier to habitat suitable for *C. chlorostoma*.

L. intermedia, on the other hand, has become very well established in the presence

of *Rhizophora stylosa*. *Littoraria intermedia* has a widespread distribution throughout the Indo-Pacific region, including Moorea (Reid 1986). It has been extensively studied in mangrove forests, where it is often the most abundant gastropod species. Furthermore, it prefers forests dominated by *Rhizophora* (Reid 1985). Thus it is not surprising that it has proliferated so successfully in the mangroves on Moorea. Although this success indicates that *L. intermedia* may have been introduced with *R. stylosa*, there are records of the presence of this species in the Society Islands prior to the introduction of *R. stylosa* (Reid 1986).

The fact that five gastropod species were found only in mangroves suggests that the introduction of *R. stylosa* has created the opportunity for the expansion of those species' natural distribution on Moorea. For example, *Puperita reticulata*, which was not found in rocky intertidal habitats with *Hibiscus*, has been observed in large numbers on coral conglomerate platforms (personal observation), the diversity of which was not the focus of this study. Furthermore, the data indicate that an ecological expansion as well as an expansion of local distribution has occurred with respect to *L. intermedia*.

In conclusion, the presence of *R. stylosa* has changed the habitats that it has invaded, which has had a dramatic effect on microhabitats as well. Microhabitat can have a strong influence on the spatial distribution of organisms (Crowe 1996). As a result, the compositions of organisms are likely to change, making the habitat inhospitable to organisms that would have lived in that environment prior to the introduction, while at the same time creating a new environment to be colonized by other species. Although the analysis of microhabitat preference was not within the scope of this paper, it would be interesting to characterize the original microhabitats and how they have been affected as a result of the mangrove introduction.

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Burrowing Ecology and Behavior of the Land Crab *Cardisoma carnifex* in Moorea, French Polynesia

Sarah Ann Bickel
Bioresource Science
Department of Environmental Science, Policy and Management
University of California at Berkeley, 94720

ABSTRACT. Investigations of burrowing density and the burrow-entrance-clearing behavior of the land crab *Cardisoma carnifex* were conducted on the island of Moorea, French Polynesia. A strong correlation (r^2=.729) was found between crab carapace width and burrow diameter measured at the narrow-point cross section of the entrance; this correlation enabled using burrow diameter as an indication of crab size for density studies. Burrow density per unit area is strongly inversely correlated with average burrow size, using Spearman's rank correlation test and a significance level of 1 per cent. Burrow density per unit area was not correlated with distance from water. Three separate tests were conducted to investigate a striking behavior of this species in which it clears the ground surrounding its burrow entrances of debris; the crabs consume any edible material surrounding their burrows and they also move most inedible material away from the burrow entrances.

Keywords: *Cardisoma carnifex*, land crabs, burrowing ecology, burrowing behavior

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Introduction

Land crabs, members of the crustacean order Decapoda, are a fascinating group of organisms that have adapted to varying degrees of life on land. Because they occupy the top of the energy pyramid in many tropical islands where vertebrates are absent, they offer unique opportunities for ecological research (Burggren and McMahon 1988). These crabs are also studied by physiologists for their complex adaptations for gas exchange, and by biologists for whom these crabs present a remarkable example of the evolutionary transition from water to land.

Burrowing crabs play important roles in the systems they inhabit. Through their burrowing behavior, these crabs contribute to the turnover and aeration of soil, leaf litter breakdown, and the rate of energy flow (Alexander 1979). In addition, land crabs are often a significant human food source on many tropical islands (Burggren and McMahon 1988).

On the island of Moorea, *Cardisoma carnifex* is a common burrowing land crab that is observed very frequently in communities of burrows located near the shore, roadside, or further inland in coconut groves (Battersby and Denhoy 1992). Mangroves, which were introduced in 1937 and have since established themselves on the island (Stoddart, pers. com.; 1997), may be providing additional food and habitat resources for the species. Very few studies have been conducted of this species on Moorea.

In fact, little has been studied about the population and burrowing ecology of this species worldwide. Virtually nothing is published about the behavior in which these crabs clear debris from the area immediately surrounding their burrow entrances. This study examines several aspects of burrowing behavior and ecology in *C. carnifex*. First, the hypothesis that burrow size is correlated with crab size is tested. Next, factors influencing the density of *C. carnifex* burrows are investigated; specifically, the study tests the possibilities that burrow density is correlated with crab size and distance of the burrows from the shore. Finally, the behavior in which the crabs clear debris from the area surrounding their burrows is addressed by the investigation of what types of materials the crabs preferentially clear.

Materials and Methods

Study Organism

Cardisoma carnifex (Herbst, 1794), in the family Gecarcinidae, is a large terrestrial crab

common in the tropical Indo-West Pacific from East Africa to the Pacific islands (Hartnoll 1988). In the Society Islands, these crabs are known as tupas and are enjoyed as food by the locals. Individual tupas construct and live in burrows in a variety of habitats, including coastal mudflats, coconut groves, and the terrestrial fringes of mangroves (Macintosh 1984). Burrows are always located near fresh or saline water or wet mud and generally reach the water table, often ending in an enlarged chamber (Hogue and Bright 1971). The crab prefers to construct burrows in a hard, dry mud substratum under plant cover; burrow entrances collapse approximately every three weeks and are rebuilt while the deeper parts of the burrow, which probably do not frequently collapse, remain inhabited (Micheli, Gherardi and Vannini 1991). *C. carnifex* scavenges on a variety of organic materials, including fresh or fallen leaves, other plant parts, detritus, and mud (Grubb 1971; Alexander 1979). *C. carnifex* is also believed to regulate the distribution and abundance of plants through fruit and seed dispersal of certain plant species and through consumption of seeds and seedlings of other species (Lee 1988).

Study Site

All research was conducted on the island of Moorea, in the Society Archipelago of French Polynesia, during October and November of 1997. The primary sites used for determining the relationship between burrow size and crab size were located on or near the property of the University of California's Gump Biological Research Station. The site used for burrow clearing experiments was located on Gump Station property adjacent to the bay and just south of the dock, while multiple sites representative of *Cardisoma carnifex* habitat were used for density sampling (Figure 1).

