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

**University of California at Berkeley  
Interdepartmental Studies 158**

**Fall 1992**

**Moorea Course Report**





DEPARTMENT OF INTEGRATIVE BIOLOGY

BERKELEY, CALIFORNIA 94720

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## 1992 Moorea Class Report

15 December 1992

Berkeley, California, U.S.A.

Dear Reader:

The University of California at Berkeley Department of Integrative Biology and Department of Geography are proud to present this report from its 1992 Moorea field course. This report compiles the 11 individual reports and 2 joint reports prepared by the 15 undergraduate students of the 1992 UC Berkeley course entitled "Tropical Island Ecology and Geomorphology."

This course focused on the ecology and geomorphology of terrestrial and marine environments on tropical islands and included a 7-week field component on Moorea, French Polynesia. With the help of UC faculty and graduate students, each student conceived and conducted an independent research project on the island. This compendium of reports represents a diverse range of topics reflecting the diversity of interests among the students.

We would like to thank the following faculty and graduate students for their special efforts in making this course a success: George Barlow, Roy Caldwell, Mary Gleason, Carole Hickman, David Lindberg, Jere Lipps, Werner Loher, Mary Power, Stuart Siegel, Wayne Sousa, Larry Vaughan, and Jan Washburn. In addition, we would like to give special thanks to Frank Murphy, Acting Manager of the UC Richard C. Gump South Pacific Biological Field Station on Moorea, for helping the course to run smoothly, and Bernard Salvat and Rene Galzin of the Centre de l'Environnement d'Opunohu Antenne EPHE/Museum on Moorea for their generosity.

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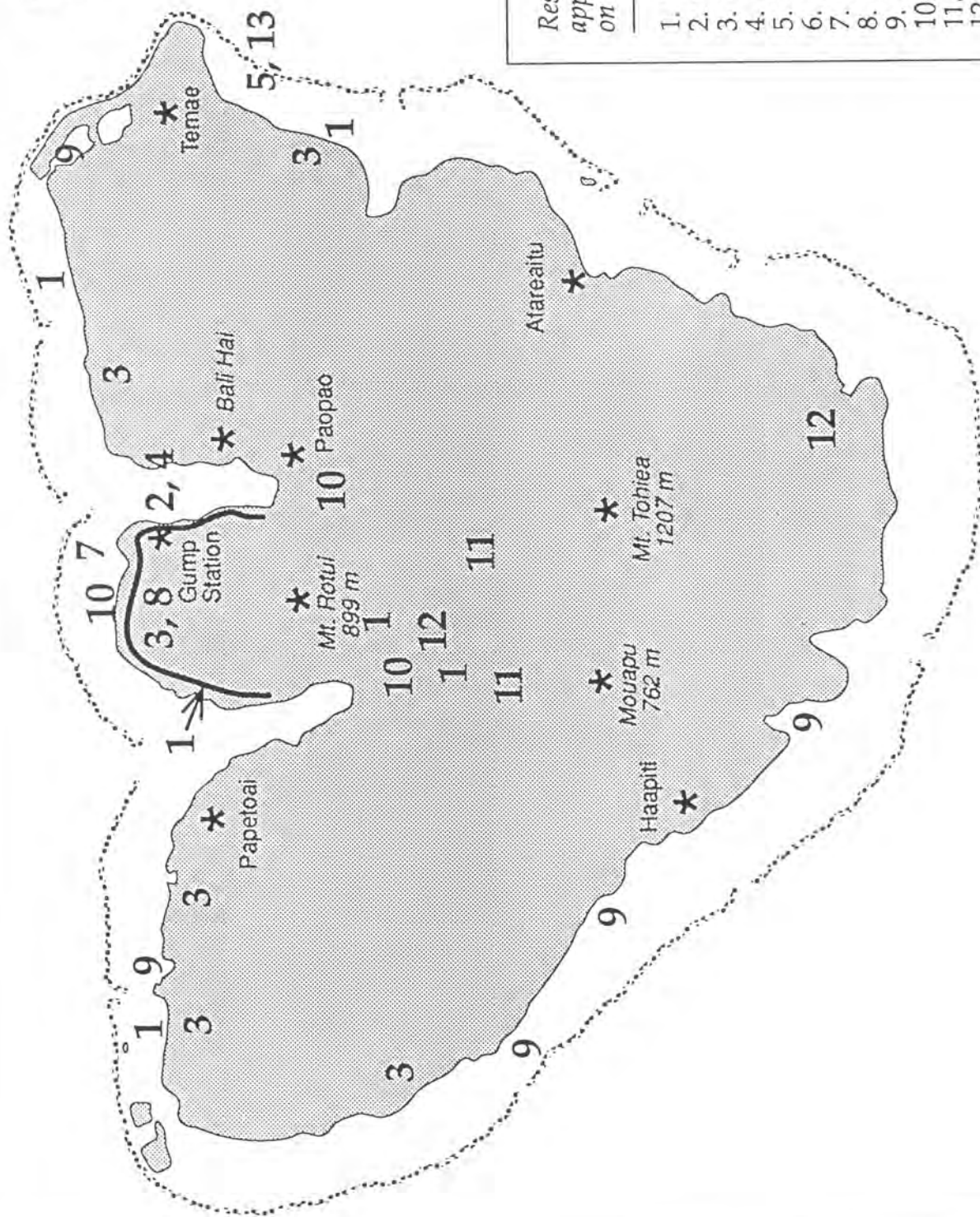
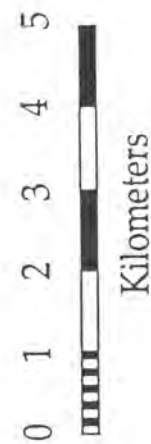


Tropical Island Ecology and Geomorphology  
University of California at Berkeley Interdepartmental Studies 158  
Fall 1992

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Researcher [number identifies approximate project location(s) on map]

1. Becker, J.
2. Churcher, T.
3. Denhoy, R. and G. Battersby
4. Elmquist, G.
5. Engel, L.
6. Ferris, L. (entire island)
7. Gilchrist, M.
8. Graff, J.
9. Kramer, M.
10. London, S. and L. Tucker
11. Santiago, I.,
12. Shiley, S.
13. Shima, J.

Source: Adapted from

1. Carte Géologique des Territoires d'Outremer, Polynésie Française 1966;
2. Polynésie Française Archipel de la Société, Îles du Vent, Moorea 1989

## Locations of 1992 Moorea Class Research Sites



Factors influencing distribution of larval  
mosquitoes of the genera *Aedes*, *Culex* and *Toxorhynchites*  
(Diptera:Culicidae) on Moorea and the relative  
importance of coconuts and roadside trash as  
breeding sites

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## Abstract

Sampling of larvae-positive water-holes on the north side of Moorea in French Polynesia showed that the amount of canopy cover and the type of container were the most significant factors affecting distribution of *Aedes*, *Culex*, and *Toxorhynchites amboinensis* larvae. *Aedes* was the dominant genus in heavy canopy cover. *Culex* preferred sites with no-canopy or light-canopy over heavy-canopy sites. *T. amboinensis* preferred heavy-canopy sites over no-canopy sites. *Aedes* preferred natural containers over artificial ones, while *Culex* preferred artificial containers over natural containers. Preference for a container type was not shown in *T. amboinensis*. In exposed rock holes the presence of leaves on the water affected *Aedes* presence. Insignificant factors for all genera were: volume of water, area of container aperture, water cleanliness, tree species for tree holes, altitude, and dominant forest species. Sampling in coconut groves revealed 4th instar mosquito production in coconuts to be 0.36 individuals/100 m<sup>2</sup> in human-tended groves and 88.93 individuals/ 100m<sup>2</sup> in untended groves. 69% of the larvae were developing in rat chewed coconuts. The difference in production between tended and untended groves was due to more breeding sites/m<sup>2</sup> and more larvae/breeding site in the untended groves. Road-side trash produced 2.9 4th instars/100m<sup>2</sup>. This value was smaller than that for untended groves due to there being less potential breeding sites/m<sup>2</sup>.

## Introduction

On Moorea, in French Polynesia, there are three genera of mosquito: *Aedes*, *Culex*, and *Toxorhynchites*. *Aedes* is a container breeder notorious for its ability to utilize a wide range of water sources in the larval stage. *Aedes polynesiensis* Marks, and *Aedes aegypti* L., the two mosquitoes in this genus on Moorea, are vectors for both dengue fever and *Wuchereria bancrofti* filariasis. *Culex quinquefasciatus* Say, the common house mosquito, and *Culex annulirostris* are also vectors for filariasis. These species are commonly thought of as artificial container breeders that live in close proximity to human developments (Rakai, et al 1974). Both of these genera are worldwide pests and their natural history and biology has been much studied due to their importance in the spread of diseases.

*Toxorhynchites amboinensis* Doleschall, the only species in this genus on Moorea, is a predatory mosquito introduced to the island in 1975 (Riviere 1979) in the hopes that it would significantly reduce *Aedes* populations. The success of this program on Moorea has not been assessed but in Central Java experiments have shown *T. amboinensis* to be unhelpful in this



regard (Annis, et al 1990). Field studies by Riviere(1976) have shown that *T. amboinensis* can reduce a specific breeding site's *Aedes* populations by 50 to 70% and its *Culex* populations by 65%. But, Focks, et al(1976), have found that location of breeding sites is one of the three most important factors determining the amount of mosquito control effected by *T. amboinensis*. *Toxorhynchites rutilus rutilus*' utility for biocontrol is questioned by Focks et al(1983b) though it reduced predator-positive container *Aedes* and *Culex* populations by 74% in field studies (Focks, et al 1982). They found later that *T. r. rutilus* orients toward vegetation resulting "in low levels of oviposition in ground-level containers not associated with vegetation."

This study defines some of the major parameters determining the distribution of these three genera on the North side of Moorea and reveals the extent of overlap between *T. amboinensis* and its two prey species. The relative importance of fallen coconuts in coconut groves and road-side trash as mosquito breeding sites is also examined. The importance of human tending in coconut groves is discussed in terms of breeding sites and 4th instar mosquito larvae produced per meter. The importance of rat-chewed coconuts as breeding sites is determined.

## Materials and Methods

This study is divided into two parts which I will now refer to as general habitat survey and productivity survey. The sampling techniques were different in these two areas. Areas of sampling are recorded in figure 8.

### GENERAL HABITAT SURVEY

All three genera of mosquito are container breeders by the criteria given in Bates(1949) except for *Culex*, which is also known to be a transient ground pool breeder (Singh et al 1983). I classified the breeding sites by the following micro-habitat and macro-habitat factors.

1. **Micro-habitat**. The micro-habitat factors were: volume of water, area of container aperture, water cleanliness, container type, leaf presence in water, and tree hole type. **Water volume** was broken into seven categories: 1. less than 10ml, 2. between 10ml and 50ml, 3. between 50ml and 200ml, 4. between 200ml and 500ml, 5. between 500ml and 2000ml, 6. between 2000ml and 5000ml, and 7. greater than 5000ml. These values were chosen to allow for classification by visual estimation without having to remove all the water from a breeding source. I estimated about 60% of all samples. My confidence is high that estimations were accurate given the scale. **Area of aperture** was roughly determined by treating the aperture as either a circle, square, or triangle and then recording the appropriate measurements. **Water cleanliness** had four

categories: 1. Clean water (I was able to see clearly to the bottom of the water and could see any mosquitoes that were present), 2. Intermediate water (there was some suspended mud in the water or the water was slightly brown), 3. Dirty water (dirt and rotting leaves were so thick that I could not see through the water and had to pour it onto a glass plate to determine if there were mosquitoes present), 4. Filthy water (this was found in rotting coconuts where the water was syrupy, opaque, and putrid smelling.) **Container type** had the following categories: tree hole, rock hole, coconut shell, metal, plastic, glass, and general artificial which included items such as juice cartons and ceramic basins. Ground pools were not included as a category of container type. Bates(1949) has classed this as a separate habitat from container habitats. Crab holes were not sampled since the necessary apparatus was not available. The container type categories were also separated into the two larger categories of artificial and natural containers. **Leaves present** was a yes or no variable that was recorded where appropriate. **Tree-hole type** was recorded if the water source was in a tree-hole. Categories were: mango, *Inocarpis edulis* (Tahitian chestnut), *Hibiscus tiliaceus*, and coconut.

2. **Macro-habitat**. The macro-habitat factors I recorded were: Canopy cover, type of forest, and altitude. **Canopy cover** was divided into three categories: heavy-canopy, light-canopy and no-canopy. Evaluation was subjective. A heavily forested site that possessed a strip without canopy reaching it from an unforested area was classified as light-canopy. Coconut groves were most often classified as light-canopy. Exceptions were where other trees such as guava and *Hibiscus tiliaceus* were mixed in with the coconuts. *Inocarpis edulis* forest sites were usually classified as heavy-canopy. Exceptions were where roads or other human disturbances abutted *I. edulis* sites without the typical *H. tiliaceus* intermediate zone. **Type of forest** had the same categories as tree hole type. The dominant tree type was recorded in heavy-canopy and light-canopy sites. **Altitude** was recorded with an electronic altimeter on two sampling days. I sampled from 2 meters to 250 meters. Altitudes above 250 m are not associated with human establishments and were not sampled.

I sampled during walks though the various habitats that I wished to test. Water sources were searched and if they contained mosquito larvae they were recorded. The survey began at the beginning of the wet season when uncolonized water sources were fivefold the number colonized. For this reason uncolonized sources were ignored and this method of recording breeding sites was maintained throughout the survey though the percent of uncolonized holes dropped as the weeks continued. In the beginning of the survey I chose sampling areas haphazardly but as the study progressed I chose to sample certain areas in order to fill gaps in my data. Mosquito larvae were removed and placed in 60% alcohol for microscope identification in the lab. I removed all larvae unless this was not possible as in the cases of large pools, deep limb-crotch water-holes, and breeding

sites that contained over 50 larvae. In these cases a representative sample was taken. The total number of mosquito larvae present was not important to this survey.

When the values for a factor were non-continuous (e.g. canopy cover) a Chi-square contingency table was used to determine whether that factor contributed significantly to the genus' distribution. When the values were continuous (e.g. aperture area) a rank order test was performed. I tested each factor against each genus. In all cases, unless noted in Results, all data was included in the statistical tests.

#### PRODUCTIVITY SURVEY.

This survey was designed to determine the importance of three different breeding habitats: tended coconut groves, untended coconut groves, and road-sides. I defined tended coconut groves as those where a human had made an attempt to clean up the unused coconuts and fronds dropped by the trees. Burn sites, where coconut garbage is destroyed, and new rat bands on the trees were also signs of tending. I defined untended groves as those showing a thick collection of rotting coconuts and fronds, no burn sites, and either old or no rat bands on the trees. Road-side was defined as the vegetation free shoulder as well as the first meter of vegetation on both sides of the road.

In the coconut grove transects I recorded: # of coconuts, # of potential breeding sites (i.e. coconuts that held water), # of coconuts positive for mosquito larvae, # of rat-chewed coconuts, # of trees, # of larval 4ths both in rat-chewed coconuts and in all other coconuts. All values except #trees were divided by the area of transect to determine these values per  $m^2$ . The number of trees per meter was determined by dividing the total number of trees in the grove by the area of the grove. I sampled two transects in each of five tended groves and five untended groves. The total area sampled was 465  $m^2$  tended, and 430  $m^2$  untended.

At the road-side I recorded: # of potential breeding sites, # of positive for mosquito larvae, # of larval 4ths. These numbers were also divided by the area of my transect to determine the values per  $m^2$ . I sampled one stretch of the main circuit road and two side roads that totaled 2560  $m^2$  and 3540  $m^2$  respectively for a total of 6100  $m^2$ .

I tested the comparisons between tended and untended coconut sites for significance using a rank order test. Most often the comparisons I make are between per tree values rather than per meter<sup>2</sup>. Comparisons between road-side and coconut groves are made between per meter<sup>2</sup> values but were not tested for significance due to the different sampling methods.

## Results

### GENERAL HABITAT SURVEY

I examined 91 larva-positive water-holes. *Aedes* was present in 70 (76%) of these water-holes. 22 (24%) were positive for *Culex*, and 12 (13%) were positive for *Toxorhynchites amboinensis* (Figure 6). 5 (5.5%) of the water-holes were positive for both *Aedes* and *Culex*. 7 (7.7%) were positive for both *Aedes* and *T. amboinensis*. 1 (1.1%) water-hole was positive for both *Culex* and *T. amboinensis*. There were no water-holes positive for all three genera. (Figure 7)

Most of the factors I used to classify the water holes did not prove to significantly explain distribution (Table 1) The insignificant factors for all genera are: water volume, area of aperture, and water cleanliness, forest type, tree hole type, and altitude. Leaves present was only tested for *Aedes* in exposed rock-holes.

1. **Container type.** The most significant micro-factor affecting distribution was the type of container (Table 2, and Figure 1).

#### a. *Culex*.

(1). Artificial versus natural water-holes. *Culex* preferred artificial container water-holes over natural container water-holes ( $df\ 1, X^2=6.133, n=42, 0.01 < p < 0.025$ ). As with the chi-square tests for preference between tree-holes and other water holes, only light-canopy and no-canopy data was used for the same reasons as stated below. All 3 of the 16 natural container water-holes that contained *Culex* were coconuts (Table 1).

(2). Tree-holes versus other natural and artificial water-holes. *Culex* was never found developing in a tree-hole. Testing the significance of this factor required the removal of all heavy-canopy data. *Culex* was never found in a heavy-canopy site so the high percentage of tree holes in these areas could have falsely made the artificial versus natural categories look significant. It would have seemed as if *Culex* were avoiding natural containers when in fact *Culex* was avoiding the heavy-canopy containers, a high percentage of which were natural containers. Data from light and no canopy cover were used alone because no preference was shown in *Culex* between these two categories of canopy cover. This data revealed a preference in *Culex* for all other water-holes over tree-holes ( $df\ 1, X^2=4.257, n=42, 0.025 < p < 0.05$ ).

#### b. *Aedes*.

(1). Artificial versus natural water-holes. *Aedes* preferred natural water-holes over artificial container water-



TABLE 2	CONTAINER TYPE				CANOPY COVER			LEAF	PRESENCE
	Natural	Artificial	tree	other	heavy	light	none	present	not pres.
Aedes	14 (88) n=16	15(58) n=26	not sig	not sig	38(91) n=42	19(76) n=25	13(54) n=24	10(91) n=11	2(33) n=6
Culex	3(19) n=16	5(58) n=26	0 (0) n=5	18(49) n=37	0(0) n=42	8(32) n=25	14(58) n=24	no test	no test
Toxo.	8(16) n=50	4(10) n=41	not sig	not sig	9(21) n=42	3(12) n=25	0(0) n=24	no test	no test

TABLE 1: Significant factors explaining genera distribution on Moorea. The first horizontal line shows the significant macro and micro-factors. The second horizontal line shows the significant categories within each factor. Sample size is the number of samples that were classed within the given category. Sample sizes may differ due to reasons given in Results.

holes ( $df=1, X^2 = 4.111, n=42, 0.025 < p < 0.05$ ). As with the tests for *Culex*, only data from light-canopy and no-canopy sites was used. This had the effect of reducing the chi-square. *Aedes* showed no other container type preferences (e.g. tree-holes versus rock-holes).

c. *Toxorhynchites amboinensis*. There was no preference in *T. amboinensis* between natural container water-holes and artificial container water-holes ( $df=1, X^2 = 0.767, n=91, 0.50 < p < 0.25$ ). A larger sample size might have revealed a preference for natural container water-holes over artificial container water-holes.

2. **Canopy cover.** The only significant macro-factor affecting the distribution of all three genera was canopy cover (Table 2, and Figure 2).

a. *Culex* strongly preferred no-canopy water-holes over heavy-canopy water-holes ( $df=1, X^2 = 31.096, n=66, p < 0.001$ ), and light-canopy water-holes over heavy-canopy water-holes ( $df=1, X^2 = 15.260, n=67, p < 0.001$ ). No preference between no-canopy and light-canopy was apparent ( $df=1, X^2 = 3.432, n=49, 0.10 < p < 0.05$ ).

b. *Aedes* showed no preference between no-canopy sites and light-canopy sites ( $df=1, X^2 = 2.576, n=49, 0.25 < p < 0.10$ ), though it was the dominant species in heavy-canopy areas. Preference between light-canopy sites and heavy-canopy sites could not be tested due to my method of sampling. As discussed in methods, I recorded only water-holes that contained at least one larvae. Because *Culex* was completely missing from all heavy-canopy sites, any larva-positive water-hole found in heavy-canopy sites was, almost without fail, an *Aedes*-positive water-hole. The rare exceptions were where a water-hole contained a solitary *T. amboinensis*.

c. *Toxorhynchites amboinensis* strongly preferred heavy-canopy water-holes over no-canopy water-holes ( $df=1, \chi^2=5.957, n=66, 0.01 < p < 0.025$ ). No preference between no-canopy and light-canopy sites ( $df=1, \chi^2=2.545, n=49, 0.25 < p < 0.10$ ) or between light-canopy and heavy-canopy sites ( $df=1, \chi^2=0.970, n=67, 0.50 < p < 0.25$ ) was apparent for *T. amboinensis*. A larger sample size might have revealed a preference between no-canopy and light-canopy sites.

**3. Leaf presence.** Presence of leaves was significant factor predicting presence of *Aedes* in heavy-canopy exposed rock holes ( $df=1, \chi^2=6.188, n=17, 0.050 < p < 0.025$ ). I performed a quick survey where all exposed (i.e. no rock overhang or low vegetation cover) rock holes with more than 10 ml of water were examined for presence of *Aedes* and presence of leaves.

#### PRODUCTIVITY SAMPLING ( Table 3)

**1. Coconut groves.** Human tended coconut groves had greatly reduced numbers of larval 4ths/tree breeding in the fallen coconuts (Kruskal-Wallis,  $n=10, p=0.034$ ). They also had greatly reduced numbers of rat-chewed coconuts that contained mosquitoes (Kruskal-Wallis,  $n=10, p=0.034$ ). Tended sites had many less coconuts/tree and rat-chewed coconuts/tree than did untended sites (Kruskal-Wallis,  $n=10, p=0.009$ ). The rat-chewed coconut was the most important coconut breeding site within the groves (63% of all larvae). 80% ( $n=5$ ) of tended sites had new rat-bands and 0% ( $n=5$ ) of untended sites had new rat-bands.

**2. Road-side.** The road-side production of larval 4th instars/100m<sup>2</sup> was only slightly larger than that in the tended groves and was substantially smaller than in the untended groves (Figure 5). The density of water-positive containers was substantially lower than that for untended groves as well as for tended groves (Figure 4). The density of breeding sites/100m<sup>2</sup> along the road was substantially lower than that for untended groves, as well as for tended groves (Figure 3). The average number of larval 4ths/breeding site was larger along the

TABLE 3	coco-nuts/tree	rat-chewed nuts/tree	larval 4ths/tree	breed-ing sites per tree	%H2O+ contain. coloniz	H2O+ cont./ 100m <sup>2</sup>	breeding sites/ 100m <sup>2</sup>	4ths/ breeding site	larval 4ths/ 100m <sup>2</sup>
Tended	4.6	0.62	0.2	0.20	38	1.25	0.48	1	0.47
Untended	74.0	7.90	40.3	0.93	27	8.15	2.17	43.1	93.80
Road-side	n.a.	n.a.	n.a.	n.a.	14	0.34	0.05	60.7	3.00

Table 2 : Data from sampling of mosquito breeding sites in coconut groves (both tended and untended) and road-side containers. Areas sampled are 465m<sup>2</sup> (tended), 430m<sup>2</sup> (untended) and 6100m<sup>2</sup> (road-side). Some data is presented in similar ways to make comparison possible between: 1. the two types of coconut groves and 2. between coconut groves and road-side areas.

road-side than this value for both tended and untended groves, though not by much in the case of untended groves (Figure 5).

## Discussion

### GENERAL HABITAT SURVEY

**Aedes.** Bonnet (1958) classifies *Aedes* as a breeder in both artificial and natural sites. This was true on Moorea. *Aedes* was the most widespread of the three genera, and was present in all water-hole classification categories. *Aedes* did show a preference for natural container water-holes over artificial container water-holes but was still often present in artificial container water-holes. In fact, *Aedes* was present in artificial container water-holes in exactly the same proportion as *Culex* (58%) (Table 2). Basically, *Aedes* is the dominant genus on Moorea and utilizes the highest percentage of all categories of water-hole without exception.

An absence of leaves in exposed rock-holes in heavy-canopy sites did seem to limit *Aedes* colonization. I tested this factor after having read an observation by Focks, et al (1976) that a light rain was enough to "bounce" *T. amboinensis* eggs out of a container. The rains on Moorea can be intense and can violently pelt an exposed water-hole. Possibly there is enough force to bounce larvae out of exposed rock-holes. The rock holes with leaves may have had a higher percentage of colonization because the leaves provide a place to hide from the rains. It is also possible that at the beginning of the wet season, when this survey was performed, the only water-holes that had had water for a long enough time to develop mosquitoes were the ones with leaves to slow down evaporation. Though this was not my original hypothesis it seems the most likely to me now. It is also possible that the leaves are acting as an attractant to ovipositing females. Lindly (1988) found that *T. amboinensis* oviposits preferentially in oak-leaf infusion water over distilled water. Perhaps something similar is occurring here.

**Culex.** Singh, et al (1983), have found *Culex* to prefer artificial container water-holes as well as ground pools formed by human disturbance (e.g. trash ditches). They found pits filled with garbage, human waste and wash water to be "the most important breeding sites for *Culex quinquefasciatus*." They also noted the importance of artificial containers such as "discarded artifacts and automobile parts. . . ." In all cases, the human factor seems to be very important in determining *Culex* distribution. These findings agree well with those found during this survey. The preference of *Culex* for artificial containers was strong. The genus seemed to completely avoid tree-holes even when they were not in heavy-canopy areas. The most natural sites that *Culex* colonized were side of road ground pools (not classed as containers) and rat-chewed coconuts (Table 1). Not all

ground pools were colonized, but only those caused by human disturbances (e.g. pools formed along the drainage ditch of graded roads). All three of the natural container water-holes positive for *Culex* in no-canopy and light-canopy sites were coconuts (n=16). This is 42% of the 7 coconuts that were in this sample. Though the coconut is obviously a natural container it seems to break from the artificial/natural distinction for *Culex*. Though the rat-chewed coconut is a natural phenomena, the places where it occurs are usually in close proximity to human developments. The majority of coconut groves grow at lower altitudes where humans live and work. It is typical to find a house bordered on two sides by coconut groves.