Crab Size versus Burrow Size

Crabs of the species *C. carnifex* were caught at night using nets as they scampered toward their burrows. It was necessary to know which burrow each crab lived in, so when a crab was found out of its burrow, the net was placed over

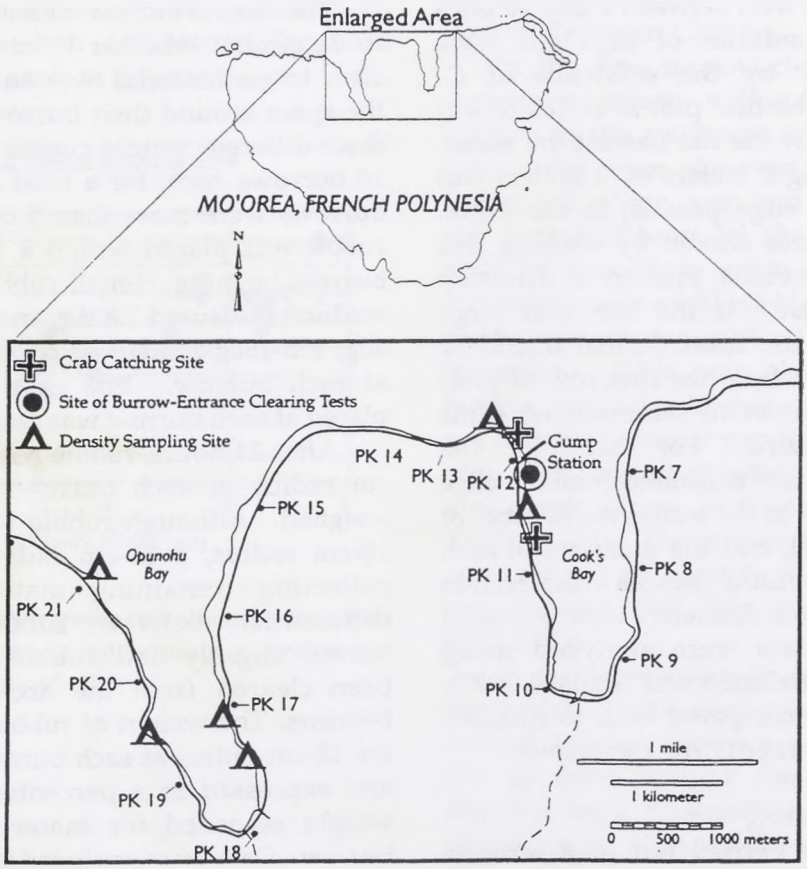

Figure 1. Map of Moorea, French Polynesia showing the location of study sites on the island.

the burrow that appeared to belong to that crab. If the correct burrow was netted, the crab would run into the net as it attempted to enter its burrow. Crab size was expressed as carapace width and was measured at the widest point of the carapace. Crabs were marked to prevent recaptures. Burrow diameter was measured twice, once over the widest cross section and again over the narrowest cross section of the burrow. These measurements were taken at the point where the burrow opening constricted the most, up to a few inches deep, since this is the point which would limit crab size. Preliminary measurements showed that carapace width correlated best with burrow diameter measured at the narrowest point, so narrow-point diameter measurements were used to establish the correlation. Data were analyzed using regression.

Crab Size versus Burrow Density

The relationship between burrow size and burrow density was investigated by measuring and comparing these two traits within $4m^2$ plots. Burrow size was used as an indication of crab size because it was much easier to measure than crab size for multiple burrows. Sampling was conducted at 6 sites, with between 2 and 10 plots per site. The boundaries of each site were delineated visually by the existence of *C. carnifex* burrows. The first plot at each site was located at the edge of the site nearest the water. A quadrat measuring 2 meters by 2 meters was then laid, with the edge parallel to the shore. Subsequent plots were chosen by walking five paces from the previous plot in a direction parallel to the coast. If the site was large enough, plots were also taken further inland by walking five paces in from the first row of plots and doing another row in the same manner as the first, as space allowed. For each plot, the distance to the water was measured from the edge of the quadrat closest to the water, the number of burrows was counted, and the diameter of each burrow at the narrowest accessible cross section was measured. Burrow diameters were averaged over each plot. Data were analyzed using Spearman's rank correlation test (Pollard 1977); burrow density was compared both to distance from water and to average burrow diameter.

Burrow-Entrance Clearing

Three tests were carried out to determine what types of materials *C. carnifex* preferentially clears from the ground just outside of its burrow entrance. For all experiments, the test area surrounding each burrow was first cleared of organic and inorganic materials down to the mineral soil, with a radius of approximately 30 cm. In the first tests, edible and inedible materials were placed around different burrows. Edible material consisted of *Hibiscus tilaceus* leaves, and inedible material consisted of marked coral rubble. Twenty five grams of whole *Hibiscus* leaves, equaling between 4 and 9 leaves, were placed around each of 15 burrows, while 270 grams of marked coral rubble of different sizes was placed around each of 15 different burrows. All burrows were 5 cm wide or greater. The volume of material placed at each burrow was approximately the same for both treatments and measured about 500 mL. Leaves and rubble were placed within a 15-cm radius of the burrow opening. Leaves were weighted down with minimal amounts of dirt and small pebbles to prevent them from blowing away. After 17 hours, all remaining material with the 15-cm radius was removed and weighed. Data were expressed as percentage of material left around the burrows and were analyzed using a Students' t-test.

The second burrow-clearing test was designed to determine whether *C. carnifex* preferentially clear larger material over smaller material from the space around their burrows. Coral rubble of three different weight classes was placed around 10 burrows each, for a total of 30 burrows. All burrows were more than 5 cm in diameter, and rubble was placed within a 10-cm radius of the burrow opening. Small rubble measured 1-10g, medium measured 10-25g, and large measured 25-40g; 155-160g of marked coral rubble was placed at each burrow. The exact mass of material placed at each burrow was recorded.

After 24 hours, rubble remaining within a 15-cm radius of each burrow was collected and weighed. Although rubble was placed within a 10-cm radius, a 15-cm radius was chosen for collecting remaining material in order to differentiate between rubble that had been moved slightly and rubble that had actually been cleared from the area surrounding the burrows. The weight of rubble remaining within the 15-cm radius at each burrow was determined and expressed as a percentage using the exact weight recorded for material placed at each burrow. Data were analyzed using ANOVA.

The third burrow-clearing experiment tested whether crabs clear different types of plant

material preferentially over other types. Material was collected from three genera in three different families: 1. leaves of the tree *Terminalia catappa* (Combretaceae), 2. leaflets from the fronds of the coconut *Cocos nucifera* (Arecaceae), and 3. stems and leaves of the ground-covering herb *Wollastonia trilobata* (Asteraceae). These genera were chosen because they are very common components of the coastal strand habitat of *C. carnifex*. Material was placed around the burrows within a 10-cm radius of the hole and was weighted down with a minimal amount of dirt and small rocks. Each treatment was comprised of 10 burrows; each burrow in the treatment received 30 g of plant material from the same genus. After 24 hours, remaining material within 15 cm was to be collected and weighed.

Results

Crab Size versus Burrow Size

Burrow size, measured as the narrow-point diameter, correlated strongly (r^2=.729) with crab carapace width (Figure 2). While collecting data to substantiate this relationship, I often observed that individual crabs became confused and disoriented when threatened by field biologists trying to capture them with nets.

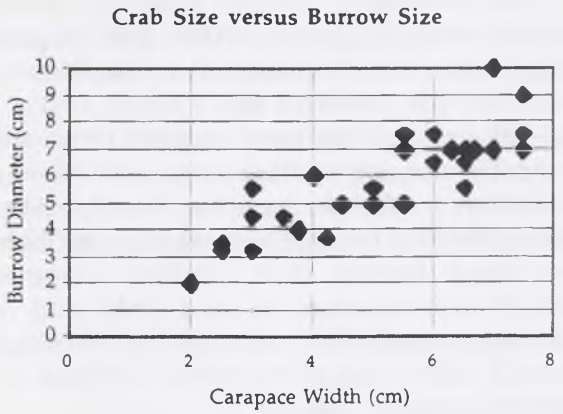

Figure 2. The relationship between crab size, measured at the widest point on the carapace, and burrow size, measured as the narrow-point diameter (r^2=.729).

Crab Size versus Burrow Density

Using Spearman's ranking correlation test, burrow size was correlated with burrow density per unit area at the 1 per cent level of significance (r_s=.950 with n=30) (Figure 3). No relationship was found between burrow density and distance from water.

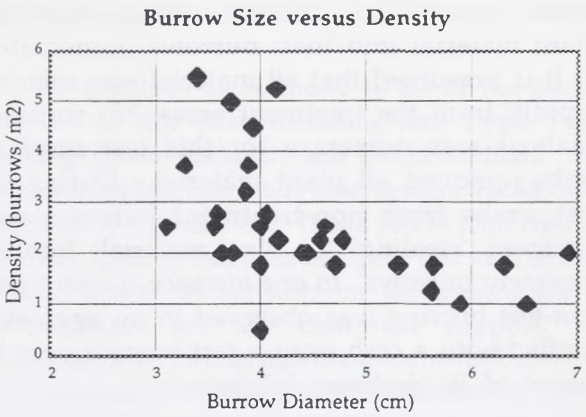

Figure 3. Relationship between burrow size, expressed as the narrow-point diameter, and burrow density. Spearman's rank correlation coefficient r_s=.950. The 1 per cent critical region is r_s>.425, so result is significant at the 1 per cent level.

Burrow-Entrance Clearing

In the first burrow-clearing test, no plant material remained within the test area of any burrow in the treatment after 17 hours. Many tupa crabs were observed eating the *Hibiscus* leaves and taking them into their burrows within the first half-hour of the experiment, so all material was likely eaten within a few hours. However, some coral rubble did remain at all of the burrows in the rubble treatment. In several instances, rubble was also found within the burrow entrance. In these cases, the rubble was not collected, since it was impossible to collect all of it. The amount of rubble remaining in the test area ranged from 14.4% to 87% and averaged 43.9%, while the amount of plant material remaining at all burrows was 0%. A student's t-test showed that this result was significant (P=3.04E-6).

In the second test, in which coral rubble of three size classes was placed in the test area around different burrows, some rubble remained for all three weight classes (see appendix). ANOVA found no significant result in the amount remaining for each weight class. Marked rubble was observed inside several treatment burrows after the duration of the test. This rubble may

have fallen in or may have been taken in by the crabs dwelling in those burrows for some reason. It appeared in one burrow that the rubble was placed in such a way as to make the opening smaller.

In the third test, in which different types of plant material were placed in the treatment areas, no material remained after 18 hours. Again, tupas were observed eating and taking plant material into their burrows immediately, so it is presumed that all material was removed rapidly from the treatment areas. No statistical analysis was necessary for this test since the crabs removed all plant material. During this test, crabs from non-treatment burrows were observed "stealing" the plant materials from the treatment burrows. In one instance, a crab from a non-test burrow was observed in an aggressive conflict with a crab from a test burrow over the leaves of *Wollastonia trilobata*.

Discussion

Burrow Size versus Crab Size

Individual crabs of the species *C. carnifex* live in burrows they excavate themselves, so the burrows are built to the individual's size specifications. Burrows that were too large would be a wasteful expenditure of time and energy (Dunham and Gilchrist 1988) and may also make a small crab more vulnerable to takeover by larger individuals. A crab could not live in a burrow that was too small. Furthermore, Battersby and Denhoy (1992) found that individuals of *C. carnifex* demonstrate burrow fidelity; that is, each individual burrow belongs to a single crab, and under normal circumstances crabs do not enter other burrows.

However, this relationship may not be so straightforward in all circumstances: in this study I observed that under duress, confused or threatened crabs often attempted to escape into the closest burrow they could find, even if that burrow was too small, too large, or was already occupied. In addition, takeover of a smaller crab's burrow by a larger member of the species has been observed in some crabs such as the western Atlantic species *Ocypode quadrata*, which would then enlarge the burrow (Wolcott 1988), and could also happen with *C. carnifex*. Burrows vacated by a dead or reproducing crab could be taken over by a crab of a different size. Because this study investigated the relationship between crab size and burrow density by using burrow size as an indication of crab size, a correlation between crab size and burrow size had to be established conclusively. Now documented, this correlation may also be helpful for future research on *C. carnifex* ecology.

Crab Size versus Burrow Density

Large organisms need more food and space than smaller organisms; hence, smaller organisms are in general more abundant per unit area than larger organisms (Smith 1974). This study found a strong correlation between burrow density and average burrow size. This suggests that competition for resources such as food and space may play a major role in structuring *C. carnifex* communities. For example, during this study multiple instances of direct competition among tupas were observed in which individuals stole leaves of the species *Hibisicus tileaceus* from one another, often in aggressive interactions.

The correlation found between average burrow size and density of burrows per unit area does not provide a complete answer for how density is determined in tupa communities. There are probably many more contributing factors. Battersby and Denhoy in 1992, found an inverse correlation between burrow density and depth of the water table (r^2=.57). Other factors may include territoriality, canopy cover, and quality of substrate for burrow excavation.

For example, *C. carnifex* generally prefers to burrow under the cover of trees and, in general, fewer burrows are located in the open than under trees (Micheli, Gherardi and Vannini 1991). This may be because the trees provide food, shelter from the sun, protection from predators, or a combination of these benefits. Further research into *C. carnifex* ecology may shed more light on the many factors that regulate community density and structure in tupa crabs and other burrowing organisms.

Burrow-Entrance Clearing

This study shows that tupas will likely consume anything edible immediately surrounding their burrows, thus clearing the area of plant materials. However, the results also show that this is not the only reason that an area is cleared of debris around the burrow entrances of *C. carnifex*. The crabs quickly and often thoroughly cleared the surrounding ground of coral rubble, a common and inedible material comparable to small rocks. If given more time, the crabs may have rid the entrance radii of all

rubble placed there for these tests.

Strong competition for food leads the closely-related species *Cardisoma guanhumi* to clear the vegetation around its burrows and to immediately seize any freshly fallen leaves or berries, often dragging them to their burrows to feed (Herreid and Full 1988). This is consistent with observations of C. *carnifex* on Moorea. However, this is the first study conducted on this aspect of *C. carnifex* behavior, and more conclusive results may follow from future studies.