*Culex* larvae were also never found in a heavy-canopy water-hole. In many cases this habitat segregation was quite striking. Along the Vaioma River on the north side of Mount Rotui there is a graded road that dead ends at an altitude of 85 meters. The river has heavy canopy while the road has light canopy or no canopy. Rock pools along the road at high, middle, and low altitudes all contained *Culex quinquefasciatus* and the middle altitude also contained *Culex annulirostris*. *Aedes* was not present in these water-holes. But, of ten rock hole samples taken along the river at different altitudes, some places only 20 meters away from the road, all were positive only for *Aedes*. Similar to these findings are those of O' Meara, et al (1989) who found that there was less oviposition by *Culex* "in the woods than in more open areas." It may be possible that *Culex* exhibits this preference as another adaptation to living in proximity to human developments. Heavy canopy cover is not usually associated with human developments so it may be advantageous, given a preference for artificial container water-holes, to avoid heavy-canopy areas.

***Toxorhynchites amboinensis*.** The range of *T. amboinensis* seems to be limited mainly by canopy cover. Water-holes without canopy cover (i.e. no-canopy water-holes) never contained *T. amboinensis* (n=24) (Table 2). These findings support the conjecture by Focks, et al (1976) that "... container location with respect to vegetation and structures also may affect oviposition. ..." To illustrate, they relate that during releases of *T. amboinensis*, "one 4-liter plastic bucket located in the vegetation near a fence received predator eggs every week while another, which never contained predator eggs, was located in the middle of a backyard in a more open situation away from vegetation."

There are other observations by researchers that might also be explained by the finding of this study that *T. amboinensis* strongly prefers heavy-canopy areas over sunny or no-canopy areas for oviposition. Focks, et al (1985), has observed that *T. amboinensis* mosquitoes did not move far from where they were released in a urban neighborhood. In the aerial photo of the field site the streets are not lined with big trees. The streets form a grid of a sunny or no-canopy lines that might



have strongly inhibited *T. amboinensis* movement between blocks. Focks, et al (1983a), found more predator eggs in water-sources that stayed wet throughout the study. This might simply be due to *T. amboinensis* avoiding sunny or no-canopy areas combined with the possibility that in these areas water-holes are more ephemeral due to a higher rate of evaporation caused by more direct sunlight.

*T. amboinensis*' strong preference for heavy-canopy cover over no-canopy cover might seriously reduce its effectiveness as a biological control agent. Both *Aedes* and *Culex* readily occur in no-canopy areas. These are areas where control should be great because they are usually associated with human developments.

One finding was encouraging for biocontrol efforts. *T. amboinensis* distribution does not seem to be limited to either artificial container or natural container water-holes. This species was found in a wide range of containers from soda cans to rock holes. Focks, et al (1976) in a release experiment in New Orleans, found that *T. amboinensis* oviposited "in virtually every commonly found type of container. . . ." This study is in agreement with their findings.

#### PRODUCTIVITY SURVEY

**Coconut groves.** The greater number of coconuts/tree found in untended groves versus tended groves (Table 2) was a result of the fact that coconuts/tree was one of subjective the criteria I used to originally define the sites I chose. The difference between the number of immature 4th instars being produced was due not only to the difference in the average amount of breeding sites/tree available ( .93 breeding sites/tree in the untended groves and .20 breeding sites/tree in the tended groves) but was also due to the difference in the average number of larval 4th instars/breeding site (43.1 4ths/breeding site in untended groves and 1.0 4th/breeding site in tended groves). In other words, not only are there more breeding sites but there are more larvae per breeding site in untended sites. This trend is possibly due to a feedback effect where more breeding sites produce more mosquitoes that in the next generation will oviposit more eggs/breeding site. The combination of both factors makes tending of coconut groves that much more important.

The rat-chewed coconut was the most important coconut breeding site within the groves( 63% of all larvae). New rat-bands designed to reduce the loss of coconuts to tree or roof rats (*Rattus rattus* Linn.) were only present in tended coconut sites showing that the motivation for utilizing them is mainly economic. Placing rat-bands around trees in untended sites would have the two-fold benefit of reducing overall rat populations, which may or may not migrate between groves, as well as reducing the number of mosquito breeding habitats due to there being less rat-chewed coconuts.

**Road-side.** The difference between the number of larval 4ths/100m<sup>2</sup> produced at roadside and in untended groves was mainly due to the much smaller density of potential breeding sites/100m<sup>2</sup> (i.e. water positive containers) along the roadside (0.34) compared to that in untended groves (8.15) (Table 3). Also contributing is that the percentage of road-side water-positive containers that are colonized (14%) is about half that in the untended sites (27%). It is possible that these two factors are positively related so that as the density of water-positive containers drops so does the percent of these containers positive for larvae.

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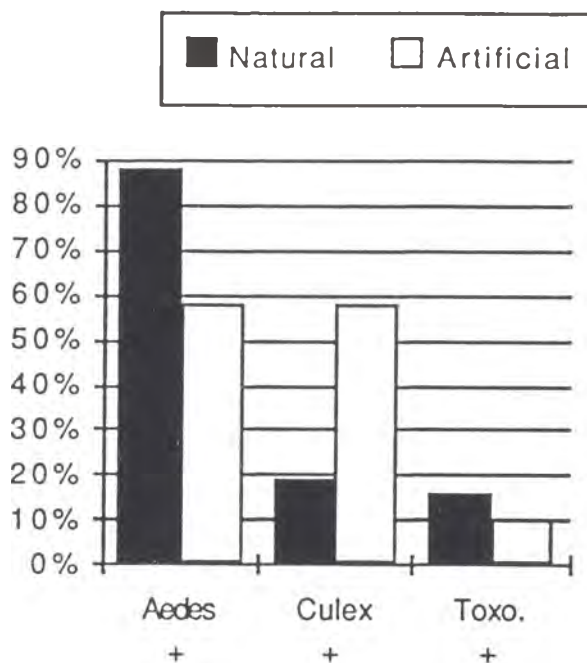


Figure 1 :Percent of artificial and natural containers positive for each genus. Sample sizes available in Table 1

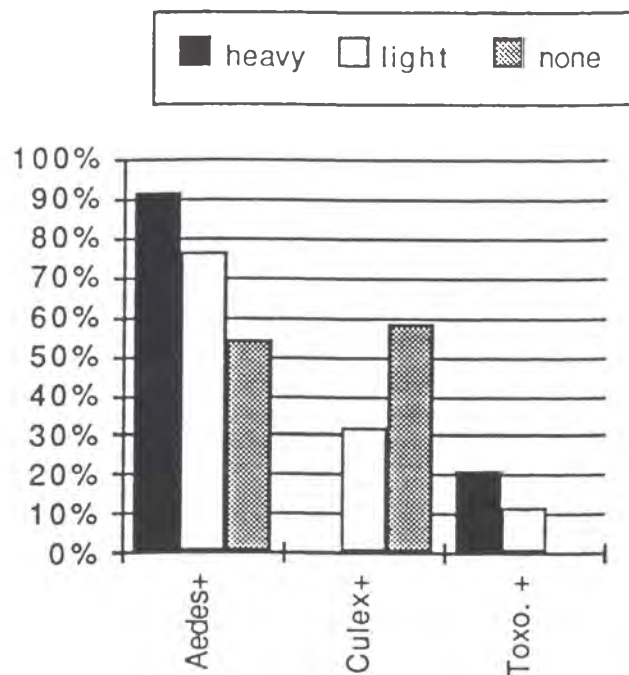
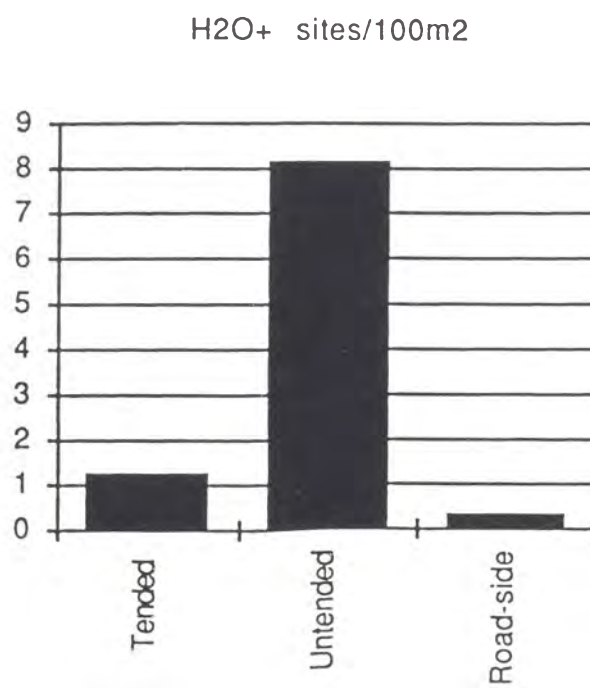
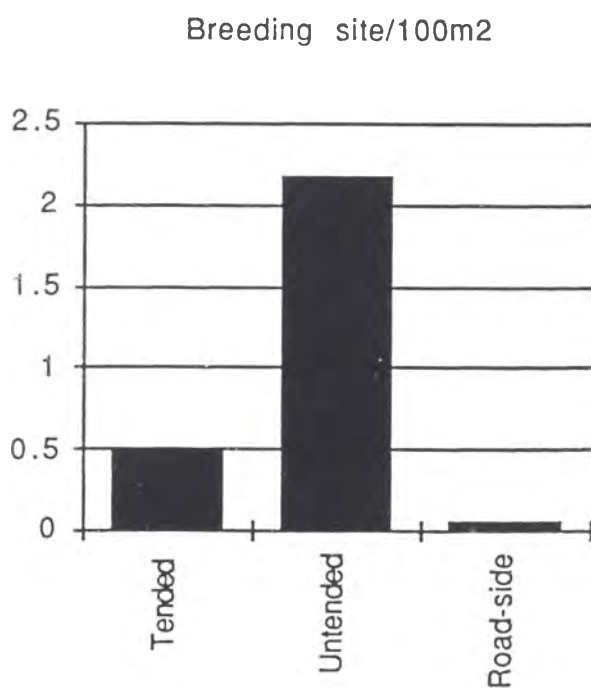


Figure 2 : Percent of heavy, light and no-canopy sites positive for each genus. sample sizes available in Table 1



Figures 3(left) and 4(right): Number of breeding sites and potential breeding sites (i.e. H2O+ sites) found in tended(n=465m2) and untended(n=430 m2) coconut groves and road-side areas(n=6100 m2), expressed by 100m2

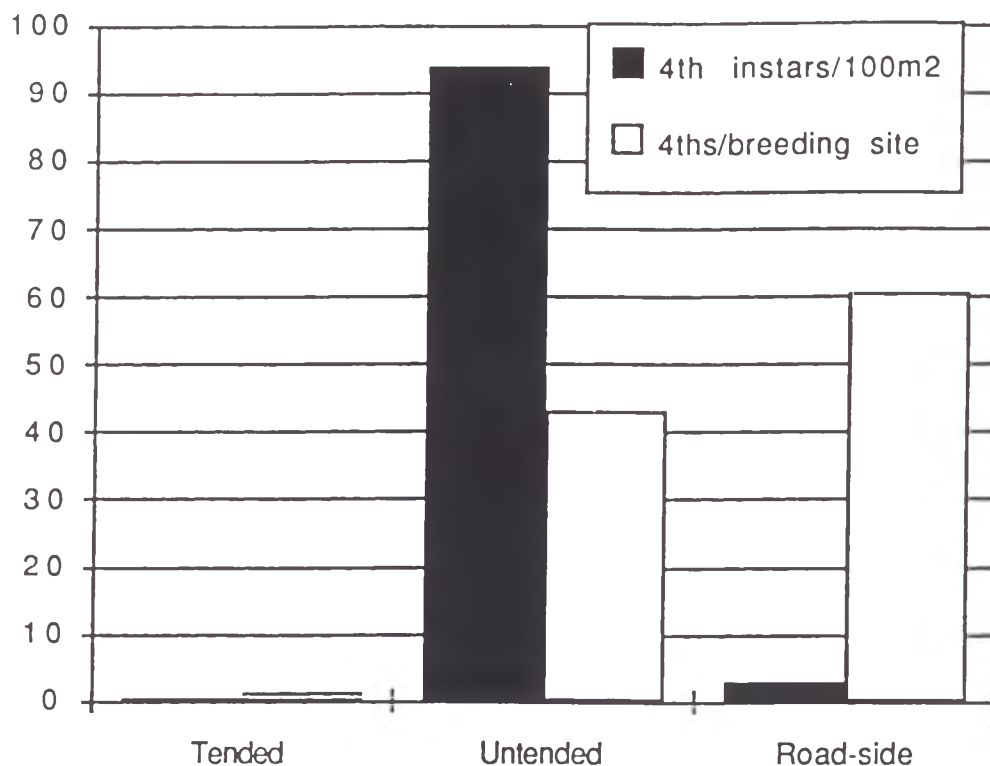


Figure 5 : Production of mosquito larval 4th instars in coconut groves (both tended and untended), and road-side area expressed by m2 and by breeding site. Sample size identical to that of Fig. 3&4.

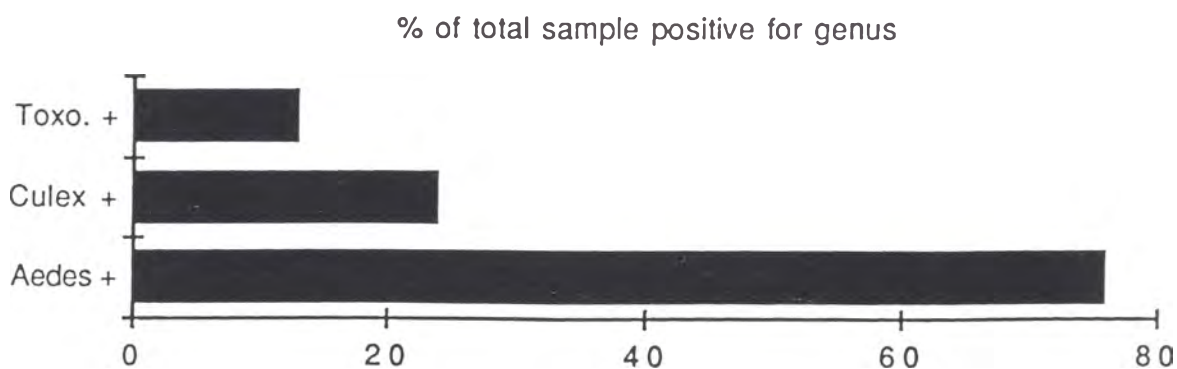


Figure 6: Percentages of total sample of larvae-positive water-holes that were positive for each genus.

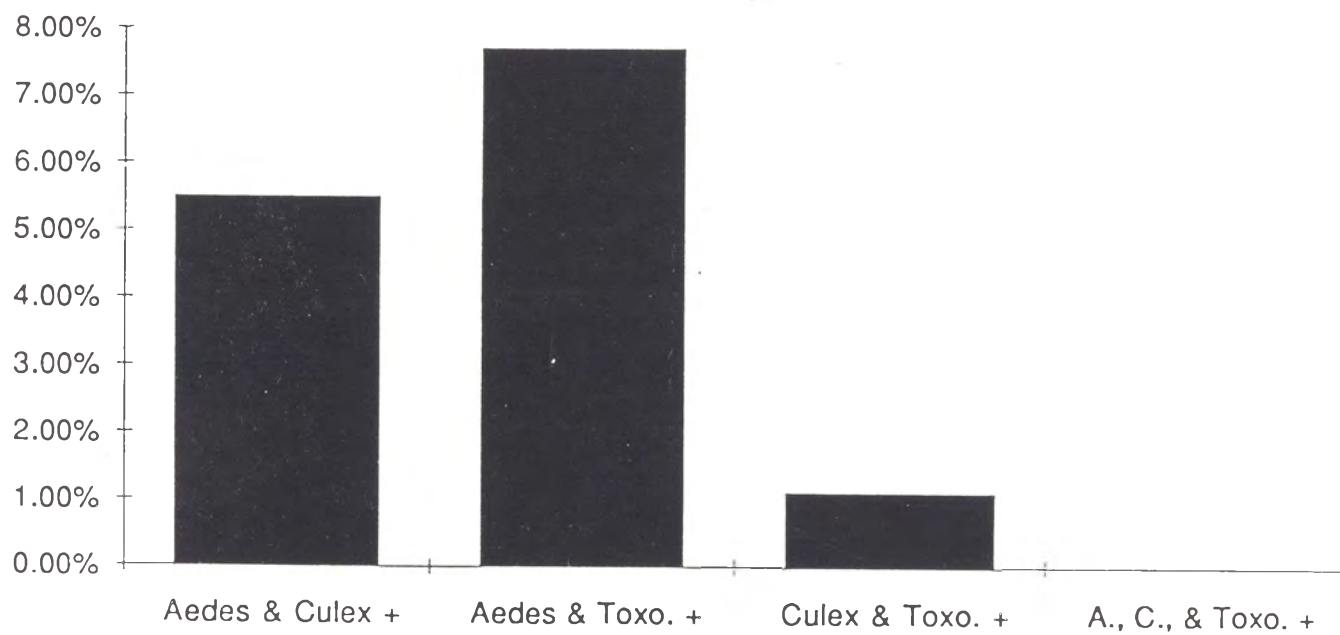


Figure 7: Percent of habitat survey samples containing two or more genera.



overall factor	classes	w/i fact	Aedes positive	Culex positive	T. amboinensi
Water volume		1	67% n=3	0% n=1	33% n=3
		2	88% n=17	40% n=5	6% n=17
		3	80% n=30	26% n=19	10% n=30
		4	67% n=15	58% n=12	7% n=15
		5	100% n=3	0% n=1	33% n=3
		6	40% n=5	100% n=2	40% n=5
		7	43% n=7	75% n=4	0% n=7
Aperture area	range found in		2.4-5000 cm3	2.4-7850 cm3	2.4- 177 cm3
Water cleanliness		1	74% n=46	24% n=46	11% n=46
		2	73% n=26	26% n=26	12% n=26
		3	86% n=7	28% n=7	0% n=7
		4	75% n=4	50% n=4	50% n=4
Container type	tree-hole		83% n=23	0% n=5	26% n=23
	rock-hole		94% n=16	0% n=2	6% n=16
	coconut		78% n=9	42% n=7	22% n=9
	metal		75% n=28	43% n=14	11% n=28
	plastic		62% n=8	50% n=6	0% n=8
	glass		100% n=1	0% n=1	0% n=1
	gen. artificial		50% n=6	75% n=8	25% n=12
Tree-hole type	mango		100% n=3	na	33% n=3
	I. edulis		82% n=11	na	18% n=11
	H. tiliaceus		80% n=5	na	40% n=5
	coconut		100% n=2	na	50% n=2
Forest type	mango		93% n=14	0% n=4	14% n=14
	I. edulis		88% n=17	0% n=1	18% n=17
	H. tiliaceus		42% n=7	100% n=4	14% n=7
	coconut		66% n=18	57% n=14	17% n=18
altitude	range found in		0-236 meters	0-71meters	0-236 meters

Table 1: Factors that do not significantly explain mosquito distribution. Sample sizes may vary for reasons stated in Results. Data for significant factors are in Table 2.

# Moorea, French Polynesia

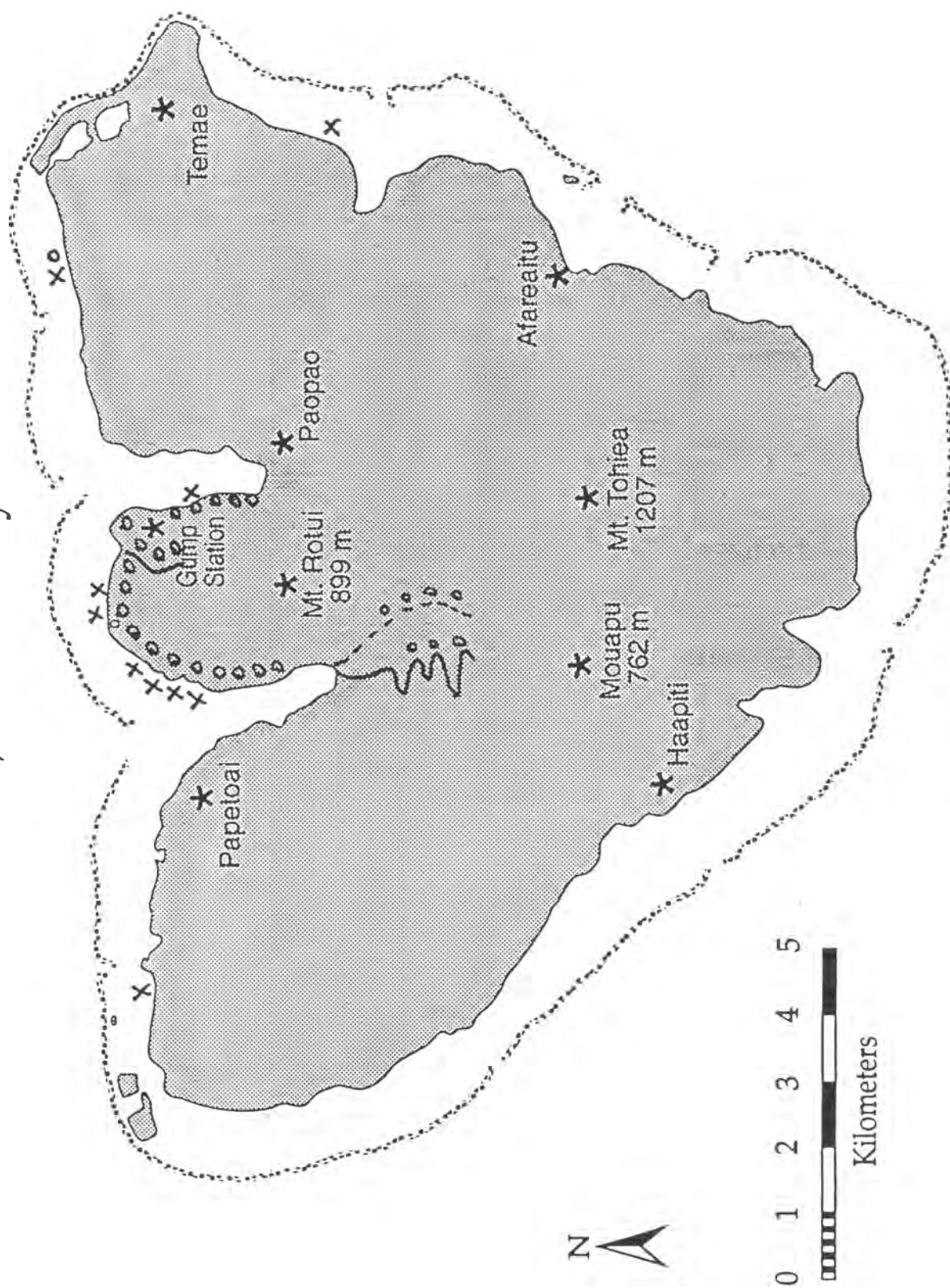


Figure 18 Study Site Location

○. habitat survey sites

×. productivity survey sites





The Localized Effect Upon a Marine Environment From  
a Small Manufacturing Effluent on  
Moorea, French Polynesia.

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## **Abstract:**

This research was conducted to evaluate the biological impact of the effluent from a small manufacturing plant on the marine environment. The project consisted of characterizing water quality, particle size of sediment, counting indicator organisms, algae percent cover and diversity, and calculating the volume of fresh water and amount of pineapple pulp entering the bay from the effluent. By comparing a control site with similar topographic and physical characteristics to the discharge area, the data collected show a localized impact upon the marine community in the immediate area of discharge from the effluent. Although the results did not prove the disturbance to be extremely harmful to the marine environment, some significant differences were found in the sediment particle sizes, and benthic species living in the sediment.

## **Introduction:**

Human-related development in tropical climates has caused the nearshore marine environment to deteriorate. Common types of disturbance include industrial growth, intensification of agricultural production, recreational use of waters, and domestic and industrial exploitation of shore properties. Recently, numerous studies have documented the affects of sediment and sewage input into marine environments resulting in accelerated eutrophication which causes changes in plant and animal life (Clark,1991). On the isle of Moorea in French Polynesia the increase in human development and agriculture has directly affected the marine environment.

The objective of this research project was to determine the biological impact of a small pineapple juice factory effluent. The Moorea Juice Factory (fig.1) is the second largest industry on the island, next to tourism. The factory produces 15,000 one-liter bottles of juice per day. Forty tons of pineapples are used each week, and roughly 10% of the pineapples (as pulp) are dumped into the effluent which enters Cook's Bay. Cleaning fluid and freshwater also enter the bay (Personal interview, Mr. Pierre Gros).

The deposition of pineapple pulp onto the marine sediments may adversely affect the resident organisms by producing an anoxic environment due to the consumption of available oxygen during the decomposition of the deposited organic matter in the sediment or by alteration of other chemical and physical features of the habitat

(Bayne,1985). A common change in the environment as a result of eutrophication could be excessive growth of algae and larger aquatic plants (Clark, 1991). Such growth chokes the open water, possibly making it nonpotable, thus greatly increasing the cost of filtration. The excessive vegetation decomposes, fouls the air, and consumes the deep-water oxygen vital for fish and other animal life.

This study was designed to examine the effect of pineapple effluent on physical and biological features of the nearshore environment. By characterizing the affected marine habitats close to the effluent and comparing it to a control area not experiencing effluent this study seeks to address the question as to whether or not there is a localized effect upon a nearshore marine environment from this small manufacturing effluent.

## **Methods and Materials:**

### **Effluent Characterization**

The location of the factory effluent entering the bay is at site#1(see fig. 1). The Moorea Juice Factory operates five days a week producing exotic fruit juices and liquors. The factory dumps pineapple pulp into a ditch and monitors the amount of pulp that then enters the freshwater effluent stream. The pulp is dumped after fermentation without alcohol, but with cleaning fluid (Personal interview, Mr. Pierre Gros).

The effluent was monitored in two ways: (1) by measurements and calculations based on the operating characteristics of the plant, and (2) by periodic manual sampling and laboratory analysis of the effluent.