Conclusion

Despite many possible confounding factors, there is a strong correlation between crab size and burrow diameter. In addition, a strong inverse correlation was found between crab size and burrow density. Other factors such as food availability and habitat quality may also play an important role in determining population densities of the crab and may be studied in the future.

The ground-clearing behavior of *C. carnifex* behavior remains largely unstudied. Future studies may examine whether this behavior is competitive, territorial, or if it serves another purpose such as allowing faster access to burrows or easier burrow identification. Observations made during this study also raise the question of what types of materials, if any, tupa crabs harbor in their burrows, and what purposes these materials may serve.

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Shell Preference of *Calcinus* sp. (Crustacea, Decapoda) Based on Aperture Geometry

Emily Hatley
Department of Integrative Biology
University of California, Berkeley
emilyhat@uclink3.berkeley.edu

ABSTRACT. Forty-one specimens of *Calcinus* sp were collected in the mangroves near Haapiti, pk 24, on Moorea, French Polynesia, and introduced to containers with shells of five aperture shapes to determine a ranking of preference for each type. The shells' aperture lengths were kept constant while the widths were increased. My hypothesis was that the crabs would prefer the widest aperture. From thinnest to widest the gastropod families tested were Cypraeidae (cowry), Conidae (cone), Strombidae (strombus), [Muricidae, Cymatiidae, and Colubrariidae, which had similar aperture shapes and made up one group] and Neritidae (neritid). I found that the group with three families, which I called the oval-shaped aperture group was the most popular choice for hermit crabs. Strombus was second, neritids were third, cones were fourth and cowries were the last choice. Further sampling was done in the mangroves to see if the crabs' choices were limited by the availability of shell types.

key words: hermit crabs, French Polynesia, *Calcinus*, aperture, shell selection, Crustacea, Decapoda

Introduction

Hermit crabs are soft-bodied crustaceans that inhabit empty gastropod shells for protection from predation, extremes of salinity and desiccation (Elwood & Neil 1992) Many studies have shown that shells are limiting resources for most hermit crab species (Gherardi et al. 1994; Provenzano 1960; Bertness 1980). The poor availability of empty shells affects hermit crab growth, survival, and reproduction rates (Hazlett 1981; Gherardi et al. 1994, Imazu & Asakura 1994). Crabs are constantly searching for better homes because even if they live in optimal shells, growth forces them to search for more appropriate ones (Elwood 1995).

Hermit crabs' selection processes for shells have been studied in great detail. To find shells, crabs use their sense of touch (Goldsmith 1918) and chemical detection of dying crabs and gastropods (McLean 1974; Hazlett & Herrnkind 1980; Rittschof et al. 1992). Weight, volume, type, and quality of shell as well as center of gravity and angle of shell axis are important factors in shell selection (Orians & King 1964; Gherardi et al. 1994; Conover 1978; Scully 1979). Different species of hermit crabs in different habitats have different preferences of shells. Some populations likely choose heavy shells with thin apertures for protection from predation (Imazu & Asakura 1994; Gherardi et al. 1994) and others inhabit lighter shells with wider apertures for easier mobility (Scully 1979). Male and female size differences play a role as well in shell selection differences in some species (Imazu & Asakura 1994; Gherardi et al. 1994) yet sex differences were not a significant factor for shell selection in others (Brown et al. 1993). Shell preferences vary for different crabs based on different conditions of habitat (Scully 1979; Orians & King, 1964). Also learning behaviors effect shell selection (Hazlett 1995). Adult crabs spend much less time and energy inspecting and trying out new shells than younger crabs due to their ability to learn (Goldsmith 1918). Possibly preferences found in a particular age group of a species of hermit crabs in one habitat may differ from those in a different age group of the same species.

Although a lot of research has been conducted on hermit crabs, the shape of aperture as an important factor in shell selection has not been given a lot of attention. This experiment involved studying the importance of shell aperture geometry to shell selection in *Calcinus* sp. The hypothesis was that *Calcinus* sp. would prefer shells with the widest apertures with respect to the length, which was kept constant between different types of shells. Initial observation indicated that shells inhabited by crabs were of poor quality, (i.e. broken, with holes, and covered in

algae), and there was a lack of empty gastropod shells in the mangrove area in which the crabs were collected, thus I hypothesized that the crabs are limited by shell resources. This lack of shell supply may limit the crabs' shell aperture preferences in their natural habitat.

Materials and Methods

Empty gastropod shells were found in the Gump station and Gump house driveways, which are located near PK 12 in Cook's bay in Moorea, French Polynesia (Figure 1). Shells were also found at Temae beach, located off the road near PK 0 at the north-east corner of Moorea. Live neritids were collected at the Temae coral conglomerate at the north-eastern point of Moorea near PK 2. The shells were cleared of neritids and used for introduction for hermit crabs. Shells were collected from the following families for introduction to hermit crabs: Neritidae, Conidae, Cypraeidae, Strombidae, Cymatiidae, Muricidae, and Colubrariidae. The last three families stated have similar aperture shape and are grouped together as a choice for hermit crab inhabitancy.

Forty-one sets of five empty shells were placed in separate containers. All shells were unbroken without holes so as to control aperture shape within each of the five groups. The aperture length of the five shells was kept as constant as possible, whereas width was varied (Table 1). The first shell type with the thinnest aperture was the cowry. The second type of shell introduced was the cone shell. The cone shell's width is a little wider than the cowry. The third type of shell, the strombus, was wider than cowry and cone shells. The shells from the families: muricidiforms, colubrariidiforms, and cymatiidiforms have an oval-shape aperture and will be referred to as the oval-shape aperture group throughout this paper. Lastly the neritid has the widest aperture with respect the length; its aperture is almost round.

With a sufficient number of empty shells, hermit crabs were collected at the mangroves between pk35 and pk24 near Haapiti on the western side of Moorea on November 1, 1997 (Figure 2). They were found mostly on rocks, *Paspalum*, and mangrove tree roots just above the water level. Some crabs were also found under no more than 30 cm of water on the sea floor. They were kept in a tank with running water and fed dead gastropods and bananas until they were introduced to empty shells on November 3, 1997.

Table 1. Mean widths of aperture for each of the five shell groups.

Shell group	Mean width
Cowry	.121 cm
Cone	.174 cm
Strombus	.370 cm
Oval-shaped	.450 cm
Neritid	.520cm

Figure 1. Sites of shell collection in Moorea, French Polynesia a) Gump Station Driveway, b) Temae Coral Conglomerate, c) Temae Beach

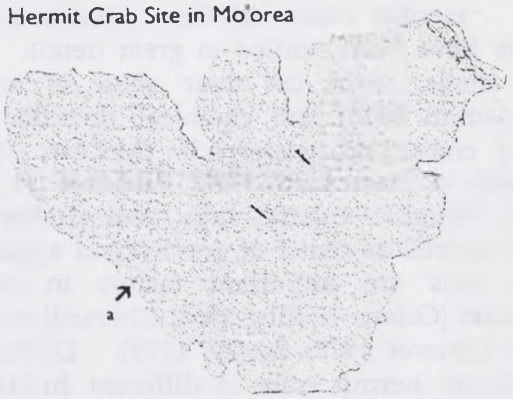


Figure 2. Site of hermit crab sampling and collection in Moorea, French Polynesia a)Crabs Sampled and Collected in Mangroves

Before the crabs were introduced to the five empty shells, each crab was removed from its original shell by placing its shell apex in hot water. The naked crab was then introduced to a container with five shells. The crab was matched to the shells by comparing the length of aperture of the shell in which it was found to the aperture lengths of the shells in each container. Aperture lengths were kept constant.

Many of the crabs inhabited a shell almost immediately, but they were given approximately twenty-four hours from when they were introduced to choose their first shell preference. Each day, after approximately twenty-four hours, for five days, an observation was made as to the preference of shell chosen by the crab. Then the crab was removed from its new shell and introduced back into the container with the remaining choices. The shell it chose was also removed. Thus, each day the crabs had one fewer shell from which to choose until the fifth day when they had only one shell to select.

The shell preferences for each of the crabs were ranked and rank agreement between samples was tested using the Kendall Coefficient of Concordance, W (Siegel and Castellan 1988). The significance of W was tested using Chi Square.

After finding the crabs' preferred shells in the lab, the mangroves were sampled between PK 35 and PK 24, (in the same area where the *Calcinus sp* were collected), for all empty shells and shells inhabited by crabs to see if the crabs' preferences found in the lab are limited in the field. This was done by laying six 30 m transects along the water line where crabs are found. Shells were counted within .5 m on either side of the transect tape along the 30 m and the types of shells that were found were recorded. The sampling took place on November 20, 1997. I also noted the type of shells in which the hermit crabs that were collected November 1, 1997 were found.

To find the availability in the mangroves of the five groups of shells used in the lab, a percentage of the total sampled on November 20, 1997 and a percentage of the total collected shells with hermit crabs on November 1, 1997 was calculated for each choice.

Results

Of the forty-one crabs observed in the lab, twenty-three selected all five shells over a period of five days. Ten of the crabs made three selections, but did not choose either of the last two shells. Eight of the crabs died before the five days were finished. Four crabs died after making their first choice, three crabs died after their second choice and one crab died after its third choice. Table 2 shows the number of crabs that chose each type of shell for their first preference, second preference, etc. It also shows the number of each type of shell that was not chosen by crabs that remained alive. Lastly it shows the number of shells that were not chosen due to death of hermit crabs. Figure 3 (a-g) shows bar graph representation of this data.

Using the preferences of twenty-three crabs that made five shell selections, ranking was charted using number one for the first choice, number two for the second choice and so on. Then I found the sum of the ranks, Ri, and the average of the ranks, Ri/k (k= number of crabs) for each type of shell. The average ranks show that the oval-shaped aperture group had the lowest rank, 1.96, which was very close to the strombus group which had an average rank of 2.09. These were the top choices. Neritid aperture had a rank of 2.96. The cone shells' average rank was 3.78 and cowries were the least preferred with an average rank of 4.22.

The Kendall coefficient of concordance, W, showing concordance between rankings of each sample was found to be .40 and Chi Squared is 36.8.

Table 3 shows percentages of hermit crab shells sampled on November 1 and November 20 for each of the five types of shells introduced to the crabs. Note that the oval aperture group makes up the highest percentage of the five studied for both samplings. All shells sampled at the mangroves were inhabited by hermit crabs.

Table 2. The number of crabs that chose each type of shell are shown for each rank. Also the number of crabs that did not choose each shell type are listed for the crabs that lived and for the crabs that died during the experiment.

rank	oval-shape aperture	cone	strombus	cowry	neritid
first choice	20	3	15	0	3
second choice	8	1	14	3	11
third choice	5	8	5	3	13
fourth choice	3	10	2	3	5
last choice	0	6	2	14	1
shell not chosen and crab alive	1	6	0	10	3
shell not chosen due to crab death	4	7	3	8	5

Table 3. Percentages of the five groups of shells sampled at the mangroves between pk 24 and pk 35 on Moorea, French Polynesia on two different days.

November 1		November 20	
Oval aperture group	30%	Oval aperture group	19.7%
Strombus	17.5%	Strombus	3.9%
Neritid	17.5%	Neritid	13.1%
Cone	7.5%	Cone	3.9%
Cowry	15%	Cowry	6.6%
other	12.5%	other	52.8%

Figure 3. a) The number of crabs choosing each type of shell as their first choice

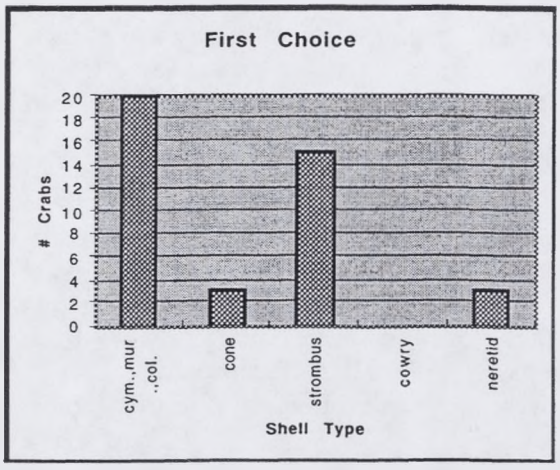


Figure 3. b) The number of crabs choosing each type of shell as their second choice

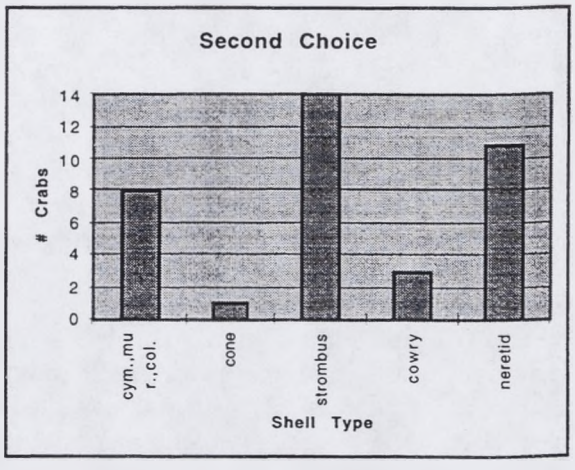


Figure 3. c) The number of crabs choosing each type of shell as their third choice