Throughout the study collecting and gathering the pulp was a problem. The nets made to collect the pulp were stolen or moved easily, and drying and accurately weighing the pulp was difficult. Ultimately, to solve the problem the net was hand held at the point of discharge into the cement-lined channel located about 1 m above the mouth of the discharge ditch. The channel cross sectional area of the ditch is .28 m. For five days I was able to collect pulp every two hours for five minutes starting at 9:00 a.m. and ending at 5:00 p.m. After gathering the pulp it was dried in an oven and weighed. Discharge velocity was measured by the ruler method; which involved placing the ruler in the water first parallel to the flow then perpendicular to the flow. Height of the water on the ruler was measured. Also, because discharge fluctuated throughout the day, as regulated by juice factory operations, data were collected throughout the day and total discharge calculated accordingly. Velocity ( $v$ ) could

be calculated according to this formula (Personal interview, Larry Vaughan):

$$v = \sqrt{981 \text{ mm/s}^2 (\text{depth } 1 - \text{depth } 2)}$$

Temperature and pH were also taken periodically simultaneous with recording data from the other two sites. Temperature of the effluent was recorded by laboratory grade glass thermometers at the point of discharge into the cement-lined channel, and pH paper was used to measure the pH of the water.

### Bay Water Quality Analysis

Figure 1 shows the locations of the two sites in Cook's Bay. Site #1 was where the effluent from the Moorea Juice Factory discharged the pulp and water into the bay, just north of the Gump Biological Station, and Site #2, the control site, was just south of it. Site #1 is a shallow shelf of 4 m in depth that extends 45 m offshore, and the control site, site #2 is of similar depth and extends 30 meters offshore. Though the control site does not extend as far offshore, it is believed that it remains equally shallow for the distance offshore within which impacts at site #1 are likely to occur.

The two site areas were sampled systematically by setting up a grid (see fig.2 and fig.3). Painted orange rocks were used to mark the intervals. The grid at site #1 had seven units 4 north spaced 10 m apart and three units at 5m, 10m, and 20m running 90 east from the imaginary shoreline. Site #1 had a total of twenty- eight sample locations. Site #2 also had a grid set up at the same intervals, but only three units running north and south, and therefore had a total of twelve sample locations.

Three different measurements were taken at Site #1 and Site#2; temperature, pH, and conductivity (salinity). Water samples were taken at each interval on the grid three times. Temperature was measured using a laboratory grade glass thermometer.

The pH of the water was measured initially with pH paper then later with a Corning Model M107 pH meter to improve data resolution. Liquid reagents for the pH meter were a year past the expiration date but could not be replaced, thereby introducing a potential systematic error in the pH data. At both sites two places on each transect were chosen to continue, after the initial sampling, measuring temperature, pH, and later conductivity. At site#1 the middle transect line was chosen at 5 m and 20 m. This line was in the center of the effluent entrance into the bay (see fig. 2). At site #2 the middle transect line was also chosen at 5 m and 20 m (see fig. 3). These measurements were taken twice. The conductivity meter was difficult to calibrate, and when testing the same solutions in



different beekers would often give different readings. This difficulty likely introduces a random sampling error into the conductivity data.

### Bay Sediment Quality Analysis

Sediments were collected at both sites. At site #1 a total of twelve sediment samples were collected from three transect rows (see fig. 2). At site #2 a total of six sediment samples were collected (see fig. 3). Samples were collected by first carefully scooping up the surface layer of sediment (less than 2 cm in depth) with a shovel. The sample was then collected from a second shovel-full of sediment taken from immediately below the cleared area. Samples were stored in plastic bags.

Sediment size distribution was measured using five U.S.A. standard testing sieves the largest sieve reported as NO. 10 (2.00mm), middle sieves as NO. 18 (1.00mm), NO. 40 (.0595mm), NO. 120 (.0125mm), and smallest sieve as NO.230 (.0063mm). After separation was completed, sediment from each sieve was baked in an oven at 100 C for three hours. Particle size distribution is reported as dry-weight percent composition.

Sediment organic matter (SOM) data were collected for four samples on the middle transect line at 5 m east at both sites (see fig.2 and fig.3). Analysis involved first obtaining the sample dry weight (100 C for one hour). (Personal interview, Dr. Jere Lipps) Samples were then placed in bleach for sixteen hours, then drained, baked and re-weighed.

The aerial extent of the pulp deposited at site #1 was mapped out with a survey tape to measure the pulp effect upon the sediment. Next, characteristics of the sediment were examined; how polluted was the sediment, the black color of the sediment, the anoxic smell in the sediment, and the number of worms in the sediment. On the grid already made at site #1 additional points on the grid were made (see fig. 5). Every 1.5 meters running north and south and east the sediment was checked and grading factor of these four parameters noted. These factors ranged from one (no effect) to three (effect), as compared to the sediment outside of the deposition area.

### Benthic Flora and Fauna

Organisms found in the sediment were counted during the sieving process.

A 1 m<sup>2</sup> quadrat divided by string into one hundred squares (0.01 m each) was used to measure the percent cover of algae at both sites. To the left of each rock on the transect rows the quadrat was placed to count species and their percent cover.



In order to acquire more information about the algae characteristics in Cook's Bay six other sites were qualitatively observed to gather more data about species richness, diversity, and evenness (see fig.1 and table 3).

## Results:

### Effluent Characterization

Table 1 shows the effluent characterization data.

Table 1. Effluent Characterization

1. Average Daily freshwater Discharge: 600m
2. Average Daily pineapple pulp discharge: 57g
3. pH: 5.5
4. Temperature: 29°C

#### Notes:

1. Data is averaged from five days of replicate characterization
2. Throughout the day fluctuation of the volume of water discharged into the bay occurred. Peak hours were 1:00p.m. - 3:00p.m.

### Bay Water Quality Analysis

Range in temperature for both sites varied from 26°C to 29°C. pH ranged between 8.14 - 8.28, and conductivity, at five parts water and one part sample, ranged from 10.08 to 13.12. ppm

### Bay Sediment Quality Analysis

Sediment samples taken from both sites showed significant differences in particle size distribution (see fig.4). The largest particle size, gathered in site #1 had a mean of 27.3% compared to site #2 63.5% composition of the complete sediment sample (Mann-Whitney  $p=.002$ ). Furthermore, the smaller sieve sizes also show a difference between the two sites. Particles measured at .0595mm in site #1 comprised a mean of 35.7% of the sediment sample whereas at site #2 only 16% was collected (Mann-Whitney  $p=.061$ ). For sieve size .0595mm there is a strong trend to have a significant difference (Mann-Whitney  $p=.061$ ). Sieve size .0125 has a significant difference (Mann-Whitney  $p=.009$ ), and sieve size .0063mm shows significant difference between the two sites (Mann-Whitney  $p=.006$ ). The effluent discharge correlates statistically with a smaller particle size of the sediment at site#1.

The composition of the sediment at site #1 contained 9.9% organic matter compared to 1.25% found at site#2.

The settlement of the pulp (see fig.5) at site #1 was strongest to the southeast of the effluent entrance into the bay.

### Benthic Flora and Fauna

The other species found at site #2 consisted of mollusks, bivalves, hermit crabs, and other crabs. Both sites had similar reef substrate, but at site #1 reef drop is roughly ten meters further away than at the control site #2. Characteristics of the marine environment at site #1 consisted of two sea cucumbers, some shoreline fish, barnacles on the rocks along the shore, and the worms in the sediment. At site #2 diadema were spotted frequently, although there were no large groupings. Other small urchins were abundant, and a variety of different fish were seen along the shoreline and further out on the substrate.

At site #2, 4 of 6 samples were found to contain a variety of different organisms (see table 2). However, the difference in number of worms between Site #1 and #2 was not statistically significant (Mann-Whitney  $p=.123$ ), perhaps because of low sample size. The worms were not evenly distributed around site #1 since worms were only collected within a 10 m radius of the effluent. The other organisms (crabs, mollusks, bivalves) found at site #2 shows that there is a statistical difference (Mann-Whitney  $p=.002$ ).

Six different species of algae were found at site #1. Only five were calculated in the mean percent cover of algae because the sixth species did not occur in the quadrat, but was observed within the study area. The *Enteromorpha* species was observed as the sixth species. The 5 m x .5 m patch of algae grows on rocks and the substrate just 1 m south of the effluent entrance into the bay. At site #2 four different species were found. The mean percent of each species and the total percent cover are in the table 2 (and see fig.6).

The Simpson Diversity index describes the probability that a second individual drawn from a population should be of the same species as the first. The index is also strongly influenced by the few dominant species, whereas the Shannon index emphasizes the rare species in the community. A comparison of the two sites suggest that the control site is less diverse by both the Shannon-Weiner and Simpson index (Table 2)(Krebs,1989). But, the impact area is more even. *Padina* at site #1 the proportion of total percent cover was recorded as 21%, whereas at site #2 it was 84%.

The Mann-Whitney U test was used to statistically compare the total percent cover of algae between site #1 and site #2. Total cover was similar among sites (Mann-Whitney,  $p<.128$ ). But, individual species responded differently to the two environments. For example *Padina* was more abundant at site #2 ( $p<.002$ ), and *Halimeda*'s was more abundant at site #1( $p<.003$ ) (see table 2 and 3).

Table 2. Bay Characterization

	Site #1	Site #2	Significant Difference
<b>Grain Size mean %</b>			
2.00 mm	27.30%	63.50%	p=.002
1.00 mm	9.60%	7.20%	p=.322
.0595 mm	18.70%	11.50%	p=.081
.0125 mm	35.70%	16%	p=.009
.0063 mm	8.90%	2%	p=.006
<b>organism count</b>			
worms	32	0	p=.123
others	0	13	p=.002
<b>Organic Matter</b>	9.90%	1.30%	
<b>Algae mean % cover</b>			
Total % cover	17.90%	12.20%	p=.128
Padina thivyl	(P 21%) 3.7%	(P 84%) 10.3%	p=.002
Turbinaria oranta	(P 1%) .23%	(P 1%) .11%	p=.041
Hypnea cernicornis	(P 14%) 2.5%	(P 6%) .7%	p=.024
Halimeda opuntia	(P 23%) 4.2%	not found	p=.003
Acanthophora spicifera	(P 41%) 7.3%	not found	p=.920
Dicotyota acutiloba	not found	(P 9%) 1.1%	p=1.00
<b>Algae Community Structure</b>			
Species Richness	5	4	
Shannon-Wiener diversity index	1.35	0.51	
Simpson diversity index	0.72	0.28	
Shannon-Weiner evenness	0.27	0.13	
Simpson evenness	0.14	0.07	
Jaccard's similarity index			0.25
<b>*Notes</b>			
p= Mann-Whitney U-Test			
(P )= proportion of total % cover			

Table 3. Algae Comparison

	Site A	Site B	Site C	Site D	Site E	Site F
<b>Species Richness</b>	3	2	2	1	2	3
<b>Jaccard's Similarity Index</b>						
Site #1	0.18	0.22	0.22	0.14	0.22	0.25
Site #2	0.2	0.14	0.14	0.16	0	0.3

## Discussion:

Since there was no previous work done at these two sites there was no information to compare site #1 to before the factory started dumping the pulp into the bay.

Although large amounts of fresh water and pineapple pulp were entering the Bay at site #1 no differences were found in the water quality analysis between site #1 and site #2. Many outside factors could have influenced these results. First, the rain and wind play a role in cleaning out the bay system. Storms frequently introduce large quantities of terrestrial sediment into Cook's Bay, some of which likely results in sediment deposition. These effects may override the relatively small volume of effluent from the pineapple plant. Another factor is the current, which changes directions thus continually relocating suspended matter and making the effect harder to detect. The amount of fresh water and pineapple pulp entering the bay is likely very small compared to all of the other factors. Thus no significant difference in water quality was detectable in this study.

Probably the most universal pollutant affecting the marine benthic community is the excess of organic matter (Gray, 1981). Benthic species and communities are the best indicators of organic pollution because of their constant presence, relatively long lives, sedentary habits, and differing tolerances of stress (Bayne, 1985). Those forms indicative of pollution have certain characteristics such as tolerance of low O levels, high biotic potential, and small size. (Hutchinson, 1969).

Sediment is one of the main factors controlling the community structure in the marine environment. Sediment with particle size of around .18 mm is the most stable since such particles are the easiest to transport, and therefore, where they occur wave and current action must be minimal. Sander's study (1958) shows that suspension-feeders (bivalves, amphipods) have higher densities at this particle size. Deposit-feeders (polychaete), on the other hand, reach maximum densities in muddy sediment. Unstable silt-clay cannot be colonized by larval suspension-feeders, and that even if it could their gill structures would be rapidly clogged by resuspended material.

Probably the variations in grain size could influence the organisms if they could in fact choose between different sizes. Yet even within the favored size range of .2 -.3mm Gray's study shows

that *P. Symbiotus* did not occur in a uniform distribution, but in patches. The organism localized in patches because it favored the species of bacteria living in the finer sediment (Gray, 1979a). The implication of this different particle size distribution affects suitable conditions for benthic organisms, algae, grazing invertebrates, and fish, and thus shows how eutrophication can affect the whole food chain within site #1.

Although I did not directly measure organic matter the reduced particle size appeared to be associated with an increase in organic sediments. In nearshore environments the organic content of the sediment typically increases with the fineness. (Gray 1979a). When there is a considerable accumulation of organic matter in an area, dissolved oxygen in the water may be partially to completely consumed, leading to anoxic conditions near sediment water interface and could ultimately cause a drop in O<sub>2</sub> available for organisms (Goldman and Horne, 1983).

Since the sediment particle size distribution differs between the two sites, one may expect that the benthic organism species composition and community structure would differ. Of the 12 samples collected from site #1 only three samples in front of the effluent contained organisms. The only organisms found were *Polychaete* worms. No worms were found at Site #2, but differences among sites were not significant (Mann-Whit,  $P < .123$ ) perhaps because of low sample sizes. Similar to pineapple pulp, sewage pollution creates sediment that is primarily fine grained (Gray, 1979a). The particles are rich in organic matter and bacterial activity is therefore high (Gray, 1979a). Gray (1979a), shows how the polychaete *Capitella* survives in polluted water because it is a classical r-selected species: it can reproduce both by planktonic larvae and by benthic larvae, has a short life-cycle, and reaches maturity from eggs in about three weeks. It can, therefore, continuously repopulate sediments subjected to pollution from organic matter. *Capitella* does not use tolerance as an adaptive strategy, but adapts to continuous disturbance by continuous reproduction. It is likely that a similar strategy might be found for the organisms collected in the samples near the effluent.

The pineapple pulp waste entering the sea may likely be acting as a plant nutrient. Studies done by R. B. Clark (1991) showed that input of organic matter into marine waters promotes the growth of phytoplankton and benthic algae and thereby affects the whole food chain. However, excessive organic matter input can lead to eutrophication. (Coler, 1989). Surface waters can acquire a high oxygen concentration because of increased photosynthesis. However,



the abundance of decaying plant material falling to the sea bed reduces the oxygen concentration in bottom waters, causing mortality or emmigration of most benthic animals. At site #2 4 of 6 samples were found to contain a variety of different organisms: these included crabs, mollusks, and bivalves. The number of non-worm taxa at site #2 was significantly greater than the number at site #1 (Mann-Whitney,  $P=0.002$ )

Nutrient rich water is an immediate stimulant for algal growth (Goldman and Horne, 1983). Recently, marine macroalgae has been used as a potential marine pollution indicator (R.L. Fletcher, 1991). The study revealed that marine macroalgae, especially in reproductive stages, are more sensitive to pollutants than some organisms. Under polluted conditions diversity of algal species are reduced, and numbers have been described as pollution indicators. *Enteromorpha* is often found in eutrophicated waters (Fletcher, 1991). More specifically Gray's study shows that in the sea water, a common sign of sewage pollution on the beach is the growth of green algae *Enteromorpha* and *Ulva* (Gray, 1979a). Although site #1 contained a small patch of *Enteromorpha*, it did not have a higher total percent cover of algae. The total cover was similar among sites (Mann-Whitney,  $p<0.128$ ). But, as one moves away from the source of pollution there is typically a sudden and rapid increase in biomass and abundance of fauna (Gray, 1979a). When mapping out settlement pattern, I observed that in the heavily affected area the total percent cover of algae at each coordinate was lower than in the less affected areas further from the effluent.

## Conclusions:

"Cultural eutrophication" greatly accelerates natural eutrophication through human impact upon the marine community (Hutchinson, 1969). The discharge of pineapple pulp from the factory effluent may be increasing organic matter content within the marine environment, and thus creating some significant differences between the impacted site and the control site. By characterizing the two habitats I was able to correlate some differences specifically in the benthic organisms living in the sediment and particle size of the sediment. Although I did not find significant differences in the water quality, or the total percent cover of algae in the community, this study does show that site #1 has been impacted locally by the discharge. I recommend in the future the continuation of the characterization of the marine habitat in order to observe changes in the environment as human development grows.



**Acknowledgements:**

I would like to thank all of the faculty for making this course possible, and specifically Dr. Carla D'Antonio, Larry Vaughan, and Stewart Seigel for helping me with all aspects of my project

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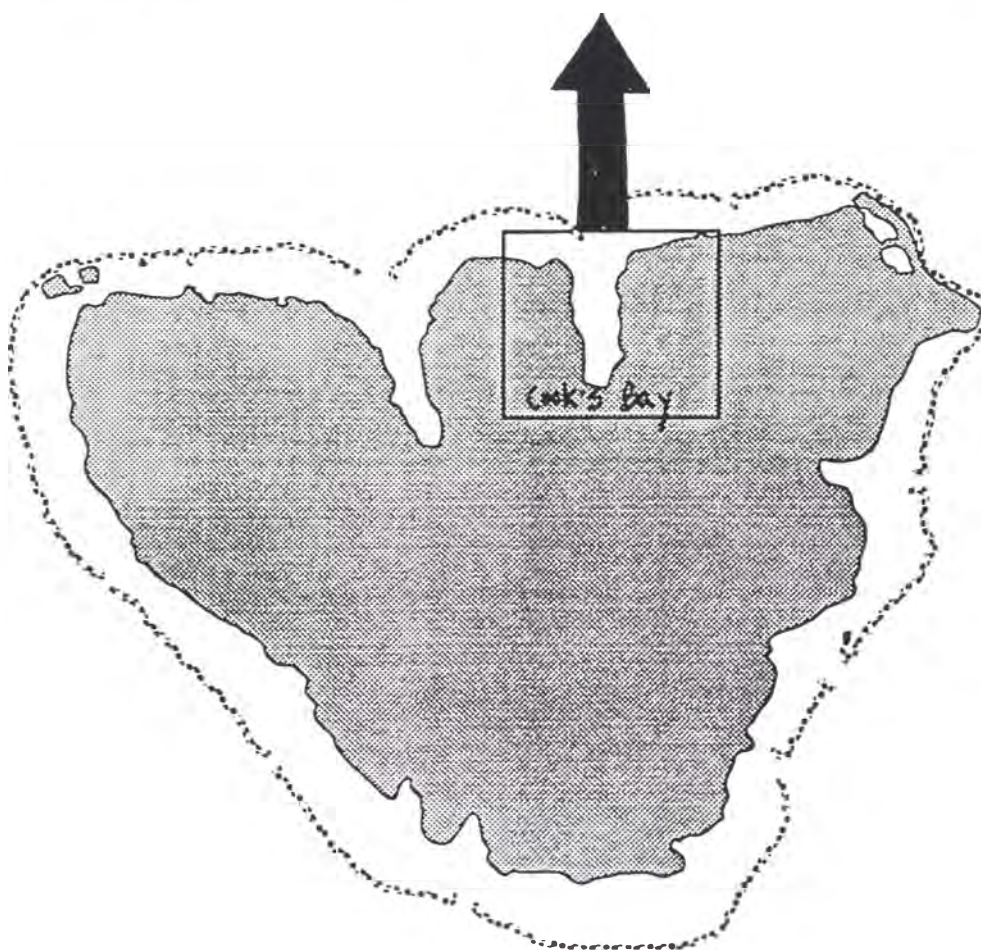
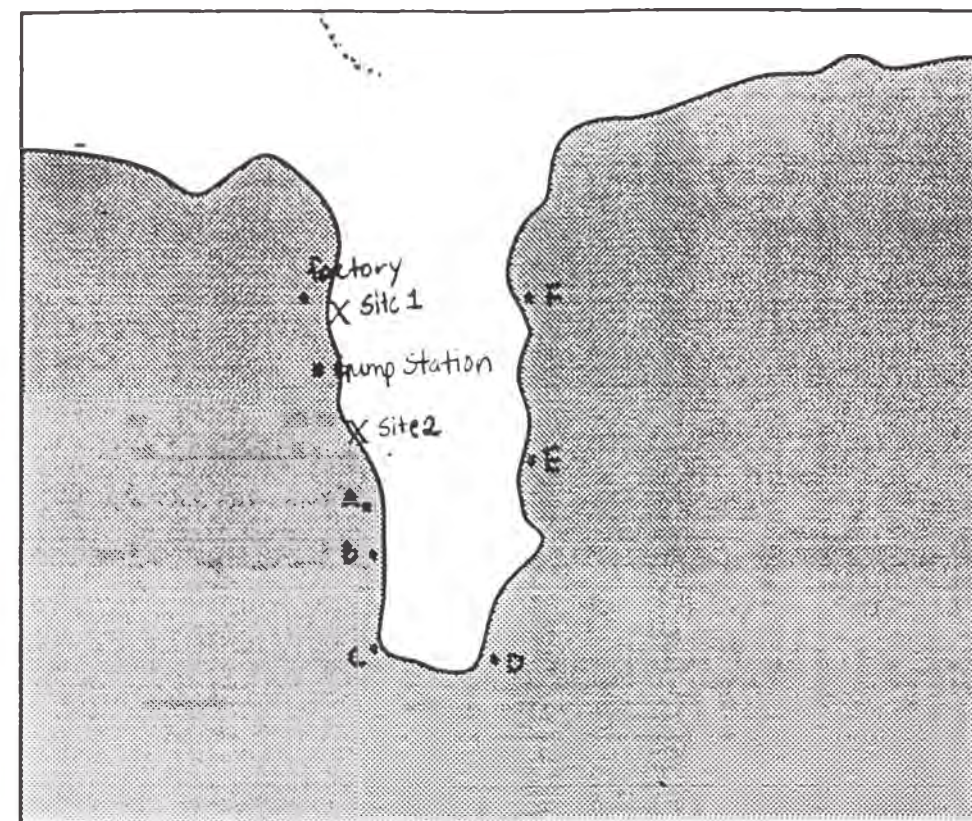


Figure 1: Location of Study Sites on Cook's Bay, Moorea F.P.