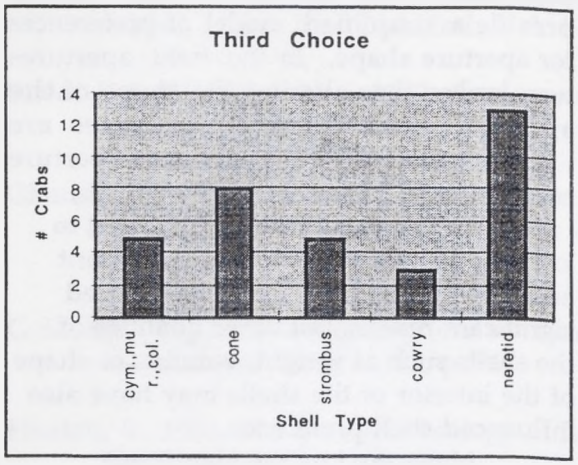


Figure 3. d) The number of crabs choosing each type of shell as their second choice

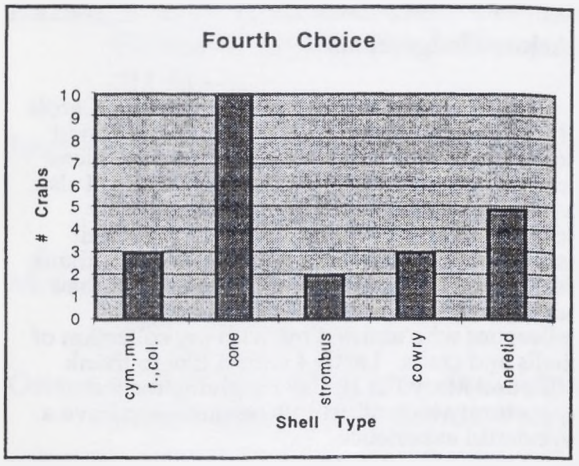


Figure 3. e) The number of crabs choosing each type of shell as their fifth and final choice

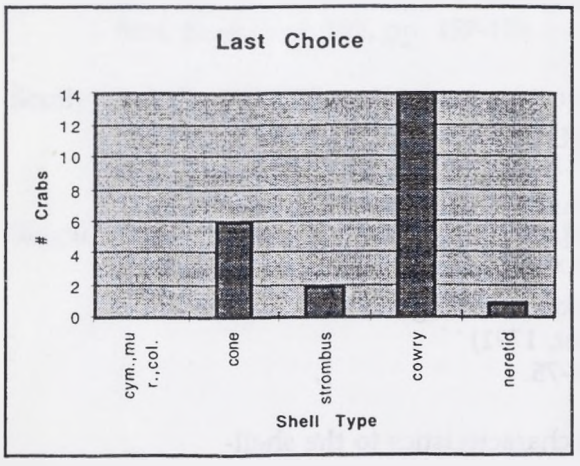


Figure 3. f) The number of each type of shell not chosen by crabs which did not die

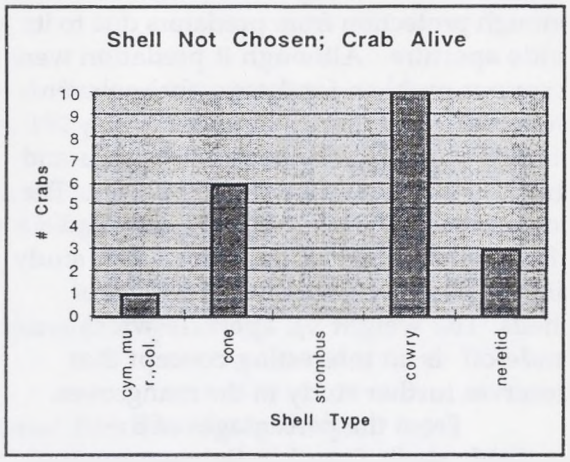
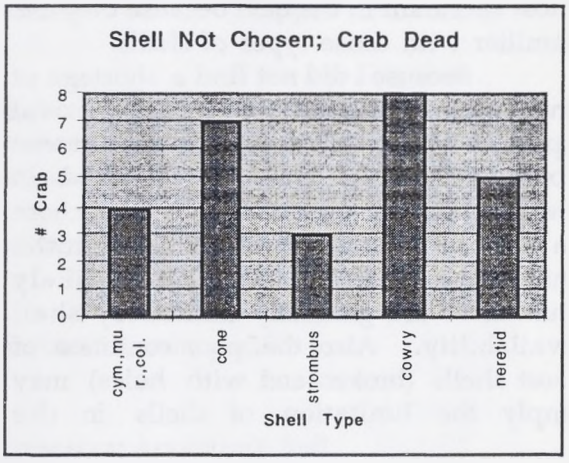


Figure 3. g) The number shells not chosen because the crabs died before the end of the experiment



Discussion

The data for all of the forty-one crabs used in this experiment contribute to the determination of what shape of shell aperture of the five types tested are most preferred. Even though eight of the crabs died, their first few choices help demonstrate a preference for the oval shaped aperture group, as does the rest of the data seen in the other thirty-three crabs. My hypothesis was that the greatest width would be picked most often, meaning the neritid would be most popular, but this did not prove to be the case. I thought cones and cowries would be last choices and this proved to be correct.

The neritid was not a primary choice because it may not have provided enough protection from predators due to its wide aperture. Although if predation were a serious problem for these crabs, an even more narrow aperture than the oval-shaped aperture may benefit the crabs and thus a cowry would be the best choice. The cowries and cones may be too heavy and affect the mobility of the crabs. This study did not measure predation or weight of shells. The weight vs. aperture width trade-off is an interesting concept that deserves further study in the mangroves.

From the percentages of the available shells found in the mangroves, I noted that both trials showed the oval-shaped aperture group was most abundant of the five shells tested. Also, cone shells and cowries were rarely found. The crabs may choose shells in the lab which were most abundant in the field because they are familiar with those types of shells.

Because I did not find a shortage of the most preferred shells, the oval aperture group, in the mangroves I cannot conclude that the crabs were limited in their habitat by the shells that they chose in the lab. Because all shells found in the mangroves. were inhabited, it is likely that crabs are generally limited by shell availability. Also the poor condition of most shells (broken and with holes) may imply the limitation of shells in the mangroves for this individual species. Because all the shells introduced in this experiment were unbroken, these results provide a simplified model of preferences for aperture shape. In the field apertures were broken thus altering the shape of the aperture. Since aperture preferences are likely, further studies might test aperture preferences of crabs using broken shells.

In this experiment I only tried to keep the length of the aperture constant and vary the width. This data showed significant results, but other qualities of the shells such as weight, volume, or shape of the interior of the shells may have also influenced shell preference.

None the less the significant ranking of five types of shell aperture geometry in Moorea, French Polynesia opens many doors for further study on hermit crabs in the mangroves.