Layout of Sampling Grid Within Study Areas

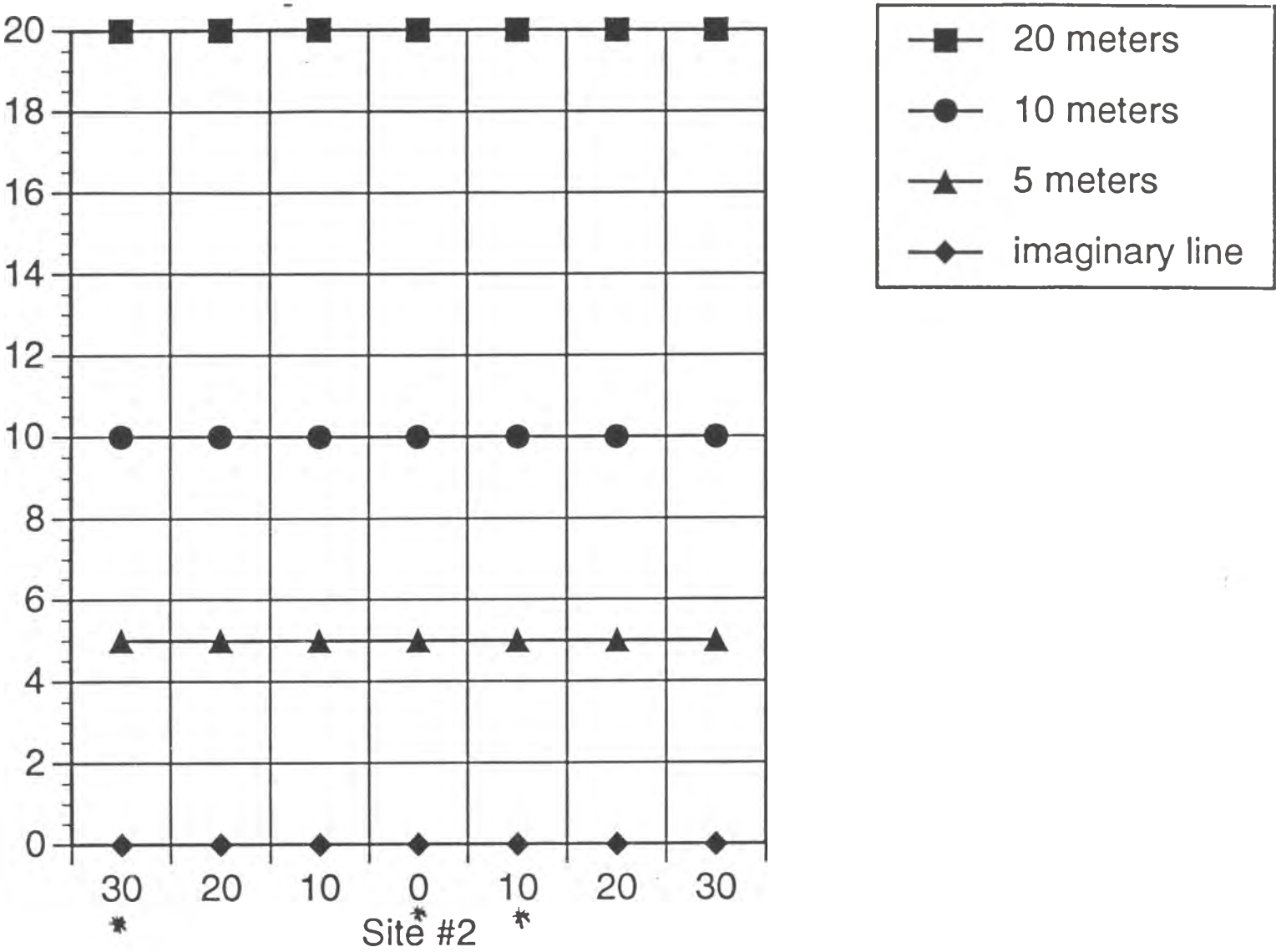


figure 2

\* sediment samples

# Layout of sampling grid within study areas

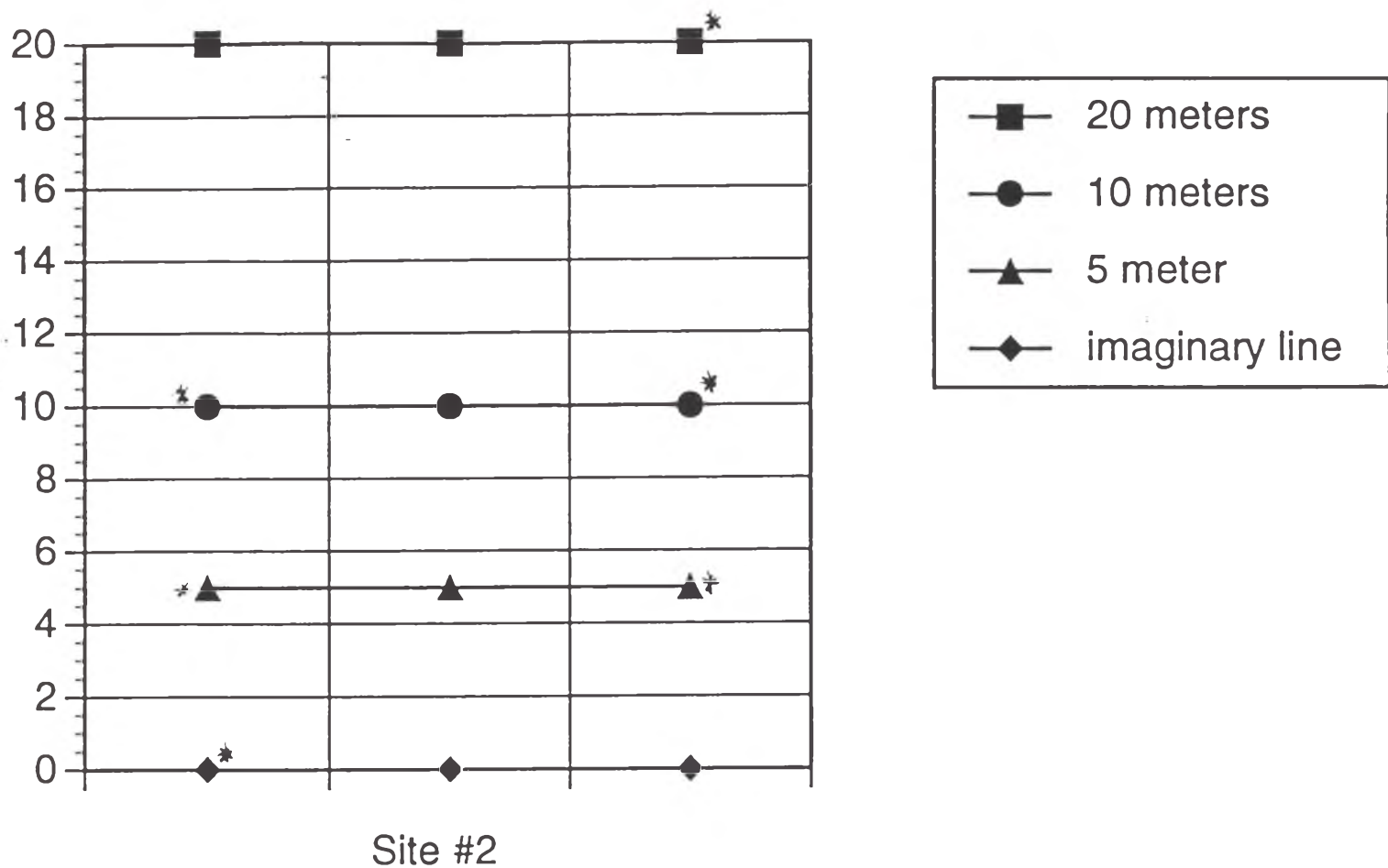


figure 3

\* sediment samples



Factors Influencing the Density and Distribution  
of *Cardisoma carnifex* in established areas,  
Including an Assessment of Burrow Fidelity  
and  
A Temporal Survey of the Road Kill of *Cardisoma carnifex*  
on the Island of Moorea, French Polynesia

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Gregory Battersby  
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University of California, Berkeley





## Abstract

We studied factors influencing the density of *Cardisoma carnifex* on the island of Moorea, French Polynesia. An assessment of burrow fidelity led us to the conclusion that each crab within a population is exclusively using one burrow. Using a food supplementation experiment, we concluded that food availability was not influencing population density during the period of this study. A strong correlation was found to exist ( $R^2 = 0.57$ ) between depth of the water table and the density of crab burrows. We also looked at movement of *C. carnifex* in relationship to phases of the moon. We found that the number of *C. carnifex* killed on the circum-Moorea road, showed a very marked increase during the three days immediately following the full moon. This supports the hypothesis that crabs are moving to the ocean at this time to spawn.

## Introduction

*Cardisoma carnifex*, (Herbst. 1794) is a poorly understood terrestrial decapod crustacean occurring in The Red Sea regions, and generally in the tropical Indo-West Pacific from East Africa to the Pacific islands. Until now no study had been conducted on the *C. carnifex* of Moorea, French Polynesia. On this island, *C. carnifex* occupies habitats ranging from roadsides and mud flats to coconut groves, varying greatly in density both within and among habitats. Wolcott (1988) hypothesized that food is possibly a limiting factor in some populations of herbivorous crabs. It has been observed on the islet of Aldabra, that in areas where *C. carnifex* is present the ground is bare; however, where the crab is absent on the islet, 10 cm of leaf litter has accumulated (Alexander 1979).

It has also been suggested that desiccation is possibly a controlling factor in the distribution of land crabs (Waterman 1960). When on land the crabs retain some "branchial water" which bathes their gills. If external water is available this pool is turned over every few minutes (Wood et al. 1983). In the absence of external water, the crabs will succumb to dehydration stress and eventually die (Hartnoll 1988). Wood et al. (1983) observed that *C. carnifex* is capable of withstanding desiccation for a maximum of 192 hours.

We investigated factors influencing the density of *C. carnifex* burrows. Specifically we looked at the relationship between burrow density and depth to water table and experimentally addressed the effect of food availability on burrow density.

Many investigations have also examined breeding and migration patterns of land crabs. Alexander (1976) observed a seaward migration of *C. carnifex*, that appears to be highly synchronized on a lunar and seasonal basis so that mass movements of the crabs occur. Thus, in addition to studying factors influencing crab density we conducted a survey of *C. carnifex* migration patterns with respect to the lunar cycle. We used the number of crabs killed in a given stretch of road as an index of nightly seaward migration.

## Study Species

*Cardisoma carnifex* (Tupa) is a common land crab found throughout the Pacific. Adult crabs are 8-13 cm in carapace width, chelipeds are unequal, especially in males (Bliss, 1968). Females must return to the ocean to deposit their eggs, juveniles return to the land quite small and remain terrestrial (ibid. 1968). *C. carnifex* usually lives in burrows that are dug to the water table, these burrows may be up to two meters in length (Micheli et al. 1991). Like other land crabs *C. carnifex* is an opportunistic scavenger, consuming a large variety of organic material. Individual crabs have been observed to travel up to 40 meters for food (Lee, 1988).

Hartnoll (1988) describes the genus *Cardisoma* as resident supertidally or out of fresh water, and active in air, most usually by night. They are generally burrowing or otherwise cryptic in habitat. They require regular access to water in which they can immerse themselves, either by visits to the sea or other sources, or to ground water in the base of the burrow, and they are dependent on water for the pelagic larval stages.

## Study Site

The main study site was located approximately 3.75 kilometers from the Gump Research Facility. This site was a representative example of *C. carnifex* coconut grove habitats seen around Moorea. The site was a well maintained grove of *Cocos nucifera* which covered a 600m x 600m stretch of the inland shoulder of the circum-Moorea ridge on the eastern side of Opunohu bay (fig. 1).

## Methods and Materials

### Burrow Fidelity

In order to determine whether the number of crab holes is a direct measure of the actual number of crabs, burrow fidelity was studied by capturing, marking and releasing crabs. Crabs were captured using box traps in the main study area (fig. 1). The trap consisted of a cardboard box supported on one end with a small stick approximately 8 cm in length, a string roughly 7 m long was tied to the stick. The box was weighted with a hollowed coconut husk and the trap was baited with pieces of bread. Crabs were seen emerging from their burrows and moving toward the trap. They entered the trap to grab the bait, at which time the string was pulled and the box would fall. Captured crabs were marked on the carapace with a number written in black permanent marker and a drop of fluorescent pink paint to make identification easier from a distance. The crabs were then released into the hole from which they emerged. The burrows were marked with a stake. The number of the crab was written on the stake as well as on a small pink flag that was attached to the stake.

Fidelity was assessed by recording any instances, during the six week period of study, when marked crabs were seen emerging or entering a burrow. The number of the crab as well as the burrow number were recorded.

### Food Supplementation

Three five meter by five meter plots were delineated in the coconut grove, that was our main study site (fig. 1). The selection of sites was meant to sample the variance of habitats in the grove. Site 1 was in a marshy area that periodically flooded, and had a considerable film of algae on the ground following flooding events. This site had a canopy of coconut trees. Site two was a barren area with no above ground vegetation and a canopy of coconut trees. Site three was similar to site two but the ground had some patches of grass and the canopy was comprised of both coconut and *Hibiscus tileaceus* trees. Each of the sites was marked with stakes and divided into quadrants. The burrows in each site were measured and mapped.

For two weeks following the initial mapping of the sites, food was introduced into two of the four quadrants of each site. The food was placed on the outer edge of the border between the two southern most quadrants. The food consisted of a pile of approximately 50 grams of flowers, grasses and leaves, and was introduced each morning. The two northern most quadrants of each sites were left as controls. Following the two weeks of food supplementation the sites were remapped and changes in the number of burrows were noted.

### Water Table

The relationship between burrow density and level of water table was investigated by the digging of holes to the water table at eight sites around the island (fig 1), and recording the density of crab burrows surrounding the holes. Sites were chosen to reflect the varying densities of crabs within the groves. The first hole in each grove was dug in an area of relatively high density, and subsequent holes were dug at five meter intervals in a direction of decreasing density. The number of holes dug at each site varied from three to seven, depending on the size of the grove. Holes were dug until the water table was reached. Once this was accomplished the hole was allowed to fill with water to a level that reflected the surrounding water table. Measurements were taken from the surface of the water to ground level.

Burrow densities were counted in one meter squared quadrats on the ocean side of the water table hole and on the side toward land. The values from the two plots were averaged to determine the density around the hole.

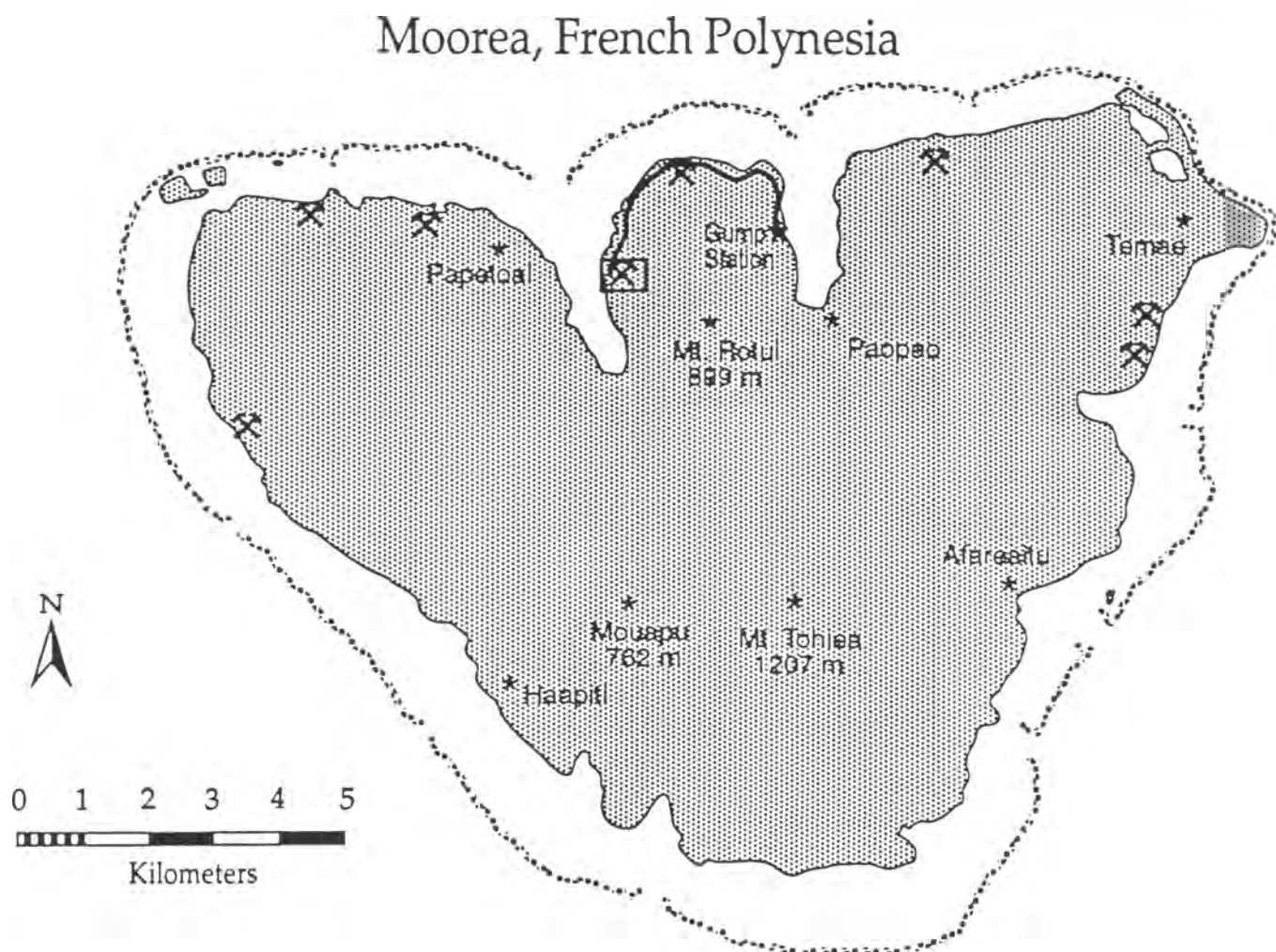
### Road Kill Survey

We used the number of crabs killed while crossing the road each night as an index of migration activity. We counted the number of dead crabs each morning on a 3.75 kilometer stretch of road extending from the Gump Biological Station to the study site used in the burrow fidelity/food supplementation experiment (fig 1). Each morning the previous night's crabs were counted and scraped off the road, so as to avoid counting the same individuals again the following day. Air temperature was also recorded for several nights.

Sexing of the dead crabs was reserved to only the carcasses that had the main body still intact. These were most often found along the side of the road. The carcasses in the road were almost always mangled, thus making sex determination difficult.



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



Site	Symbol
Food Supplementation	□
Hole Fidelity	X
Water Table	—

## Results:

### Burrow Fidelity

Over the course of our six week study, 15 crabs were captured and marked. 57 separate observations on these individuals were made. In every case the observed crab was associated with the burrow from which it was originally captured. There were no observations of crabs entering or leaving other burrows.

### Food Supplementation

Burrows were mapped and measured on October 28, 1992 and again on November 21, 1992. Burrow mapping indicated that entrance holes changed in size and location (appendix 1), but that over all numbers were more or less constant (table 1).

There was no indication that food supplementation had an effect on burrow density (table 1). There was no consistent difference between the sites that were supplemented and those that were not.

The null hypothesis for this survey was that food supplementation would not affect the density of burrows. In order to assess the statistical significance of the food supplementation results, we used a one tailed Wilcoxon's Signed-Rank Test. This test yielded the following figures: We obtained  $T_+ = 6$ ,  $T_- = 55$ , and  $T = 6$ , using an alpha value of .05, the Wilcoxon's Test allows us to say with 95% certainty that the null hypothesis, that food availability is not effecting burrow density, should not be rejected.

Table 1. Response of crabs to food supplementation.

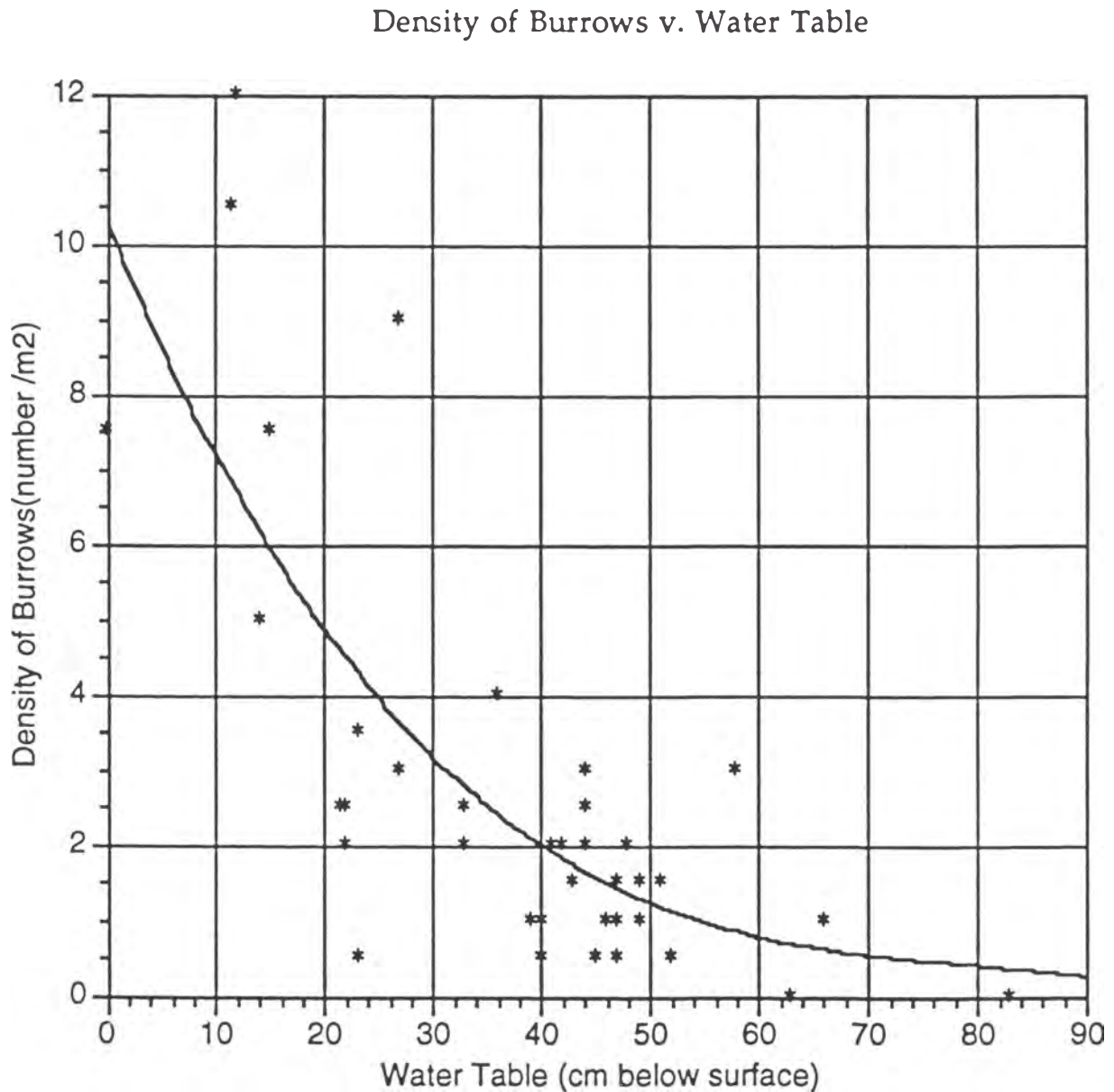
Site	Treatment	Number of Burrows		Change
		before supplementation	after supplementation	
1	control	133	178	+45
	supplemented	89	91	+2
2	control	9	10	+1
	supplemented	15	9	-6
3	control	11	14	+3
	supplemented	8	12	+4



## Water Table

In the six weeks of our study, 42 water table holes were excavated. We found a strong inverse correlation between crab density and the depth of the water table,  $R^2 = 0.57$  (fig 2). This suggests that *C. carnifex* is preferentially locating its burrows in areas where the water table is more accessible.

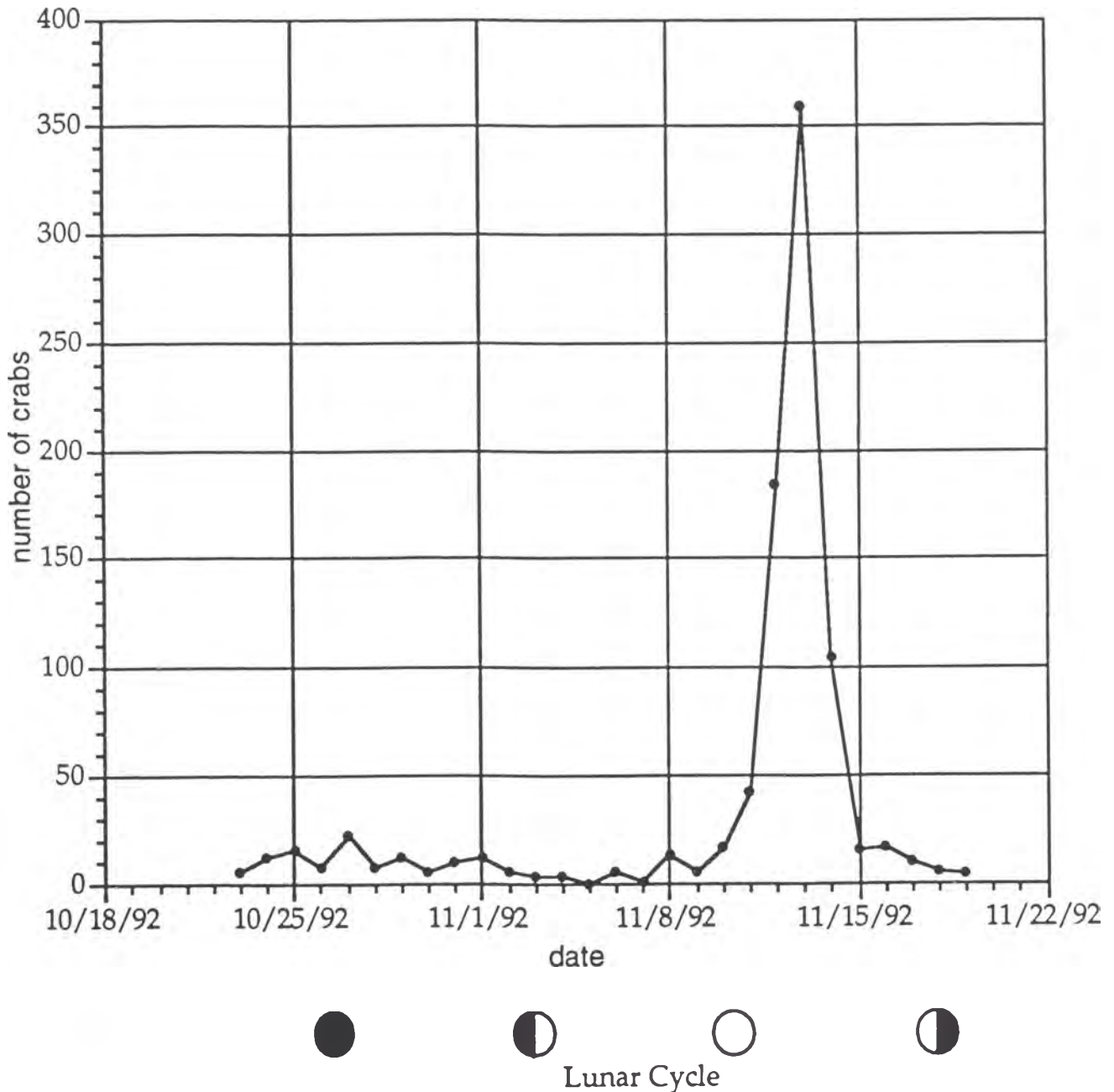
Figure 2. Relationship between water table and burrow density.



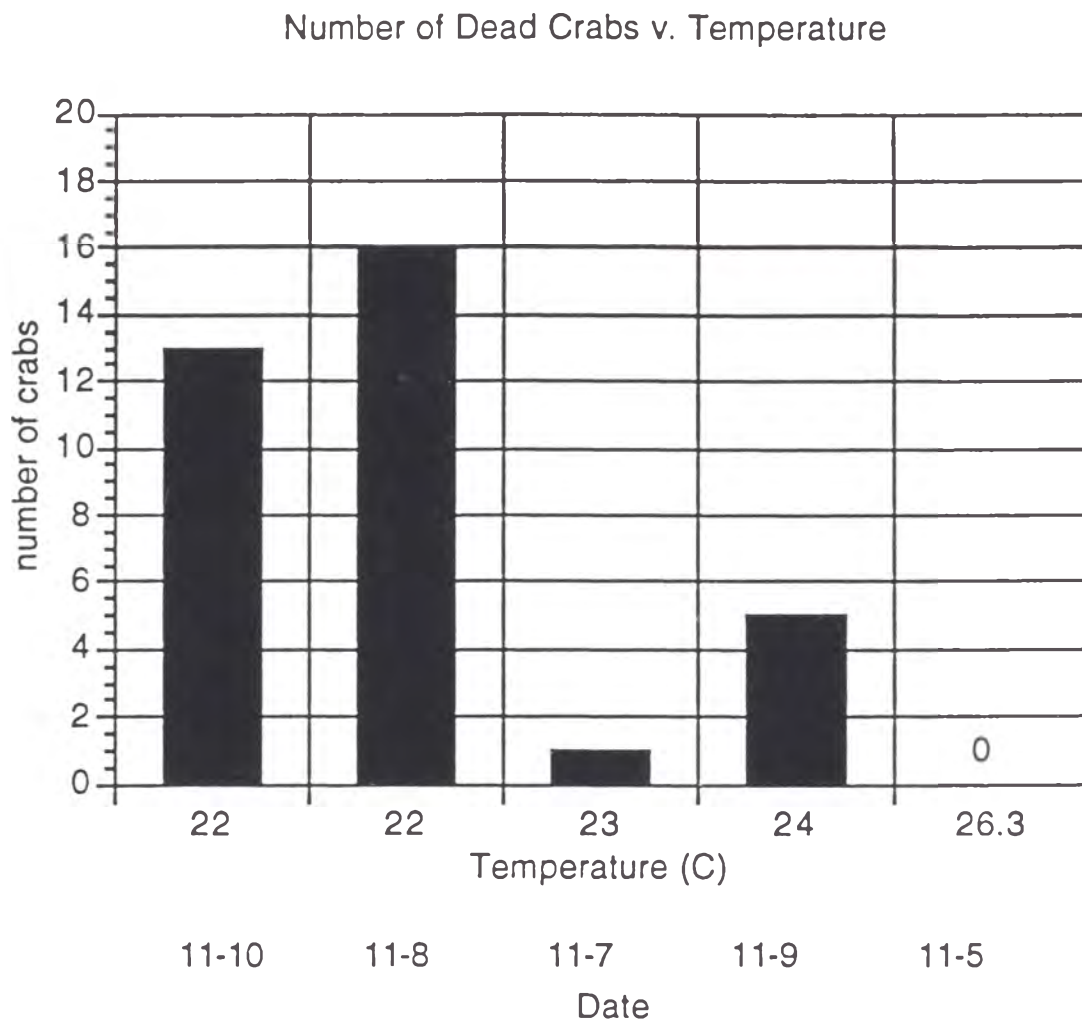
## Road Kill

Crabs killed by traffic in the road (crab migration/movement), showed a peak immediately following the full moon (fig. 3). During this four day period there were 10-30 times more crabs killed on the road than the rest of the month. Mortality during low periods may be partially explained by nighttime temperature, with fewer crabs being killed on the 3 nights where the temperature exceeded 22 C (fig. 4). While the sample size is small there appear to be more crabs killed on cold nights than warm ones, which may suggest thermoregulatory behavior. Relative proportions of male to female crabs did not vary considerably between the four days following the full moon and the rest of the month (fig 5).

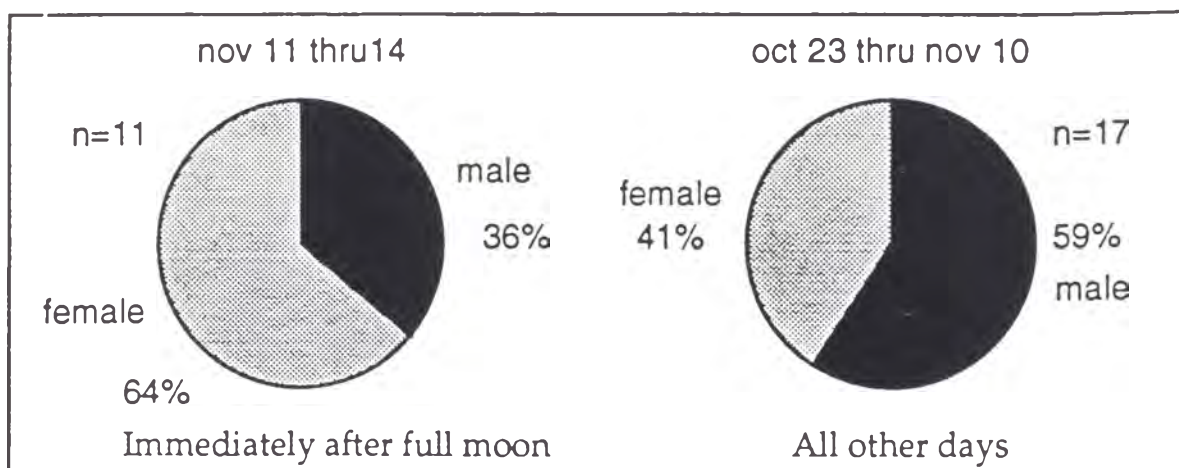
**Figure 3:** Crabs Killed per Night along a 3.75 km stretch of Road between Oct. 23 and Nov. 19, 1992



**Figure 4:** Number of dead crabs collected versus air temperature. The temperatures were recorded between 9 PM and 12 AM



**Figure 5.** The relative percentages of male versus female crabs for the four days surrounding the full moon, and for all other days.



## Discussion

### Burrow Fidelity

In the Aldabra study of terrestrial decapod crustaceans (Alexander 1979), population studies were carried out by counting the number of burrows. This census was conducted under the assumption that one crab excavated and used one hole. We set out to determine the validity of this assumption by conducting an experiment on burrow fidelity. The results obtained from our study support a one to one correspondence between crab and burrow, thus validating the techniques used in the Aldabra study and substantiating our burrow density mapping methods.

### Food Supplementation

The null hypothesis for this survey was that *C. carnifex* is not food limited and thus, food supplementation would not affect the density of burrows. The Wilcoxon's Test allows us to say with 95% certainty that this null hypothesis should not be rejected, and that food availability is not influencing burrow densities. It is apparent that the relatively short duration of this study could have been a significant factor in the results obtained. It has also been suggested that quality rather than quantity of food is a limiting factor in populations of terrestrial decapods. Herbivorous crabs appear to prefer high nitrogen food under many circumstances (Wolcott 1988). *C. carnifex* prefers to browse on the shoots of certain plants (Alexander 1979). Shoots on average have a higher proportion of non structural tissues, and thus a lower carbon:nitrogen ratio (Mattson 1980).

Our maps (appendix 1) suggest that in spite of a relatively stable population size (table 1), there is considerable burrow turnover. However, because of the dryness of the upper soil layers, burrow entrances often collapse and are dug again, while the deeper parts, which probably do not collapse as frequently, continue to be inhabited by the crabs. Therefore, only entrances are rearranged and often repositioned (Micheli et al. 1991).

### Water Table

Even the most terrestrial of land crabs have poor resistance to water loss and it is only by appropriate behavior patterns that they are able to survive out of water (Hartnoll 1988). *Cardisoma* is a pan tropical lowland genus, living in muddy soils where its burrows can reach ground water (Bruce-Chwatt and Fitz-John 1951). Thus, we hypothesized that the density of *Cardisoma carnifex* would be directly related to the level of the water table below the surface. During the course of our study, we dug 42 holes down to the water table and found that crab density is inversely correlated with water table depth (fig. 2). While it has been noted that burrows may be as deep as two meters (Micheli et al. 1991), we did not find any sites with a water table below 83 cm using our sampling technique. It is possible that these areas are too dry to support crab populations, or that crabs would preferentially dig their burrows in areas where the water table is more accessible. This question certainly deserves more attention.



## Road Kill Survey

A lunar periodicity to seaward migration in land crabs has been documented in a number of crab species. Spawning is generally programmed so that brood release occurs at a time most appropriate for the growth of the young (Adiyodi 1988). This is often concurrent with the highest tides of the lunar cycle (Wolcott 1988). Crabs of the species *Gecarcoidea natalis* release their eggs within a few hours of midnight on the days immediately following the full moon (Klaassen 1975). In *Cardisoma guanhumi*, closely related to *C. carnifex*, seaward migrations of ovigerous females to deposit larvae has also been observed (Wolcott 1988). These migrations can sometimes be as long as 8 km (ibid. 1988). The orientation or navigation systems involved in migration have not been studied in detail. In many species, males also participate in migration (ibid. 1988). Often this migration to the sea involves considerable danger. In developed areas this danger includes traffic. Hickey et al. (1984) estimate the annual road kill of *Gecarcoidea natalis* on Christmas island at 600,000 crabs per year. On Moorea, we observed a 30 fold increase in the number of *Cardisoma carnifex* killed by cars on the night three days after the full moon, compared to the daily totals preceding the full moon (fig. 3). On this day 357 crabs were counted versus an average of approximately 12 for the days before the full moon. The relative proportions of female to male crabs also increased (figure 5), suggesting that migrations are female biased, although our sample size does not allow us to draw any statistically significant conclusions.

Most crabs are limited to a modest temperature range of between 15 and 40 °C, and they use varying behavioral and physiological methods for regulating their temperature (Herreid and Full. 1988). On the island of Moorea the daily fluctuation was well within this range. However, the data in figure 4 supports the hypothesis that crabs are using the road for thermoregulation. They are ectothermic, and are being killed by cars more often on cold nights than warm ones (fig. 4). The question of whether *C. carnifex* is using the roads in Moorea for thermoregulation does, however, deserve more attention, as temperature data was only recorded for five nights.

The extent to which an increase in traffic could cause an increase in the number of dead crabs was also considered. However, given the size of the island of Moorea, a 30 fold increase in the traffic around the island would be an event that would not go unnoticed.

## Conclusions

We set out to address two primary questions in our six week study: (1) how are food and water table affecting density of *C. carnifex* and (2) is there a periodicity in the number of crabs crossing the road each night?

The density of *C. carnifex* burrows varies considerably around the island and within habitats. As part of this study we set out to address what factors influence this density difference. We first determined that burrow number was an accurate representation of population size. This was followed by a food supplementation study, from which we concluded that food availability does not effect the density of crab burrows. Perhaps if this portion of the study were to be conducted again a food

source higher in nitrogen would be preferable as quality rather than quantity of food has been previously observed to be a limiting factor (Wolcott 1988). We also investigated the hypothesis that land crab density was related to water depth, based on the observation that many land crab species are sensitive to desiccation (Hartnoll 1988), and found strong support for this hypothesis.

It has been observed in other studies that the behavioral repertoire of the family *Geocarcinidae*, to which *C. carnifex* belongs, consists of a strikingly unique and consistent breeding migration pattern. This seaward migration has been observed to be highly synchronized on a lunar and seasonal basis (Alexander 1976). *C. carnifex* on Moorea appears to behave in a way consistent with these prior studies. The large, paved road which surrounds Moorea serves as a dividing line between the lagoon and the coconut groves frequently occupied by *C. carnifex*. As such, it serves also as a reflection, in terms of road kill, of the number of *C. carnifex* moving in the direction of the sea on a nightly basis. Our survey showed a striking increase in the number of crabs participating in this seaward migration on the days immediately following the full moon. Crabs killed prior to the noted overall increase probably represent casualties that result from thermoregulatory behavior or foraging activity. This is also consistent with Polynesian myths which associate a lunar periodicity with the activity of the Tupa Au', the ghosts of the recently dead. According to this myth the ghosts possess the bodies of the crabs on the three days following the full moon, and move about the island (Bubba 1992).

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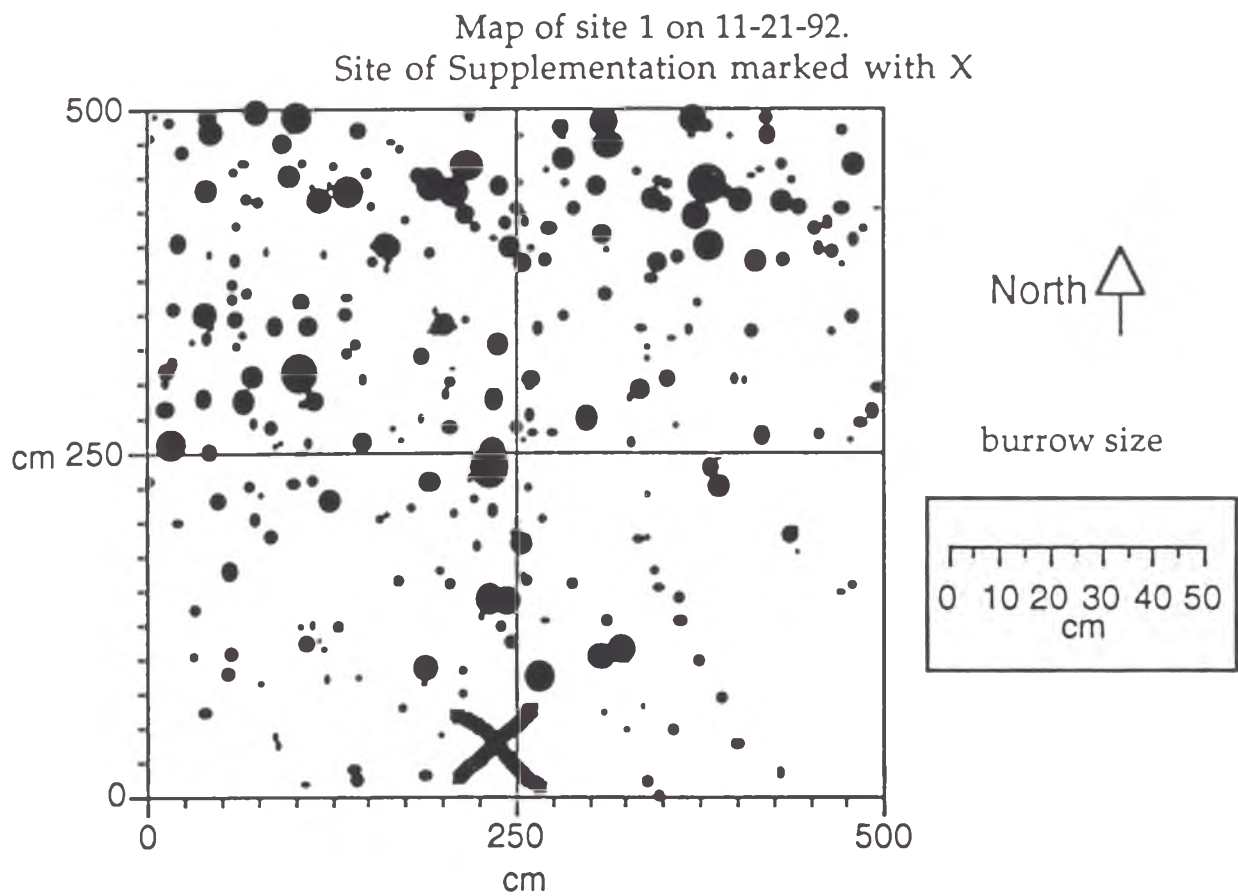
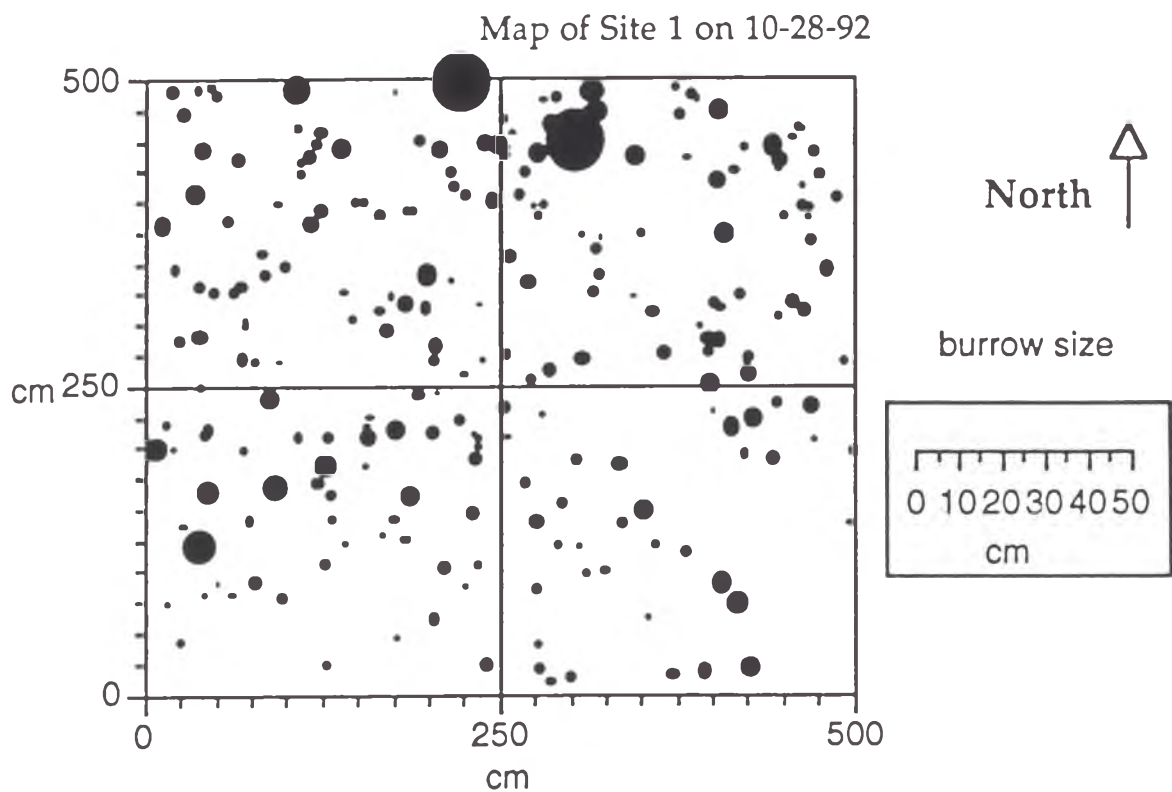


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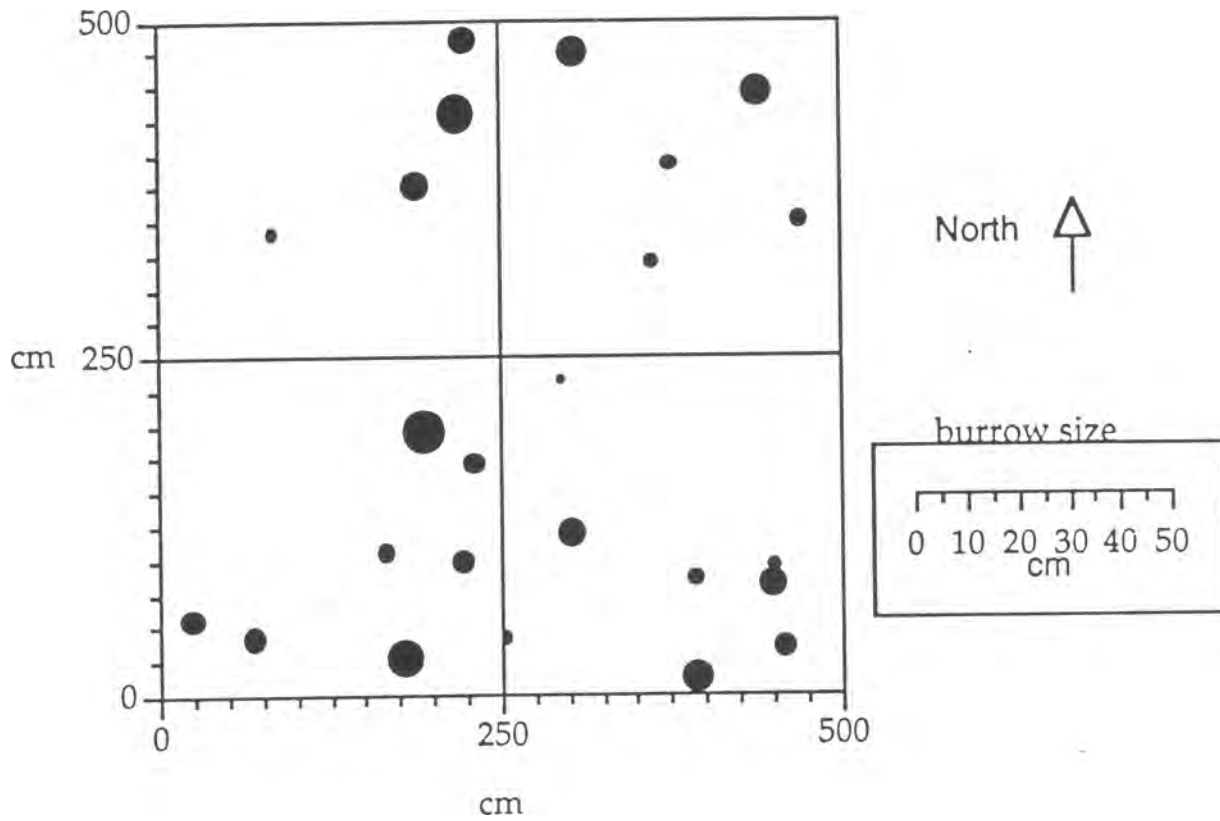
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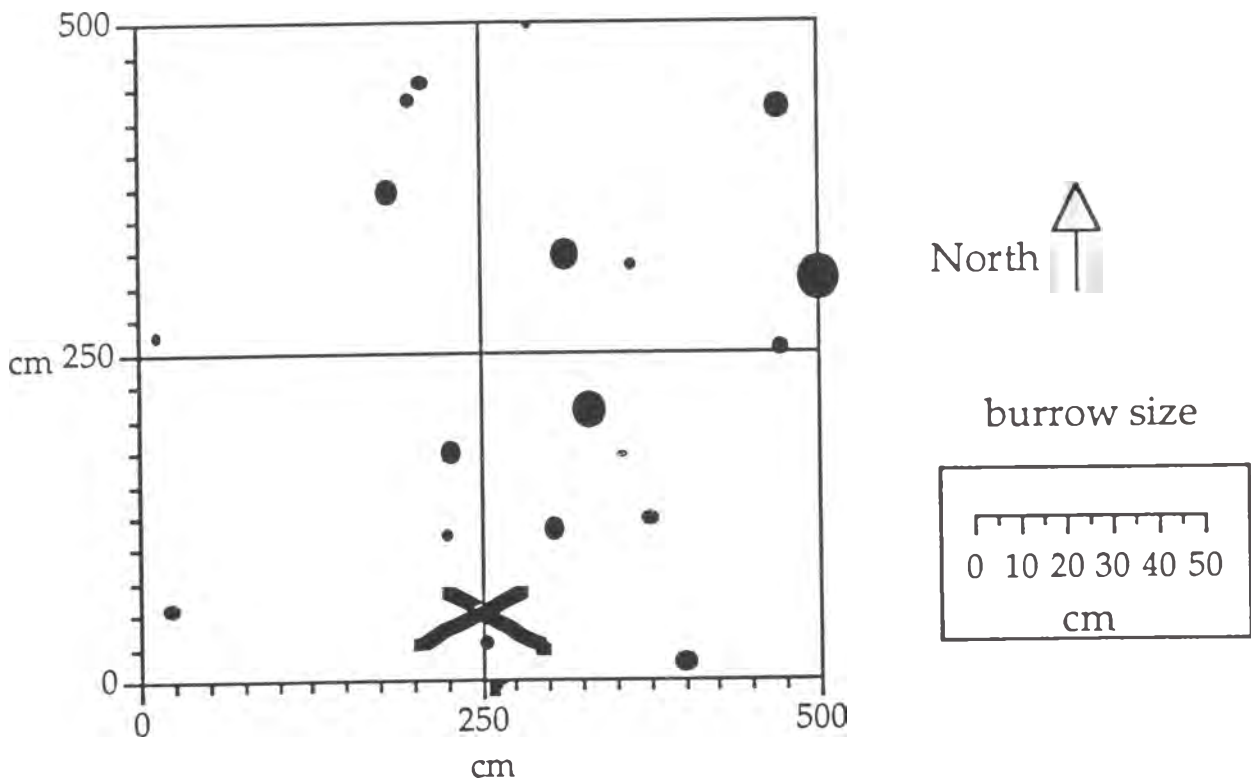
Appendix 1 Maps of sites before and after food supplementation



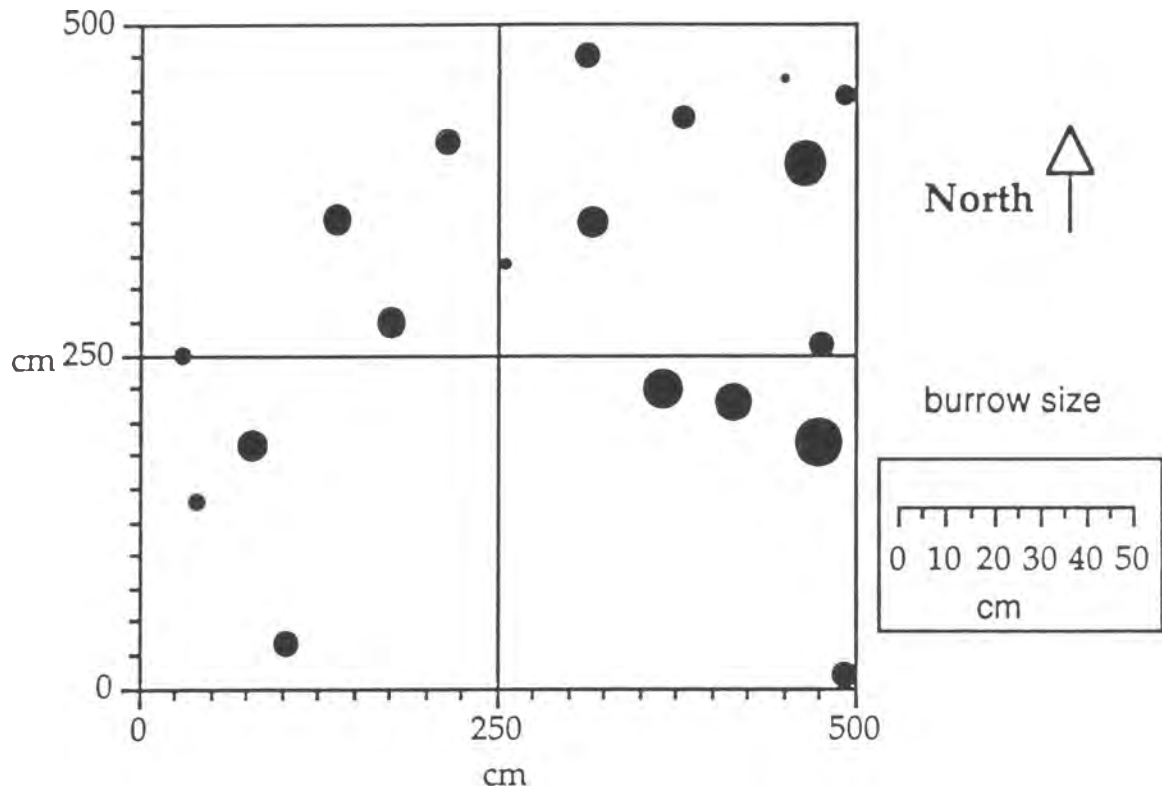
Map of Site 2 on 10-28-92



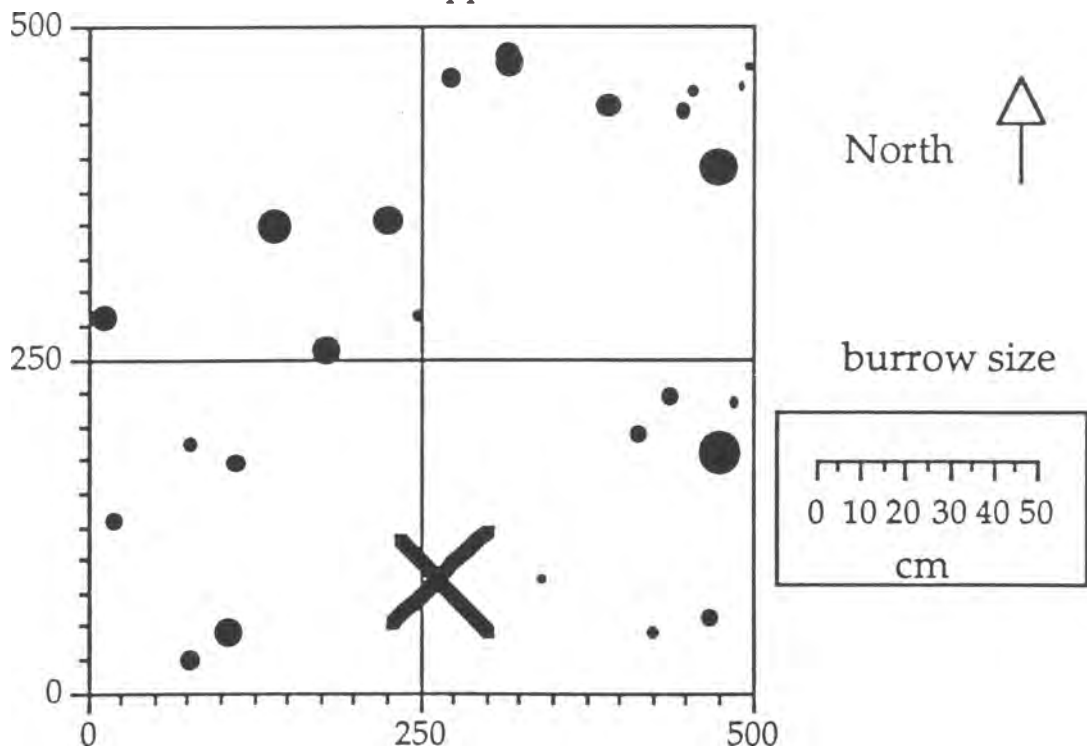
Map of Site 2 on 11-21-92  
Site of Supplementation Marked with X



Map of Site 3 on 10-28-92



Map of Site 3 on 11-21-92  
Site of Supplementation Marked with X





## Recognition Abilities of the Stomatopod *Pseudosquilla*

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## Abstract

*Pseudosquilla* (new species) stomatopods live in rock and coral cavities in the low, subtidal zone that also houses a variety of crabs, shrimp, octopus and other stomatopods. Consequently, these animals have evolved aggressive strategies that enable them to defend their territories successfully. The risk of injury or fatality in any territorial battle is great, especially when the stomatopods encounter other stomatopods ( *Gonodactylus festae*, ) other *Pseudosquilla*, or one of its competitor/predators, *Octopus joubini*. This paper will prove the ability of *Pseudosquilla* to recognize different chemical cues, classify their opponents in terms of fighting ability, and subsequently modify their behaviors accordingly to the opponent.