Acknowledgements

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Fauna associated with floating vegetation rafts in the lagoon of Paopao Bay, Moorea, French Polynesia

Rachel Shapland
Department of Integrative Biology
University of California, Berkeley 94720
shap@uclink4.berkeley.edu

ABSTRACT. Floating vegetation rafts found in the lagoon of Moorea, French Polynesia consist of two or more pieces of brown algae that has been torn from the algal ridge due to wave action. These rafts create a unique mobile habitat for invertebrates. Fauna in vegetation rafts may differ from fauna of the same species of algae at the algal ridge. Vegetation rafts and attached algae were sampled to test for differences in fauna. Significant differences were found in three species of invertebrate, and many more were observed, showing that differences between floating and attached algal habitats do exist.

keywods: vegetation raft, *Turbinaria ornata, Sargassum sociale*, microinvertebrates, nudibranch, copepod, ostracod.

Introduction

Communities of unattached algae are a common phenomenon world wide (Norton and Mathieson 1983). Drifting communities of floating algae are an intricate part of ocean ecosystems, providing habitats for many fish and invertebrates (Kilar and Norris 1988). Vegetation rafts consist mostly of unattached macroalgae and can vary considerably in what they are made of, from multiple species of macroalgae to debris from land plants and human pollutants.

Vegetation rafts can be viewed as islands because they are individual and isolated communities of various sizes surrounded by ocean, making them a possible test of MacArthur and Wilson's Theory of Island Biogeography. This theory states that as the area of an island increases, the diversity of species colonizing the island increases, and the further the island is from a mainland, the lower its rate of immigration due to the distance (MacArthur and Wilson 1967). The communities formed by vegetation rafts are unique island communities because of their ability to move within the lagoon, so that there is no fixed distance from a mainland. The rafts are driven by wind and accumulate in current eddies (Norton and Mathieson 1983).

Vegetation rafts on the island of Moorea, French Polynesia consist of two or more pieces of macroalgae floating together on the surface of the ocean. Rafts are made up primarily of two species of brown algae, both of the family Sargassaceae, *Turbinaria ornata* and *Sargassum sociale*, and often collect seeds and driftwood while moving with the current and winds. *T. ornata* and *S. sociale* primarily colonize the algal ridge, the ridge that forms the most elevated part of the reef top due to a pavement of encrusting corraline algae over the main coral fauna, upon which wave energy is high (Maxwell 1968; Nunn 1994). *T. ornata* and *S. sociale* can also be found on the fringing reef, and tend to colonize dead corals. On the island of Moorea, *T. ornata* and *S. sociale* that are unattached from the colonized corals tend to drift together in the lagoon inside of the barrier reef, forming vegetation rafts of various sizes. Both species of algae are furnished with gas bladders that keep them afloat. Many families of microinvertebrates live in the *T. ornata* and *S. sociale* attached at the algal ridge (Kingsford and Choat 1985). These invertebrates may remain attached to the algae when waves pull it from the algal ridge. The *T. ornata* and *S. sociale* found floating in vegetation raft communities may support the same microinvertebrates, or there may be differences in the epifauna of the attached and free floating algae.

Invertebrates are commonly found in the brown algae *T. ornata* and *S. sociale*, including nudibranchs, shelled gastropods, crustaceans, including amphipods, isopods, copepods, ostracods and crabs, as well as flat worms and annelids (Zyaginstev 1992). Many marine invertebrates have a biphasic life cycle, which includes a planktic larva that floats free in the ocean. Many marine gastropods have a larva known as a veliger that is free swimming, with cilia for feeding and locomotion (Barnes 1974). Floating juvenile invertebrates may use rafts to disperse, many amphipods and isopods that do not have a swimming larval stage attach to vegetation rafts, using them for protection and movement (Highsmith 1985).

It is possible that differences may exist

between the species and numbers of invertebrates found in vegetation rafts and in the same species of algae still attached at the algal ridge. The raft communities may attract different invertebrates due to their ability to move and pick up floating animals in the lagoon, or they may be carrying only the animals that were inhabiting them when they were attached. It is possible that invertebrates have been lost due to the change in their environment. The primary objective of this research was to test the hypothesis that vegetation rafts accumulate a fauna that is distinct from that of attached algae. A secondary objective was to explain differences that occurred because of the vegetation rafts unique habitat.

Materials and Methods

Study site

Paopao Bay is located on the northern coast of the island of Moorea, French Polynesia, found at latitude 17"32' and longitude 149"50' in the Society Archipelago (Figure 1). Moorea is a volcanic island surrounded by a barrier reef with multiple passes. Samples of attached *T. ornata* and *S. sociale* were taken at the algal ridge on the barrier reef of Paopao Bay, west of Avaroa Pass. Samples of vegetation rafts were taken from rafts floating within the barrier reef, in Moorea's lagoon, north and northwest of Paopao Bay.

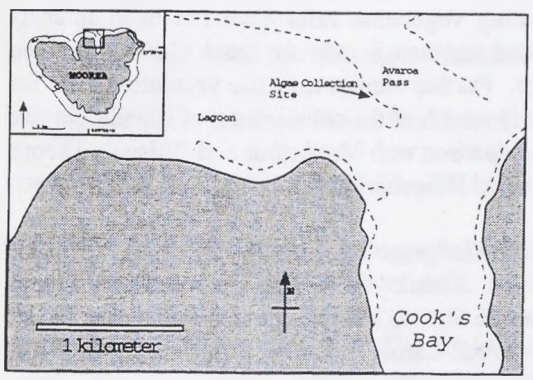

Figure 1. Map of Moorea, showing sample sites

Sample Methods

All samples were taken between October 1 and November 22, 1997. Samples of attached algae were taken by filling a gallon size bag with *T. ornata* and *S. sociale* in equal proportions from the algal ridge. Vegetation rafts found in the lagoon were sampled in two areas, at the edge of the raft and at the approximate center, also in equal proportions of the two algae and in gallon size bags. Fifteen samples were taken of attached algae from the algal ridge, and fifteen were taken of floating vegetation rafts found in the lagoon. Vegetation rafts sampled were measured and their distance from shore recorded.

Sorting of Samples

Samples taken were rinsed and agitated in fresh water to strip invertebrates from the algae. Both species of algae were combined. Invertebrates stripped from the algae were then sorted at a magnification of 20X using a dissecting microscope. Microinvertebrates were sampled by order and family whenever possible. Voucher specimens of invertebrates collected are located at the University of California at Berkeley Museum of Paleontology.

Statistical Analysis

A students T-test was run on results to find if observed differences between raft invertebrates and attached invertebrates were significant.

Results

13 orders of invertebrates were identified and compared between the algal rafts and attached algal samples. Invertebrate populations in rafts and attached algae were different, although most invertebrates were found at least once in both habitats (Table 1). Among these, microgastropods were the most abundant invertebrate found, with an average of 121.3 found per raft sample and 132 found per attached algae sample. Seven different species of microgastropod were identified, including *Sytyliferina goniochila, Pusillina marmorata, Rissoina multizona, Schwartziella triticea, Itibittium parcum*, and larval shells of *Triphora* sp. and *Cupraea* sp. The larval shells found were in both the vegetation rafts and the attached algae samples, in slightly greater numbers in rafts.