## Introduction

*Pseudosquilla* (new sp.) must constantly defend their rock cavity homes as they live in a highly populated low subtidal region. They compete for resources with several members of the community , including other *Pseudosquilla*, *Gonadactylus festae* (another species of stomatopod) and a small, cavity dwelling octopus, *Octopus joubini*.

Clearly, an ability to recognize the chemical cues exuded by these different animals would prove highly beneficial. For example, an animal that has lost his cavity could decide whether or not an entry into a presumably occupied cavity would be worth the risk of a possible battle. There is extensive knowledge of the ability of invertebrates to recognize conspecifics by chemical cues. The banded shrimp *Stenopus hispidus* ( Johnson 1977) and the clown shrimp, *Hymenocera picta* (Seibt, 1974) can recognize chemical cues given by their mates. ( Caldwell, 1979) found one species of stomtopod, *Gonodactylus festae* that uses chemical cues as an integral part of its competitive and territorial behavior with *Gonodactylus bahiahondensis*. Additionally, *G. bredini* has been reported to have the ability to recognize its competitor, *Octopus joubini*, although not on an individual basis (Caldwell and Lamp, 1981.)

This paper examines the ability of *Pseudosquilla* to recognize the chemical cues of other *Pseudosquilla*, *Gonodactylus festae*, and *Octopus joubini*. It will also explore the various responses of the animal to the chemical stimuli and any possible differences between male and female behaviors. Essentially, the paper will attempt to prove that the *Pseudosquilla* stomatopods have the ability to recognize different chemical stimuli, and consequently, the appropriate animals and apply the appropriate behaviors.

## Study Site

All animals used in the manipulations were found in the subtidal region (less than two meters in depth) at the UC Gump Field Station, Moorea, French Polynesia. All manipulations were conducted in the Gordon and Betty Moore Field Laboratory at the UC Gump Field Station. See attached map, figure #3.

## Methods and Materials

Nineteen *Pseudosquilla* were collected for the study; nine females and ten males. All animals were in the adult stage of development. The animals ranged from 20 centimeters to 24.5 centimeters in length. Ten *Gonodactylus* stomatopods and four octopus were collected. After capture, the animals were sexed, measured, numbered and placed in separate plastic containers with a mesh cover, then lowered into a flowing salt water tank. The animals were fed shrimp twice weekly. All remaining live animals were returned to their environment within four weeks of capture. Moulting animals were not used in the manipulations.

Twelve hours before the manipulations, the animals were placed outside of the water tank, still in their separate containers. One hour before the manipulations, water was removed from the octopus, *Gonodactylus* and both male and female *Pseudosquilla* containers, to be used in the experimental runs. This was to allow the animal's scent to accumulate in and disperse throughout

the water. I also wished to exclude the possibility of pheromones from the *Pseudosquilla* or any warning or aggressive chemical cues from the other animals.

For the manipulations, the animal was placed in a 12 1/2 cm X 6 1/2 cm X 3 1/2 cm rectangular plastic arena filled 3/4 full of fresh sea water. The arena had a small hole (approximately 1.5 cm in diameter) drilled in one of the long ends, and a blackened 45 ml vial could be attached. The vial contained one of the following: fresh sea water, water from the home of a *Gonodactylus*, water from the home of an octopus, or water from the home of a same-sex *Pseudosquilla*. All defined behaviors were recorded according to time. The behaviors were defined as follows:

AGGRESSIVE-

L- Lunging at hole-lunging at hole then retreating

HH- Head first, quick entry into hole

S- Sitting in front of hole, not entering (also investigatory)

DEFENSIVE-

A- Antennulation

T- Tail first approach to hole, specify whether or not entered

HESITATIVE-

HN- Head first entry into hole, slowly

INVESTIGATORY-

P- Peering around corner of hole, eyes only

S- Sitting in front of hole, not entering (also aggressive)

All "encounters" were timed from the initial entry into the tray until the animal either entered the vial completely and remained in the vial, or it refused to approach the entrance seven minutes after the last aggressive or investigatory behavior was observed. Twenty-four hours later, the same animal was placed in the arena. The water in the vial would again contain one of the previously listed types of water, obviously not the one it had encountered before. The stomatopods had a specific order of encounters assigned to them, each order being different. Between each encounter, the tray and vial were rinsed thoroughly with hot tap water and then with fresh sea water. Within four days, (and three twenty-four hour intervals,) the individual stomatopod encountered four different types of water.



## Results

### Fresh Sea Water Vial

Every Stomatopod entered the fresh sea water vial within 45 seconds of its first approach to the entrance (approach must be within 2 cm of entrance.) All but one animal entered head first, without hesitation. One animal showed aggressive behavior, four animals investigated the vial before entering and no animals showed defensive behavior.

### *O. joubini* vial

The vial containing water from the octopus home was entered by only four of nineteen animals, three of which entered after three minutes following their last approach. The animal would enter the tray, locate the entrance by lunging or peering, then retreat. Usually this behavior was followed by antennulation, moving about the tray, and approaching the entrance any number of times. The "encounter" was ended if the stomatopod failed to enter the vial seven minutes after last approaching the entrance. There was no significant difference between the entrance times for the males and females (Standard t-test -0.441, significance 0.671.) There was also no observable difference between the male and female behavior patterns.

### *Gonodactylus* vial

The vials containing water from the *G. festae* home evoked basic patterns of behaviors, involving the previously defined behaviors. Eighteen animals entered the tray and located the entrance within forty seconds. The animal would then display various combinations of the following behaviors: antennulation, lunging, peering, head first entries, tail first entries, head first approaches, tail first approaches, and sitting in front of the entrance. There was no observable difference between male and female behaviors in the *Gonodactylus* vial manipulations. There was also no significant difference between the entrance times between the males and the females (Standard t-test 0.333, significance 0.748.)

### *Pseudosquilla* vial

The vial containing water from the same-sex *Pseudosquilla* home brought about the same patterns of behavior as the vial containing *Gonodactylus* water. One animal failed to enter the vial. All animals located the entrance within 40 seconds.

Again, there was no significant difference between the male and female entrance times (Standard t-test 0.658, significance 0.529.) There were also no observable differences.

The times between first recognition of the entrance and complete entry into the vial for each animal (in each vial) were computed and compared with values for complete entry into all other vial types, for that individual animal. An animal not entering the vial after seven minutes was assigned a time of 420 seconds for the seven minute observation period. Using the Wilcoxon signed-ranks test, the following values were obtained:

Compared Vials	T value	N value	P value
Blank/ <i>O. joubini</i>	0	19	<0.001
Blank/ <i>P. (new sp.)</i>	0	19	<0.001
Blank/ <i>G. festae</i>	3	19	<0.001
<i>O. joubini</i> / <i>G. festae</i>	1	19	<0.001
<i>O. joubini</i> / <i>P. sp.</i>	3	19	<0.001
<i>G. festae</i> / <i>P. sp.</i>	15	19	<0.001

#### Figure #1

The entry times per animal are presented in terms of that individual animal. Each animal is analyzed as a discrete set of data.

#### Figure #2

The entry times are presented in terms of the type of vial that the animals entered. All data from the encounters is compiled and arranged in increasing order.

Each trial is separated, the individuals no longer remain discrete variables, and the entries are graphed as a function of time.

### Discussion

The results of the manipulations demonstrate that the *Pseudosquilla* used in the manipulations do have the ability to differentiate between various competitors and potential predators. Furthermore, these animals can identify their competitors by species. It is possible that stomatopods associate the odor of an animal with that of its ability to fight. For example, a *Pseudosquilla* (new species) is very likely to

lose in an encounter with an *O. joubini*. I observed ten *Pseudosquilla* and *Gonodactylus* encounters with *O. joubini* in the laboratory and in every instance the octopus killed and consumed the stomatopod. This association of chemical cue and the specific danger that the associated animal represents is clearly demonstrated by the fifteen stomatopods that refused to enter the vial containing water from the octopus home.

Similarly, *Pseudosquilla* was also hesitant to enter the cavity when it contained *Gonodactylus* water, but not as hesitant as if faced with the odor of an octopus. The stomatopods entered the same-sex *Pseudosquilla* vial faster than the vial containing octopus water (Wilcoxon signed ranks test  $T=3$ ,  $N=19$ ,  $P<0.001$ .) Additionally, the *Pseudosquilla* vial was entered significantly faster than the *Gonodactylus* vial ( $T=15$ ,  $N=19$ ,  $P<0.001$  Refer to figure #2.) A *Gonodactylus* may be a formidable opponent for *Pseudosquilla*, though probably not as formidable as a predatory octopus. A stomatopod can anticipate encounters with an octopus to be almost certainly fatal, as reflected in their refusal to enter the cavity they suspected to contain an octopus. However, they became increasingly aggressive when they encountered the *Gonodactylus* and *Pseudosquilla* vials, respectively. This most certainly reflects their ability to classify their opponents. A *Pseudosquilla* is a much more even match for another *Pseudosquilla* than is a *Gonodactylus*. *G. festae*, being a "smasher", has the fighting advantage against a "spearing" *Pseudosquilla*. "Smashers' " raptorial appendage has evolved as a heavily calcified dactylus heel while "spearers" have a thinner raptorial appendage equipped with two or more barbs. The strike of a smasher is much more powerful than the strike of a spearer. (Caldwell, 1989.)

Clearly then, *Pseudosquilla* is able to classify their opponents in terms of their fighting ability. I have proven their ability to recognize and differentiate between three different species of animals, and subsequently their ability to associate the odor with the aggressive behaviors of that species of animals. I suspect that *Pseudosquilla* may also recognize individuals within its species. *G. festae* has been shown to display this ability (Caldwell, 1985.) (Caldwell, 1985) has also demonstrated this ability with several members of this genus. The stomatopod can anticipate the aggressive tactics of another group of animals and adjust its strategy according to the situation. This may later be shown to be indicative of an ability of all stomatopods to recognize individuals within their species, and possibly in different genera. The advantage of this skill may prove invaluable when encountering *Gonodactylus*

individuals, for example, as its raptorial strike is potentially lethal (Berzins and Caldwell, 1983.)

The stomatopod lives in a dangerous and competitive environment, *O.ctopus joubini* being one of many aggressive neighbors and potential predators. In such a habitat, the evolution of recognition and classification behaviors is advantageous. It is also indicative of the generally held belief that with any limiting resource (such as territory) there evolves an intense competition and subsequently advanced communication tactics. A cavity provides a place to hunt, mate, moult or protect eggs, as well as to hide. A stomatopod without a cavity is extremely vulnerable. This supports the idea that communication systems are well developed in the stomatopods (Caldwell, 1982.) Additionally, it also provides new evidence for recognition and applied appropriate behaviors in the invertebrates, where examples were previously found in vertebrates.

## Acknowledgements

I would like to thank the following people for their assistance: Larry Vaughn, Roy Caldwell, David Stoddart, Carla d'Antonio, Mary Gleason, Jere Lipps, and my parents, Charles and Marilyn Elmquist.

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Entry Times Per Individual Animal

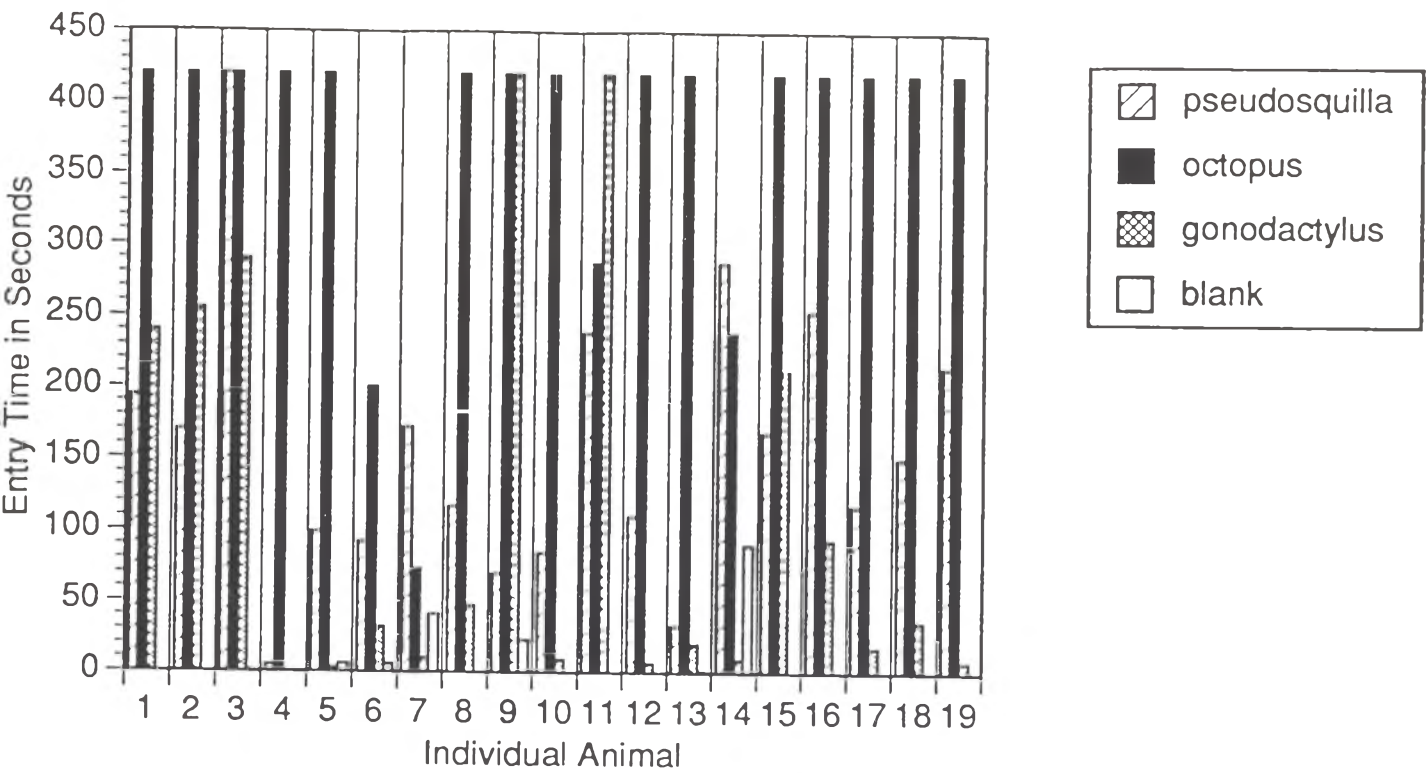


Figure #1- The entry times for the *Gonodactylus*, *Pseudosquilla*, *Octopus* and fresh water (blank) vials are charted per individual animal.

## Combined Entry Times

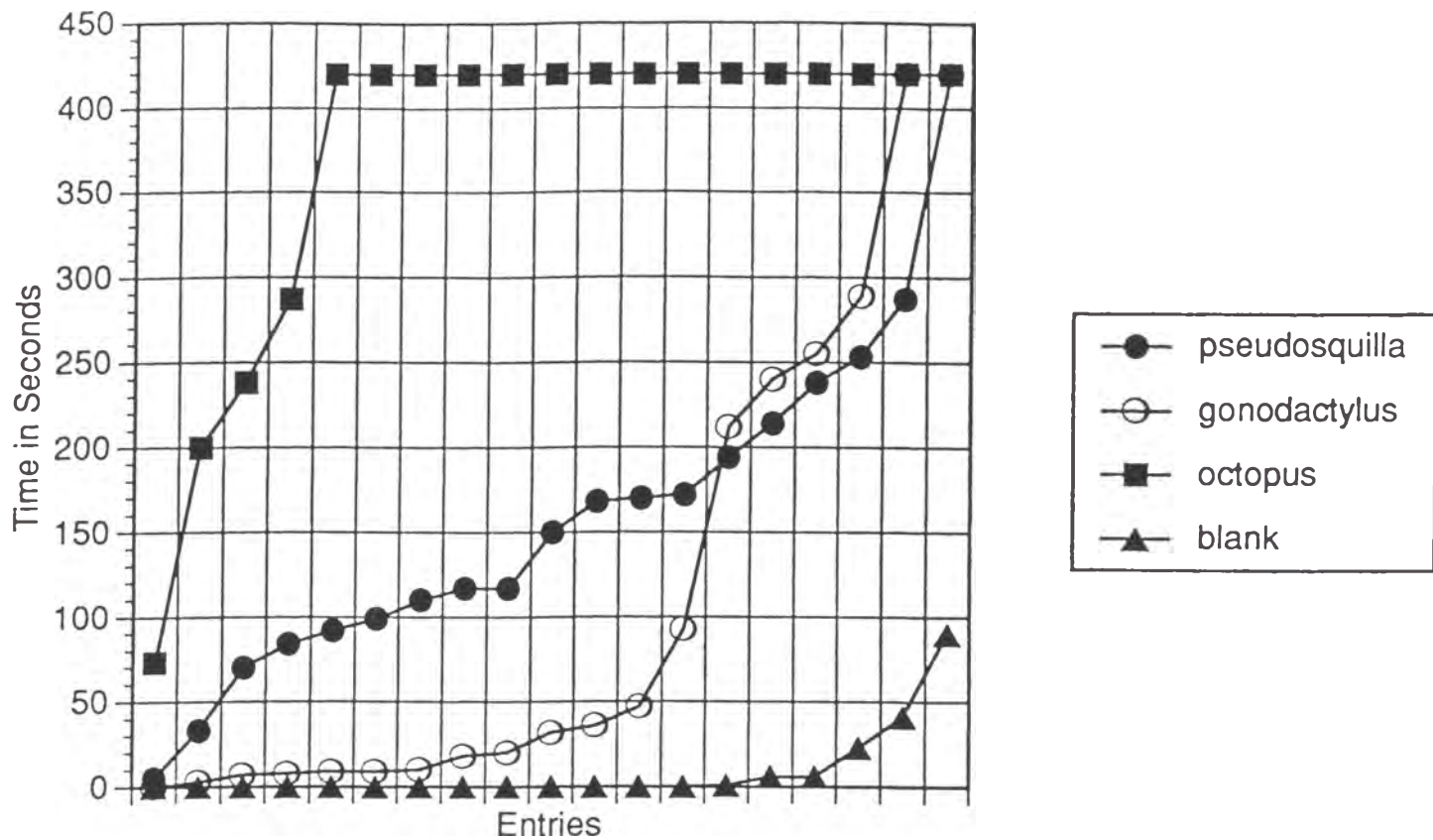


Figure #2- Animal entry times are arranged in increasing order for each type of vial (number on x-axis does not necessarily correspond to that particular animal.) Fifteen animals refused to enter the octopus vial after seven minutes. The animals entered the fresh water (blank) vial the fastest, followed by the *Pseudosquilla* vial and the *Gonodactylus* vial, respectively.

# Moorea, French Polynesia

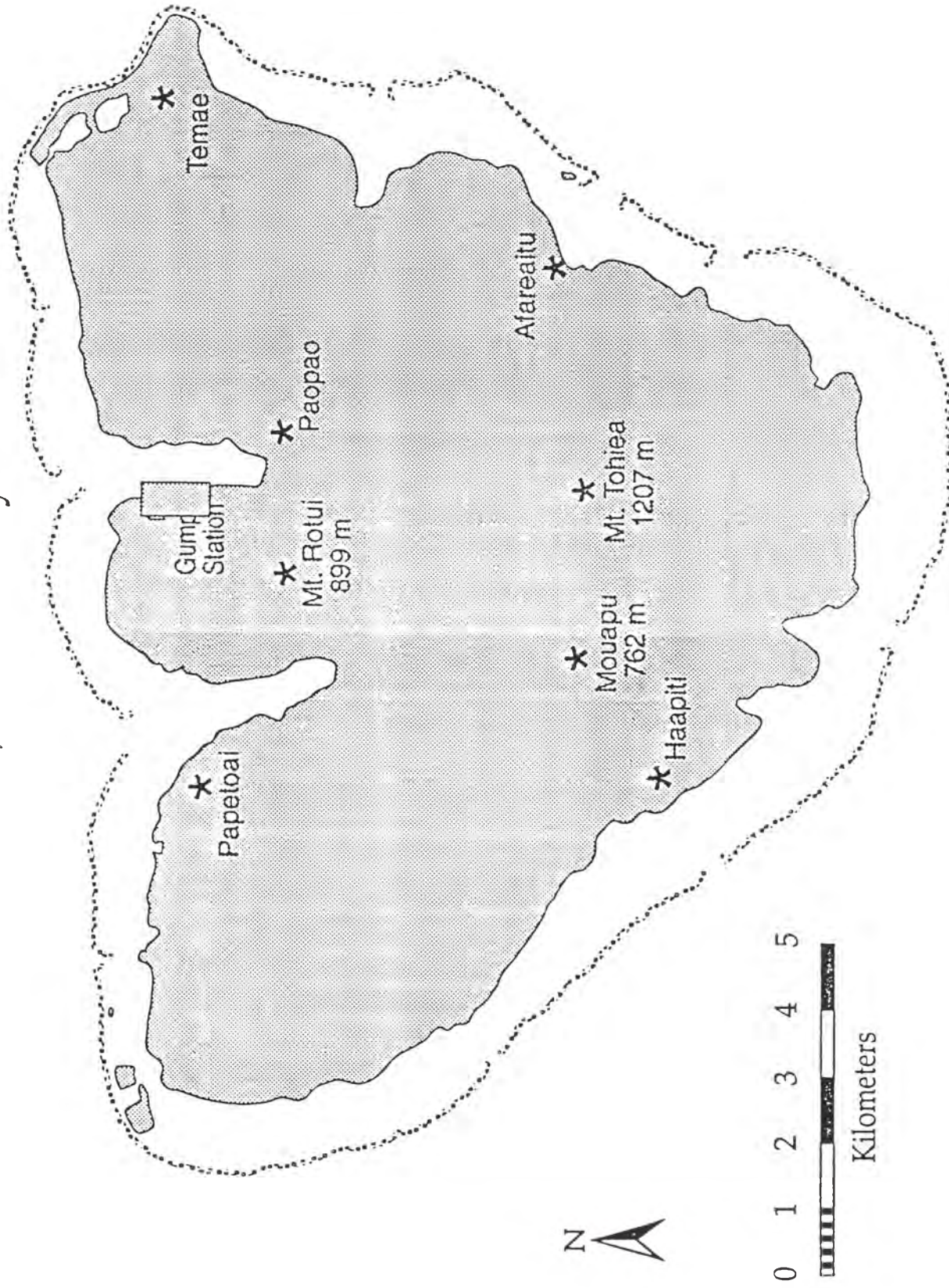


Figure #3- Study Site Location 



**Aggregations of *Diadema savignyi*: A Comparison of Their Diurnal Migration, and Group Constancy Between Two Different Habitat Types on Temae Public Beach, Moorea, and the Presence of Alarm Response in This Species.**

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Fall 1992





# Aggregations of *Diadema savignyi*: A Comparison of Their Diurnal Migration, and Group Constancy Between Two Different Habitat Types on Temae Public Beach, Moorea, and the Presence of Alarm Response in This Species

## Abstract

*Diadema savignyi* occupies two areas of the lagoon at Temae Public Beach. It is found on the sandy near-shore area and around coral heads. The behavior of these large near-shore groups of *D. savignyi* is compared to the behavior of *D. savignyi* which aggregate around coral heads. It was found that the number of groups and the number of individuals on the coral heads remained relatively constant for the 15 sample days. Conversely the aggregations on the sand seemed to vary each day. The presence of an alarm pheromone in this species was also examined and it was found that *D. savignyi* will respond by moving away when another conspecific is crushed.