Notable species differences between the raft and attached algae communities were copepods, ostracods, juvenile nudibranchs and anenomes (Figure 1). The number of copepods and ostracods found in floating vegetation rafts doubled the number of those found in attached algal samples, and 36 nudibranchs were found in rafts samples, while zero were found in attached algae samples. Anenomes on the other hand, were 9 times as abundant in the attached algal samples than in

vegetation rafts.

inverte-brates	raft only	both	attached only
shelled gastro-pods		X	
amphi-pods		X	
copepods		X	
isopods		X	
mysids		X	
ostracods		X	
poly-chaetes		X	
platyhel-minthes		X	
crabs		X	
nudi-branchs	X		
anenome		X	
acarina		X	
megalops		X	

Table 1. Distribution of Invertebrates in rafts and attached algae.

Discussion

The vegetation raft habitat not only provides food for invertebrates, it may also be used as means for dispersal and for protection from predators. Nudibranches, ostracods and copepods were found to be more abundant in floating raft communities than in *T. ornata* and *S. sociale* attached at the algal ridge. Nudibranch juveniles are nearly invisible when surrounded by *S. sociale* of the algal rafts, their morphology is very similar to the blade of the algae. This suggests that the rafts may serve primarily as protection from predators while they are in the stage of their life cycle in which they float in the open ocean. The veligers of microgastropods swim and feed on plankton before settling and metamorphosing into juveniles, and their appearance in vegetation rafts may be due to accidental entanglement while swimming, or due to a response to the chemicals of the algae. It is possible that many of the invertebrates found in the vegetation rafts are there as a result of being on that particular piece of algae when it is broken off at the algal ridge. This accounts for the similarities between the fauna of the attached and raft algae seen in Table 1. It is also seems that rafts are directly colonized by invertebrates, especially nudibranchs which are found only in vegetation rafts, leading to differences in populations of the two habitats.

In total, microgastropods and anenomes were more abundant in the algae attached at the algal ridge than in vegetation rafts, suggesting that the attached algal habitat is more suitable to their survival needs. The anenome feed by catching organisms with their tentacles, and the wave action at the algal ridge provides a constant influx of new water and food for them, which makes the algal ridge a preferable habitat for anenome. Marine gastropods tend to attach themselves to rocks and graze as adults, perhaps explaining their greater numbers in attached algae.

Statistical analysis showed that only the differences between nudibranch, copepod and anenome populations were significantly different. Despite lack of statistical significance, other differences mentioned between rafts and attached algae were evident, and with higher sample numbers could have proven significant.

Invertebrates inhabiting *S. sociale* and *T. ornata* are able to survive in both the attached and vegetation raft communities, but that different invertebrates find the two different habitats preferable. Species of invertebrates choose the most suitable habitat depending on their individual needs. Floating vegetation rafts have not been intensly studied, and there is room for much more work to be done. Further studies may use vegetation rafts for more research of the colonization of islands, for use in comparison with MacArthur and Wilson's Theory of Island Biogeography.

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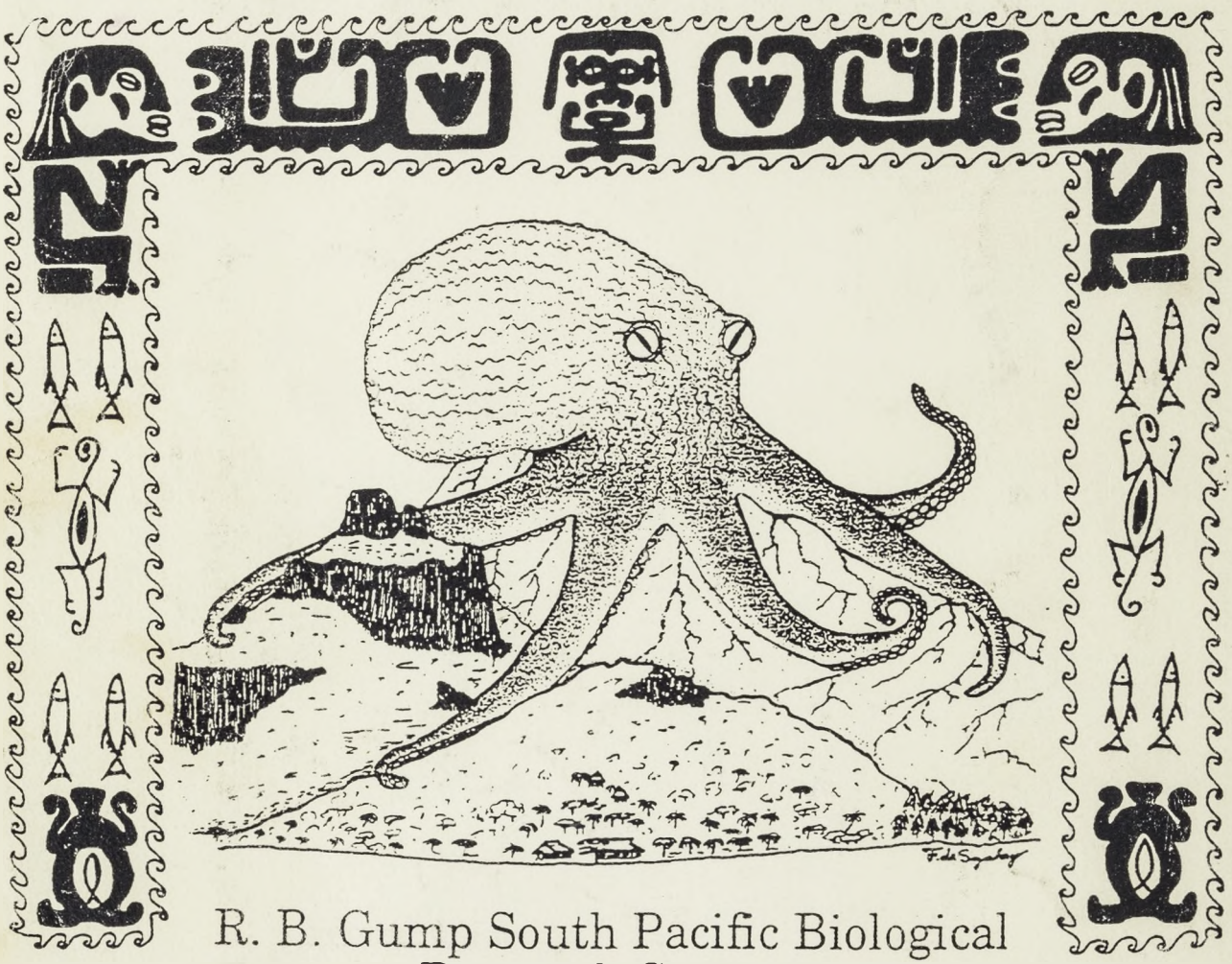

R. B. Gump South Pacific Biological
Research Station
University of California, Berkeley

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