## Introduction

Urchins in the genus *Diadema* are a common feature of coral reefs throughout the world. Their influence on algal communities is well known (Ogden 1973, Pearse 1972, Sammarco 1982, Lawrence and Hughes-Games 1971, Smith 1969, Lewis 1964, Lawrence 1975, Randall, Schroeder and Starck, II 1964, Nelson and Vance, 1979, Vance and Schmitt 1979, Carpenter 1990). The sea urchin *Diadema savignyi* occurs in the IndoPacific and can be identified by its dark black color, a bluish-purple iridescence around its test, and its long, slender, extremely sharp spines. It is closely related to the tropical eastern and western Atlantic species, *Diadema antillarum*. Fewer studies have examined the habitats, movement patterns and foraging behavior of *D. savignyi*, but it is known that *D. antillarum* inhabits rock, coral reef, mangrove roots, seagrass beds, and sand flats (Randall 1975). *Diadema antillarum* is known to

forage out from coral heads during the night (Pearse 1972) and return to the reef before daylight. This pattern appears to be common in *Diadema* (Nelson and Vance 1979) and most individuals inhabit crevices and within and around coral heads.

*Diadema savignyi* inhabits two general areas of Temae Public Beach on the island of Moorea, French Polynesia: sand flats and coral heads on the fringing and barrier reef. Larger aggregations of *D. savignyi* are found in the near-shore sand flats of Temae Public Beach than anywhere else on the island. The large aggregations of *D. savignyi* on the littoral area of the beach may be related to a lesser number of predators there (Randall 1975) or may be the result of a large population size due to factors influencing recruitment. *D. savignyi* is also found on and around coral heads further down the beach.

The questions I address are: Why do some *D. savignyi* aggregate on the sand flat while others aggregate in, on, or around crevices in coral heads? Is there group fidelity or a homing response and if so, does it change from day to night, and does it differ between the two habitats?

In addition it is also reported that *D. antillarum* possesses an alarm response when it is exposed to body fluids of another urchin (Snyder and Snyder 1970). The presence of this in *D. savignyi* was investigated.

## **Materials and Methods**

Field work was conducted during the month of November, 1992 on the northeast side of Moorea, French Polynesia. Observations were made at two areas of Temae Public Beach. The first area consisted of a 20m X 30m area starting 5m out from the shore in 2.0 to 2.5 m of water in the lagoon at Temae Public Beach. The substratum consisted mainly of sand topped with bits of dead coral covered with green algae.

The second area was down the beach to the west of the first area. It consisted of three

coral heads 6m out from the shore in 2.0m to 3.0m of water which had a much stronger current due to its relative position to breaking waves on the barrier reef. Coral head A seemed to have one good crevice, coral head B had about 11 good urchin crevices, and coral head C consisted mainly of an overhang ledge with no good crevices.

Urchin counts over a 24 hour period were taken every 4 hours during daylight and every 2 hours after dusk for the first four days and it was found that movement into loose aggregations occurs at 18:30 and reaggregation occurs between the hours of 03:50 and 04:30 at which time the groups remain constant until 18:30 again. The sunrise at 04:00 marks the beginning of a day and the sunset at around 18:00 ends it. Any count made from 03:50 to 03:00 the next morning counts as one day. After this pattern was established, urchin counts were taken 2- 4 times a day in each site, at least once in the early morning, 03:50 to 12:00 and once after dark 19:00 to 24:00. Counts were taken for 15 days over a 20 day period. The number of urchin groups and the number of individual urchins per group were counted at each time interval for both sites. An urchin group on the sand is defined day or night as the number of urchins touching each other. The definition of urchin group when applied to urchins on the coral head during the day refers to the number of urchins touching each other in a coral head or occupying crevices next to each other in the same coral head. The definition of an urchin group at night in the coral heads differs slightly and refers to any urchin foraging around or near one single coral head. For example 8 urchins around coral head B with only two touching each other would still be regarded as a group of 8 because of their orientation at night near a particular coral head.

Tiles were placed for a week on the sand around day groups of urchins to mark the site of aggregation and determine whether or not aggregations occur in the same spot each day.

Alarm response was measured in 21 urchins over 3 days. Clumps of D.

savignyi on the sand bottom, and under various coral heads at Temae Public Beach, and Kia Ora Hotel beach, were selected randomly and one urchin upcurrent from the others was subjected to various treatments. These included 1. Breaking off a couple of spines; 2. Poking the urchin with a stick; 3. Crushing a coral rock to recreate the affect of turbulence caused when crushing an urchin; and 4. Crushing an urchin and distributing its body fluids and parts over the rest of the group. Distribution was done either by holding the contents of the crushed urchin in a bag and fanning it out over the rest of the group, or by letting the contents drift naturally downcurrent and over the urchins in the rest of the group. The bag method seemed to work especially well when the current was moving very quickly. The number of urchins in each group, the number responding to each treatment, and the % urchin response to each treatment was recorded (Table 1). A response is defined as individual urchin movement away from the body fluids and parts of the crushed urchin.

## Results

Groups of *D. Savignyi* on the sand remained at a constant number throughout different time periods of daylight in the course of one day, suggesting that they do not move during daylight hours. Urchins occupying coral heads also remain at a constant number during daylight hours and orient themselves inside the crevices of the coral heads. Urchins in both areas seem to move into loose aggregations to forage at around 18:30 and regroup by 03:50 to 04:30..

Day time urchin numbers on the sand vary from day to day (App 3, 8 ). Conversely, day time urchin numbers around coral heads remained relatively constant from day to day (App 3, 7 ). Figure one also illustrates this. By looking at the standard error bar for the sand and comparing it with the standard error bar of the coral, one can see that counts for the # of urchins in the coral were more regular than counts for the urchins on the sand. The number of urchins around coral heads is different for the first



4 days than for the last 11 because urchins were collected for food by locals on the afternoon of the third day. Immediately after collection, coral head A which housed two urchins contained only one urchin, coral head B which was inhabited by 10 urchins was only inhabited by 4 urchins and coral head C which was inhabited by 3 urchins was no longer inhabited. Twenty-four hours after collection only one urchin was found in coral head A, and 36 hours later, the coral heads were recolonized. After recolonization, coral head A contained 1 urchin, coral head B contained 8 urchins and coral head C contained 0 urchins.

The number of groups on the sand also varied from day to day as did the number of urchins per group (Fig 2, 3, App 1,9) while the number of groups and the number of urchins per group on the coral heads remained relatively constant from day to day (Fig 2,3, App 2,7). The fluctuation in the number of groups and number of individuals on the coral heads can be explained by the urchin in coral head A that occupied a deep crevice. Because it was in refuge during the day it could only be seen sometimes depending on how deep in the crevice it retreated. Even on the days when it was not seen, it was present near the coral head at night thus suggesting its presence during the day.

The total number of *D. savignyi* on the sand differed from night to night (Fig 1, App 4, 8 ). The number of nighttime groups of *D. savignyi* on the sand varied over the 15 days as well (Fig 2, App 1, 6). The size (Fig 3, App 9 ) and location of the groups on the sand also were not constant. Night time groups around the coral heads after recolonization remained constant (Fig 2,4 App 2, 6), as did the number of *D. savignyi* in each group (Fig 1, 4, App 7 ).

There were fewer sand groups during the day with more urchins per group (Fig ), while there were more sand groups during the night and fewer urchins per group (Fig 3 ). The *D. savignyi* groups on the sand are scattered during the night, but they seemed to be in relatively the same location each day. However, *D. savignyi* did not

relocate precisely on the tiles put out any day of the week.

*D. savignyi* does contain an escape response to the body fluids of conspecific urchins. All 21 trials showed movement from at least some of the urchins exposed to body fluids of another urchin (Fig 5, App 10). Sixteen of the 21 trials resulted in 100% movement of urchins in the group away from the crushed urchin (App 9). No response from other urchins in the group was found when one urchin was subjected to being poked with a stick. Likewise, turbulence created from breaking a piece of coral did not elicit a response from urchins. In 7 of the 21 trials, urchins touching the one whose spines were broken moved their spines but no movement away from the urchin was recorded (table 1). Movement seemed strongest in urchins downcurrent from the crushed urchin and urchins which did not elicit a response were all upcurrent or lateral to the crushed urchin. During one of the trials a pair of butterfly fish came and picked at the crushed urchin and during another trial a balloon fish (sp?) came in to pick at the crushed urchin and in both trials the urchins began to move faster in the presence of a predator.

## Discussion

*Diadema savignyi* are nocturnal organisms which feed during the night and regroup into aggregations during the day (Randall 1964, Nelson and Vance 1979, Vance and Schmitt 1979). This behavior may be an evolutionary adaptation in response to *Diadema* predators which are active during the day (Nelson and Vance 1979). Some *D. savignyi*, on Temae Public Beach, aggregate around and in crevices on coral heads. Others group together in large aggregations on the near-shore sand flats of Temae. Both groups could serve as a means of protection from predators. Coral head crevices may provide protection from current and serve as a retreat from predators. Large groups of *D. savignyi* on the sand also serve as mutual protection, as urchins in a group are able to bring more spines against an enemy

(Randall 1964).

However, day time urchin numbers on the sand vary from day to day while urchin numbers on the coral heads remain constant from day to day (Fig 1, App 3,7,8 ). Smith (1969), worked on *D. antillarum* in Curacao and also observed that the aggregations around coral heads remained constant from day to day but urchins in areas of rubble without coral heads did not show this consistent clustering.

The constancy in urchin numbers on coral heads may be due to the limited space and limited number of ideal crevices. Urchins return to the same coral heads day after day because it is the only way they are assured of finding a daytime retreat (Nelson and Vance 1979). Ogden (1978) observed *Echinometra lucunter* aggressively attacking another conspecific which tried to take over its crevice. The difference in the number of groups and the number of individuals in the coral heads from the first 4 days to the last 11 (App 2,3,7 ) is explained by collection of *Diadema* by the locals for food. Urchins were collected on the afternoon of the 3rd day. When counts were made that night, 1 urchin was found in coral head A, 4 urchins were found in coral head B and no urchins were found in coral head C. Only one urchin on head A was found in the coral heads during the daily and nightly counts of the 4th day. However, the heads had been recolonized by the morning of the 5th day. It is not known why there were 4 urchins in coral head B after collection but no urchins found there the next day. Tristan Sherrod (1991) found a decrease in urchin numbers due to the broken spines of conspecifics. However, the alarm response tests I performed did not show any urchin movement due to broken spines. Perhaps movement out of an area in response to broken spines is not as immediate as movement in response to body fluids. Another reason for delay in movement out of the coral heads could be due to pieces of a collected urchins body left on the rubble outside the coral head which the 4 urchins were not exposed to until they went out foraging. This would explain the absence of urchins the next morning. The urchin body parts and fluids

may have washed away enough by the next day to allow for recolonization. Randall (1964), observed that when *Diadema* were removed, urchins from adjacent areas moved in fairly rapidly and within 48 hours the measured area was occupied with one-fourth the original number. One out of two urchins was collected in coral head A. Six out of 10 urchins were collected in coral head B and 3 out of 3 urchins were collected in coral head C. Coral head A only had one good crevice, coral head B had 10 good crevices and coral head C had no crevices, rather it consisted only of an overhanging ledge. Coral head A's crevice was occupied. Therefore, coral head B offered the most and best available crevices which would explain why it was recolonized with the most urchins. The fact that there were two more good crevices than urchins, in coral head B may explain why no urchins crowded into coral head A or settled for the overhang of coral head C. Tristan Sherrod (1991, unpublished) found consistency in urchin numbers on coral heads in Moorea and concluded that all available spaces on the heads she studied were occupied by urchins. Before collection, there were more urchins than ideal space so some urchins had to "overflow" into coral heads A and C.

There is no space restriction on the near-shore sand flat. Therefore urchins probably have no need to return to the same group. The surge and current that are present around the coral heads is also absent. This cuts down on the need to return to find a protective crevice day after day. The variance in number of groups, and total number of urchins (Fig 1,2 App 1,3,5,8,9) day after day also suggests lack of homing and group fidelity in urchins on the near-shore sand flat. Furthermore, urchins did not reorient in the same location each day as was demonstrated by placing tiles out and observing group orientation on them day to day. This most likely reaffirms lack of homing in aggregations of *Diadema* on the sand. However, lack of orientation on the tiles may be the result of *Diadema* selectively choosing to stay away from them due to the habitat disturbance they cause such as creating mounds of sand or covering up algae on coral fragments.

Night time groups of *D. savignyi* on the sand varied over the 15 days while night time groups around the coral heads remained relatively constant (Fig 2, App 6 ). However, these coral heads were isolated to some degree from other coral heads and thus the degree of group fidelity around coral heads at night is not exactly known. Nightly orientation of *Diadema* near their respective coral heads may be due more to the coral heads being in a relatively isolated area. Smith (1969) observed that *D. antillarum* traveled one to two meters away from their coral heads and seemed randomly dispersed.

On the sand there seems to be fewer groups with more urchins during the day while there are more scattered groups with less urchins during the night (Fig 3 ). In comparison, on the coral head, the number of day groups seems to be relatively the same as the number of night groups (Fig 4, App 2) The number of individuals occupying the coral heads is constant from day to night as well. The point of inconsistency in the number of groups and the number of individuals is due to the urchin in coral head A which could be seen some of the days but not others. However, it was always present at night. This may be explained by the deep crevice in which the urchin may take refuge during the day and thus is not visible.

The difference in numbers of urchins on the sand from day to night (Fig 1, App 3, 4, 8 ) and the variance in numbers of urchins on the sand from day to day can be explained by assuming that some urchins travel outside the near-shore sand transect while foraging and while some return back to the transect during reaggregation, others may regroup and form smaller aggregations just outside the transect. The reasons for not returning to the same group as the previous day may be due to *Diadema*'s lack of incentive to travel a long distance back to a specific group or site, as on the sand there probably is no advantage to picking one group or the other or may be due to the fact that the *Diadema* stayed out foraging too long to make it back to its original group before its cue to reaggregate. Discrepancies in number of *Diadema* on the sand from



day to day, day to night, and night to night, may also be explained by counting error. Counts when groups are relatively the same day to day, may be explained because urchins may not have broken too far apart at night and thus reaggregated together the next morning.

Of the four treatments tested, only the crushing of an urchin and distribution of its body fluids was enough to make the other urchins move away (Fig 5, App 10 ). The 5 trials which did not result in 100% movement of all *D. savignyi* away from the area were conducted on days when the current was extremely strong and the conspecific juice probably was washed away before it had a chance to reach the urchins that did not respond. In addition, Snyder and Snyder (1970) report that urchins of the species *D. antillarum* that did respond in strong currents lost their hold and were carried far away making them more vulnerable to fish predators. Any advantage for an urchin showing alarm behavior in strong currents must presumably be tempered by the risk of being swept away in the current (Snyder and Snyder 1970). Most urchins were crushed at the edge of a clump to allow the body fluids to reach the rest of the aggregation downstream. The direction most often traveled by urchins in which the alarm response had been evoked was downstream. I found that urchins to the side or upcurrent from the crushed urchin most often did not respond to the crushing probably because they were not exposed to any of the conspecific "juice." Snyder and Snyder (1970) hypothesize that if predators of *Diadema* tend to move only short distances between meals, urchins that move downcurrent in alarm could reduce their chances of falling victim to a predator at the expense of increased danger to other urchins closer to the predator but crosscurrent or upcurrent from him and unaware of his presence. Urchins on the coral heads responded in the same manner as urchins in aggregations of the sand. Furthermore, urchins were able to move upcurrent as was demonstrated when a bag was held over three urchins on their downcurrent sides. Snyder and Snyder found similar results. The presence of fish predators that were feeding on the

crushed urchin on two occasions seemed to provoke the *D. savignyi* to move faster and farther downstream. The presence of a fish predator seemed to have no effect on *D. antillarum* (Snyder and Snyder 1970).

It is not known exactly why there are such large aggregations of *D. savignyi* on the near-shore sand flats of Temae. It may be that a large number of larvae were deposited there. This large amount of recruitment combined with a low population of predators may have resulted in a large population density. Perhaps there are no coral heads left to take refuge in or perhaps the urchins would have to move too far to find an available one. These large aggregations may serve the same type of function as crevices in coral heads in that they provide protection from daytime predators. The presence of an alarm response may also add to the amount of protection from the group. Strong species specificity of the response suggests that it is an adaptation to reduce predation (Snyder and Snyder 1970). Difficulty in tagging *D. savignyi* made it impossible to accurately test homing in these urchins. However, it does appear that *Diadema* that orient around coral heads are more likely to exhibit homing tendencies than those that aggregate in large groups.

Future research which could be done includes looking at more coral heads in a less isolated area and comparing aggregations around these with aggregations on the sand. Looking at habitat partitioning in crevices and interspecific as well as intraspecific aggressiveness in maintaining crevices. More work could also be done on the alarm response in urchins, assessing whether it occurs in all species of urchins, and if one species responds to the body fluid of another species.

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## Mean # Diadema

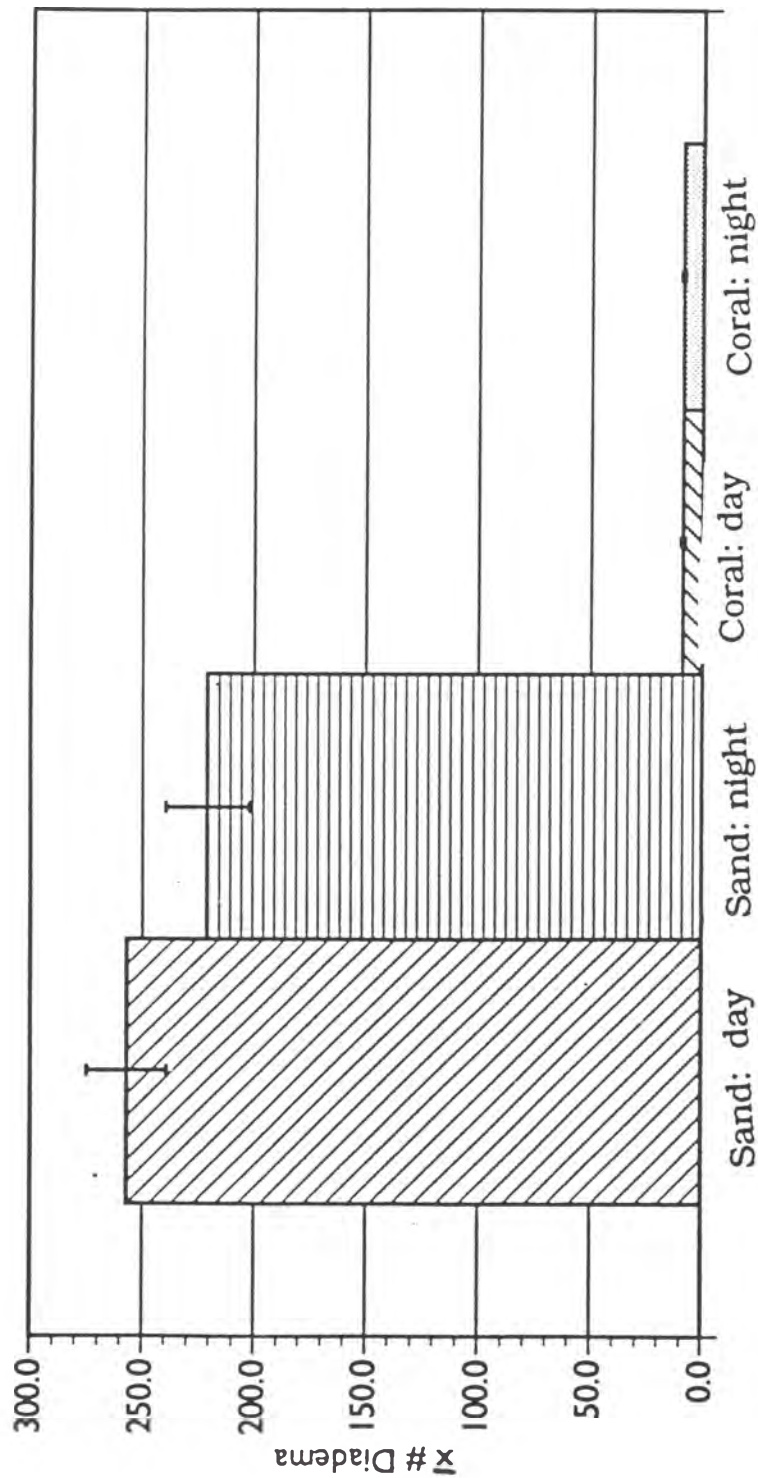


Fig. 1. Mean # of *Diadema* over 15 days. A comparison between day and night aggregations on the sand and day and night aggregations in coral heads. Mean # of *Diadema* in coral heads was found by averaging the total # of *Diadema* in heads A, B, C. Error Bar = 1 Standard Error. Standard Error of the  $\bar{x}$  # of *Diadema* on the sand during the day = 17.8. S.E. of the  $\bar{x}$  # of *Diadema* on the sand during the night = 18.7. S.E. of the  $\bar{x}$  # of *Diadema* in the coral heads during the day = .88. S.E. of the  $\bar{x}$  # of *Diadema* in the coral heads during the night = .85



# Mean # Groups

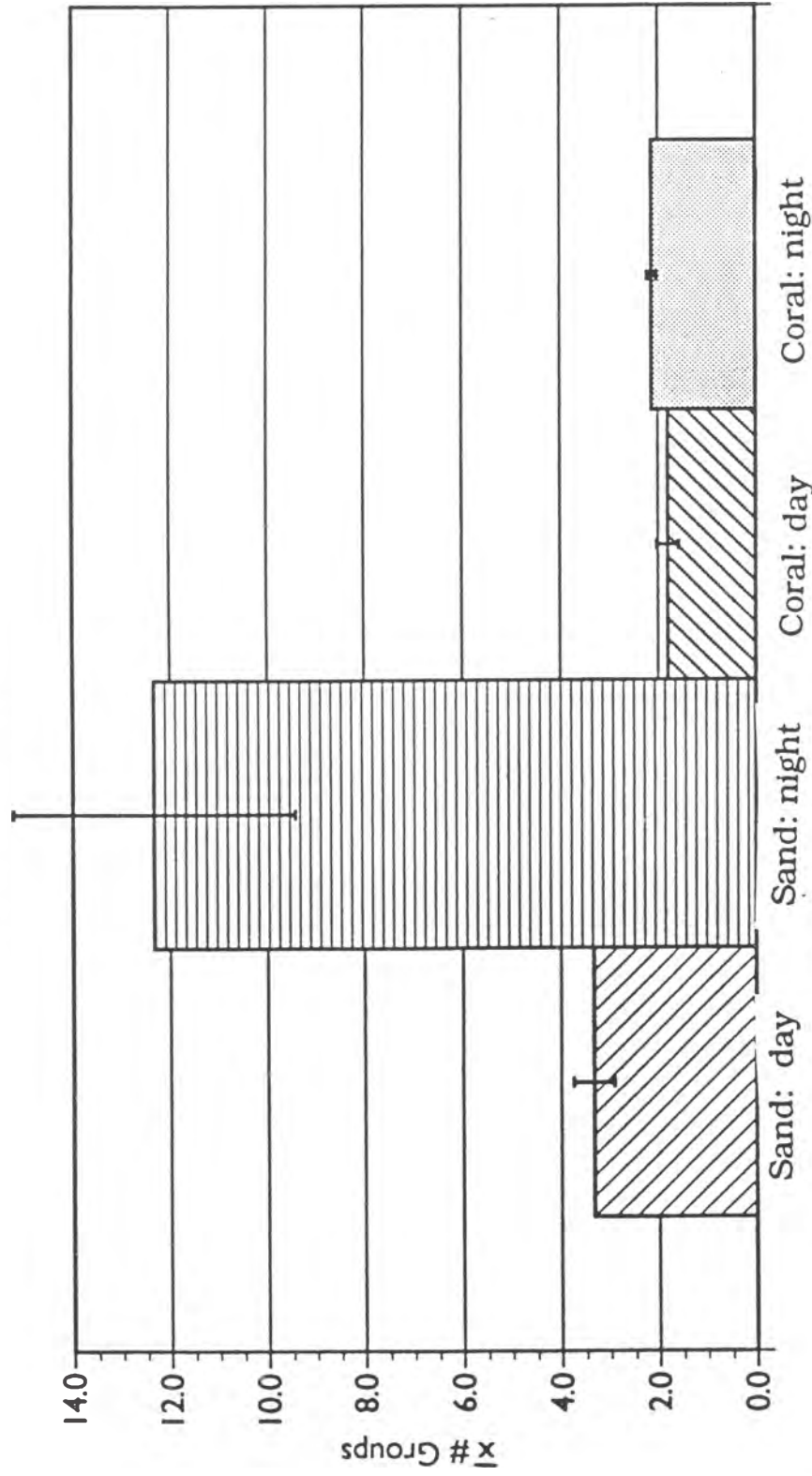


Fig. 2. Mean # of *Diadema* groups over 15 days. A comparison of the mean number of groups on the sand during the day and night to the mean # of groups on the coral during the day and night. Error Bar = 1 Standard Error. S.E. for the  $\bar{x}$  of sand groups during the day = .41. S.E. for the  $\bar{x}$  of sand groups during the night = 2.9. S.E. for the  $\bar{x}$  of coral groups during the day = .23. S.E. for the  $\bar{x}$  of coral groups during the night = .10.

Mean # Groups and Mean Group Size: Sand

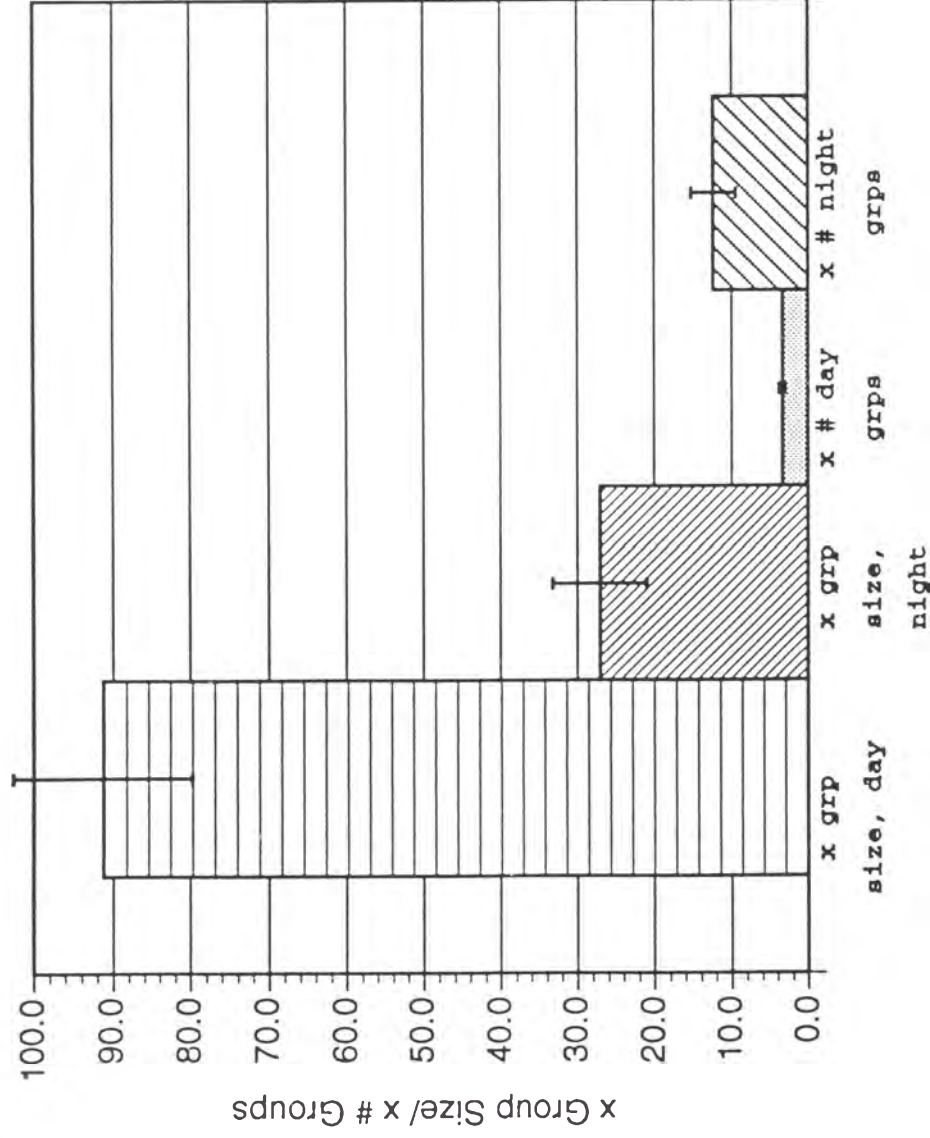


Fig 3 Mean # of Groups and Mean Group Size day of *Diadema savinyi* on the Sand: A comparison between day and night. The mean day group and night group size over 15 days and the mean number of day groups and night groups over 15 days. Error Bar = 1 Standard Error. Standard Error for x grp size, day is 11.5, Standard Error for the x grp size, night is 6.1. Standard Error for the x # day groups is 2.9. Standard Error for the x # night groups is .41.

mean # of Coral Groups and Mean #  
of Diadema per Coral Head

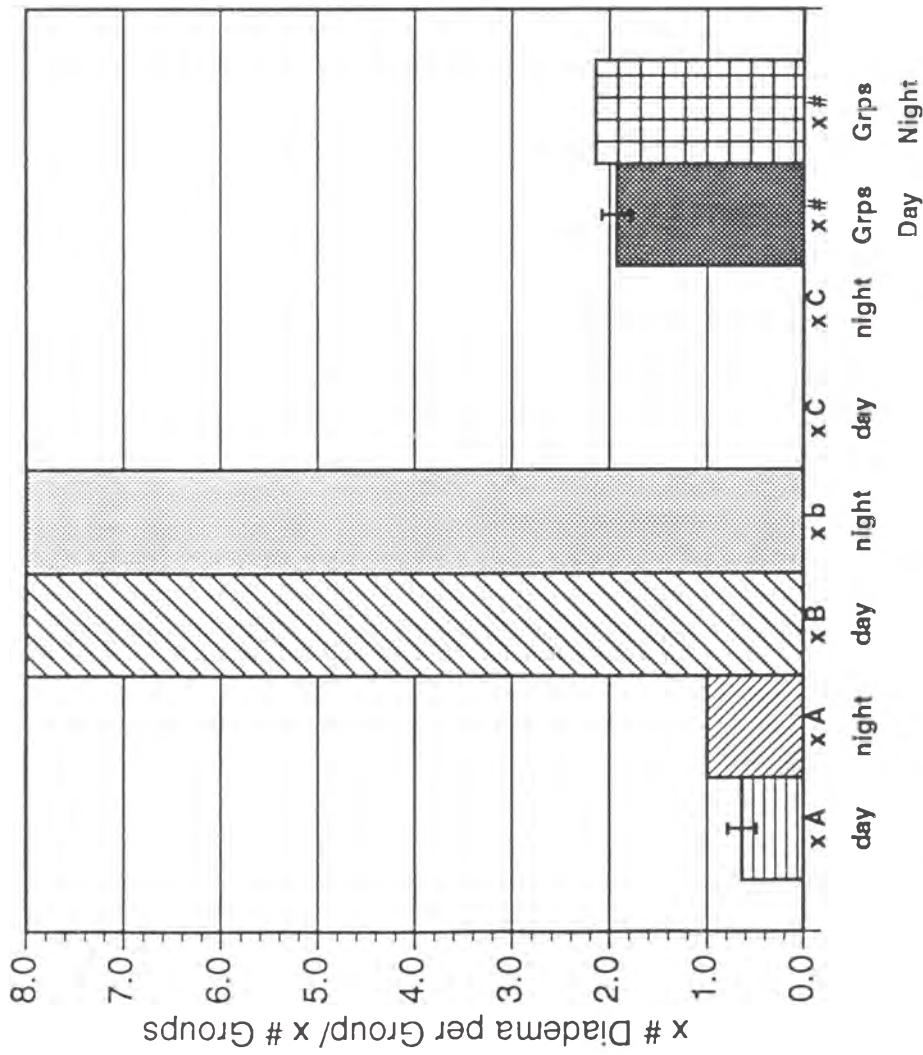


Fig 4 The Mean # of Groups in the coral heads over 11 days and the Mean # of Diadema per coral head over 11 days after recolonization. Day vs Night. Error Bar represents 1 Standard Error. Standard error for both the mean # Diadema in head A and the mean # of day groups is .15.

# Mean % of Diadema That Respond to Different Types of Disturbance

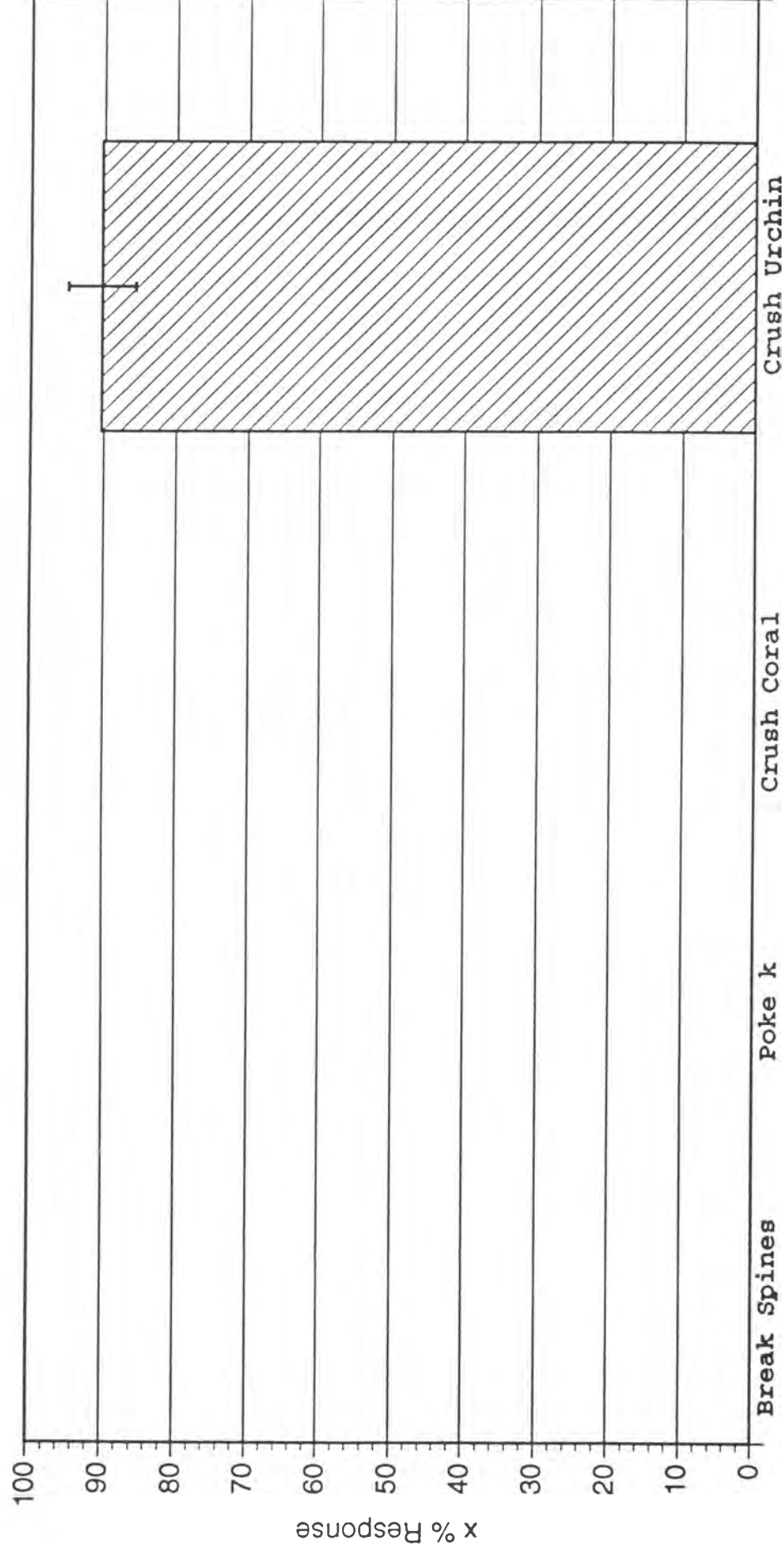
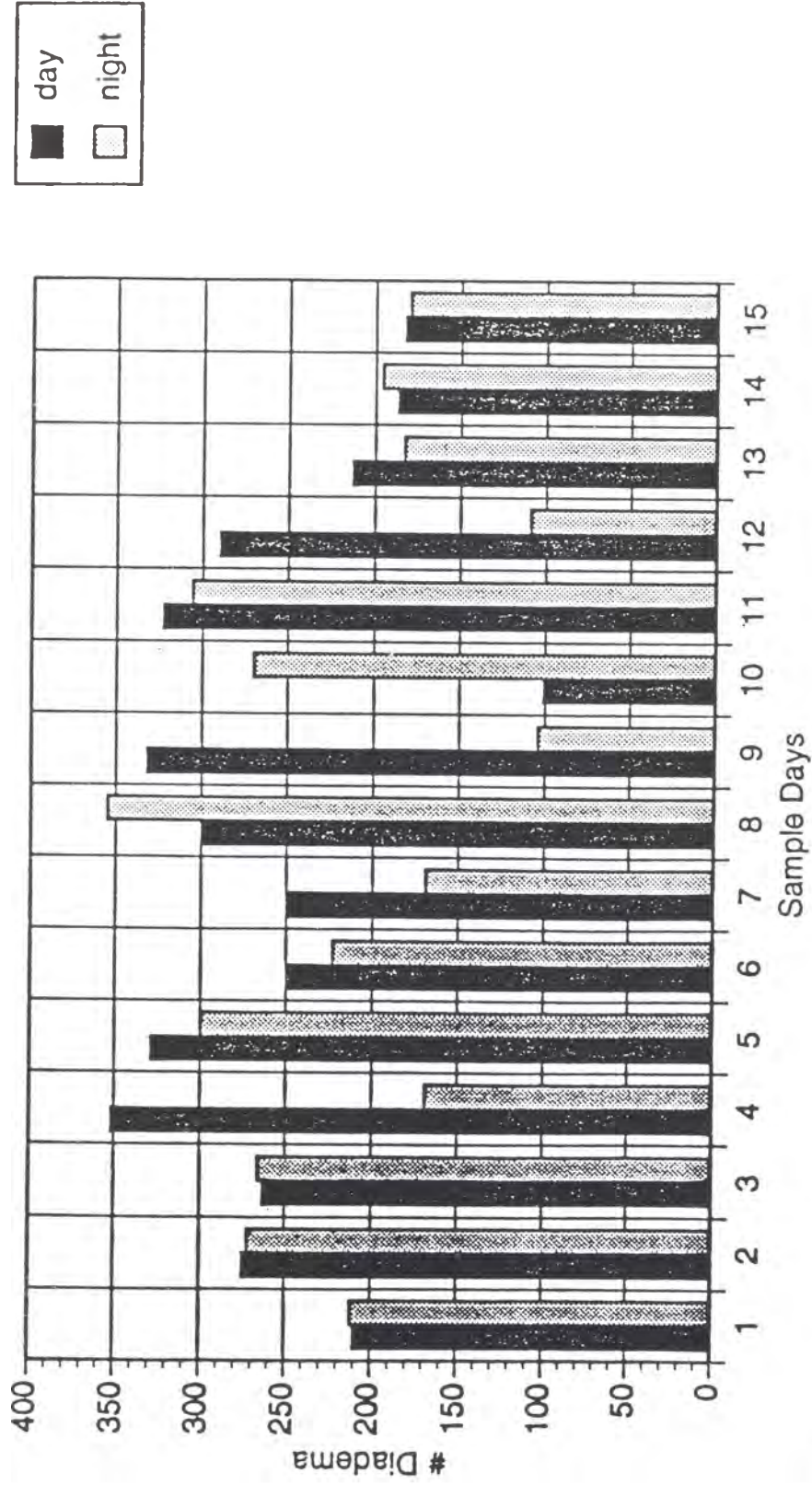


Fig. 5 The Mean % of *Diadema savignyi* that Respond to Different Types of Disturbance. Mean is taken over 21 trials and response is measured in terms of movement of an urchin away from the crushed urchin. Disturbances include breaking spines, poking with a stick, crushing coral to emulate turbulence created by crushing an urchin, and crushing an urchin with a hammer and spreading body fluids and parts over the group. Error Bar = 1 Standard Error. Standard Error = 4.6.



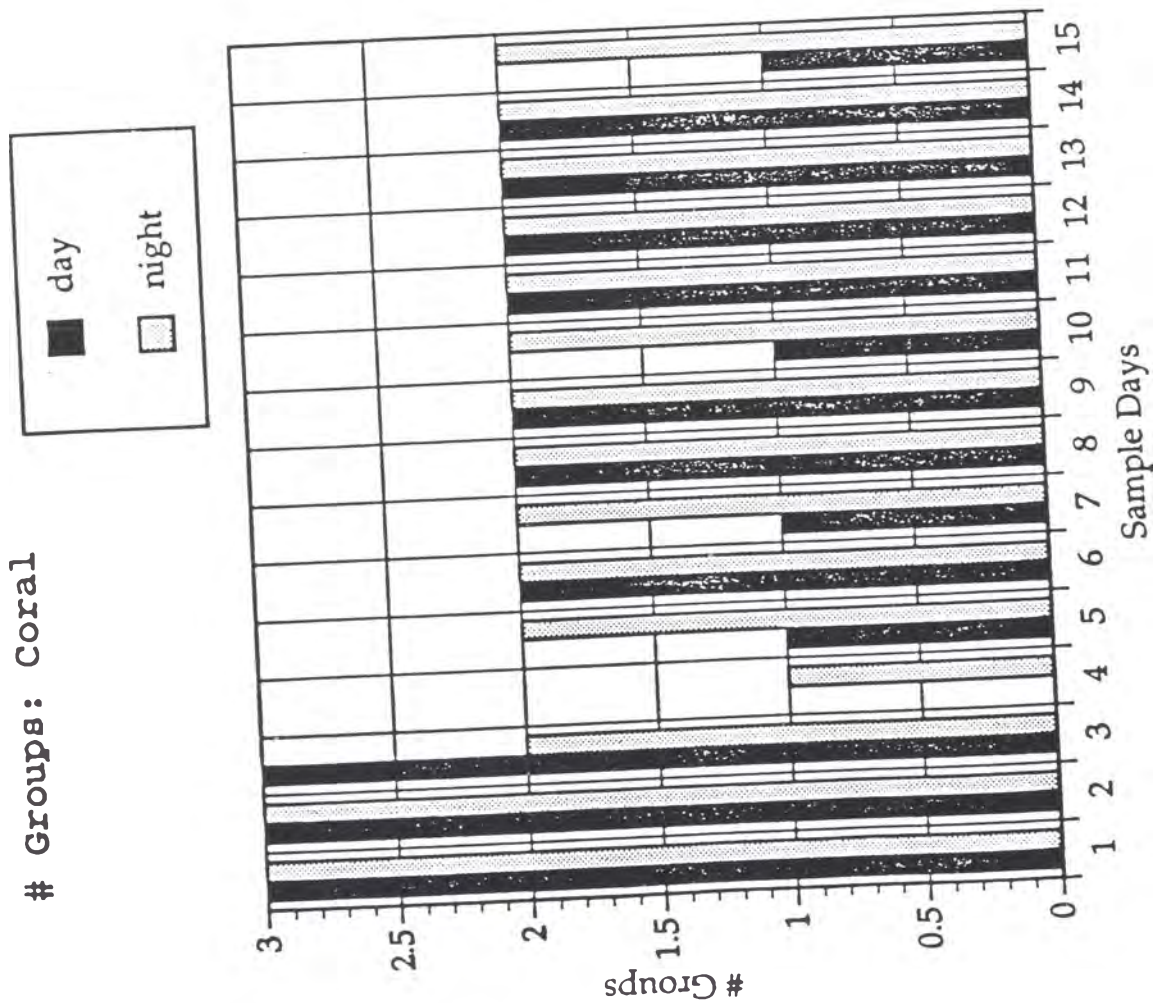
# Total # Diadema: Sand



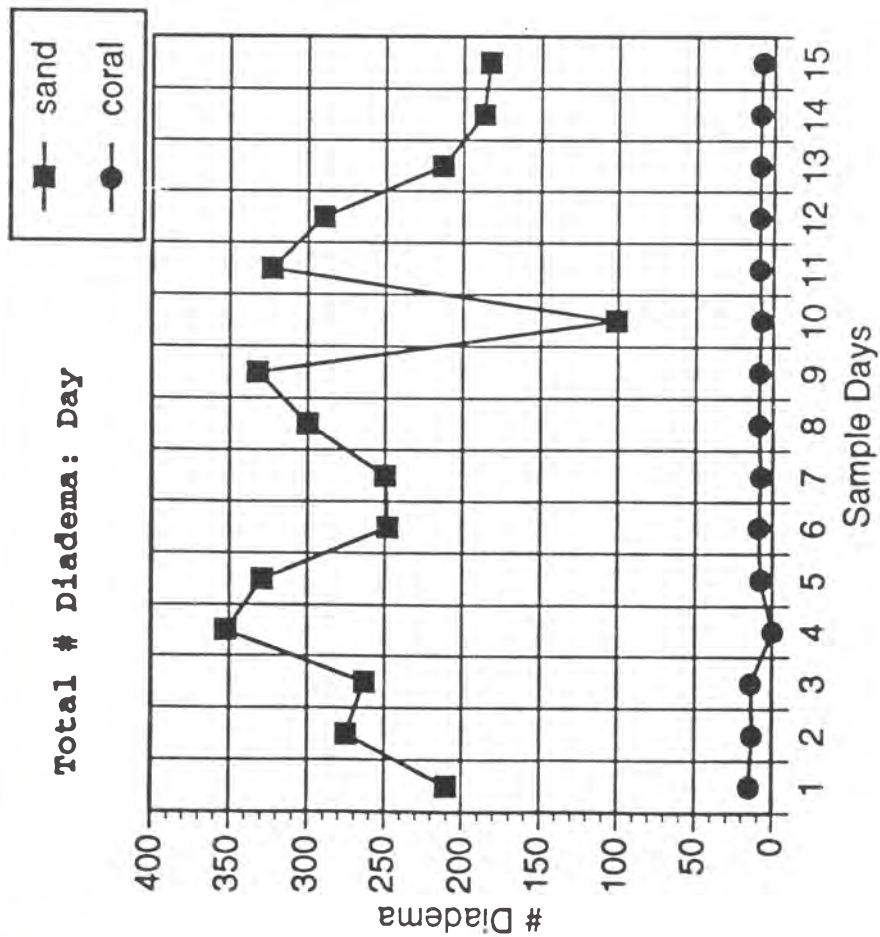
Appendix 1 The total # of *Diadema savignyi* in the sand each day. Day vs. Night.



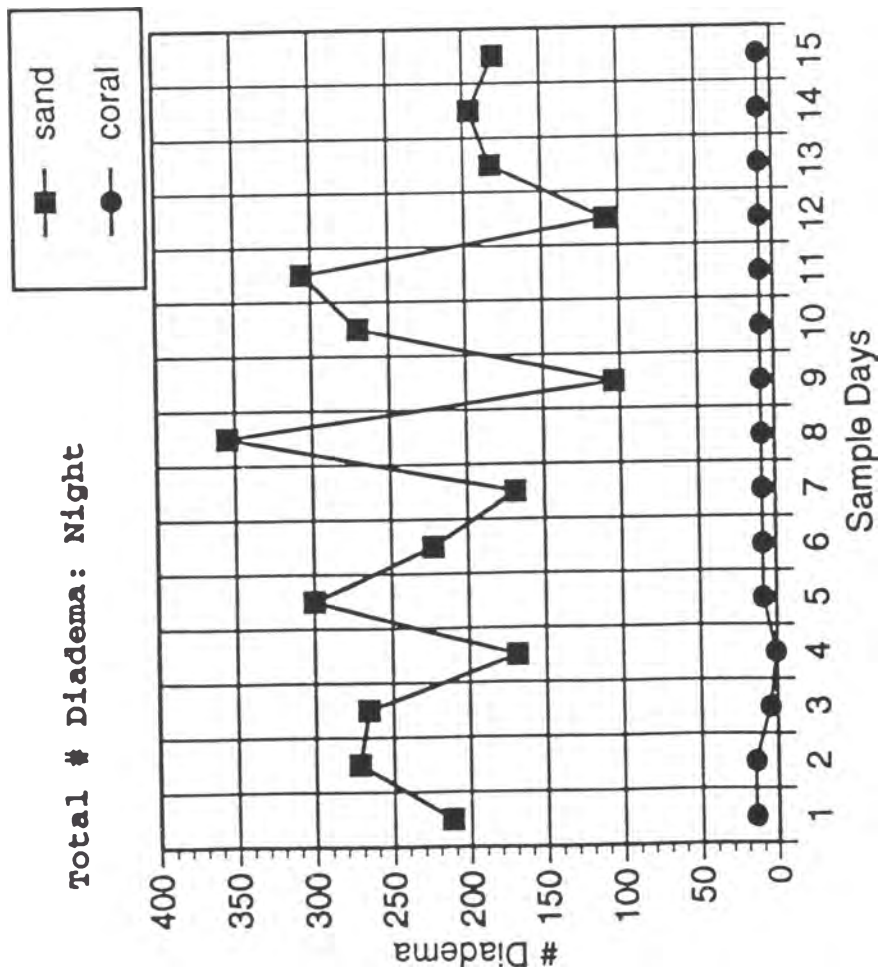
# # Groups: Coral



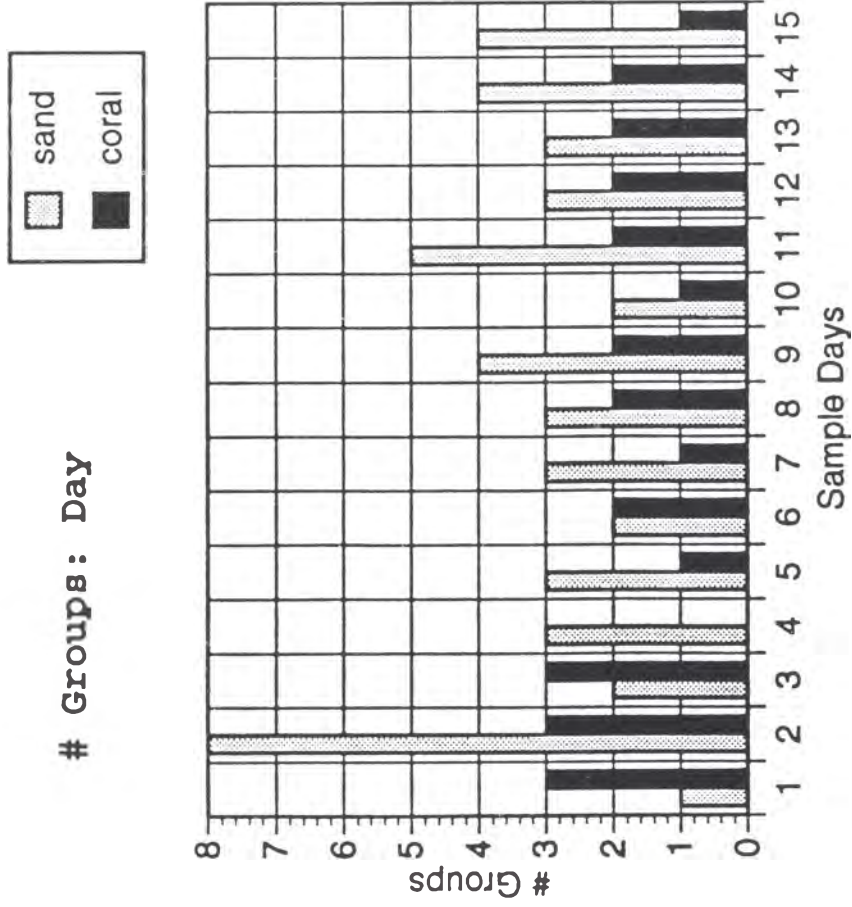
Appendix 2. The # of Groups in the coral heads. Day vs Night. The difference in the # of groups for the first four days as compared with the rest of the graph is due to the urchins that were collected by the locals for food on the afternoon of the third day.



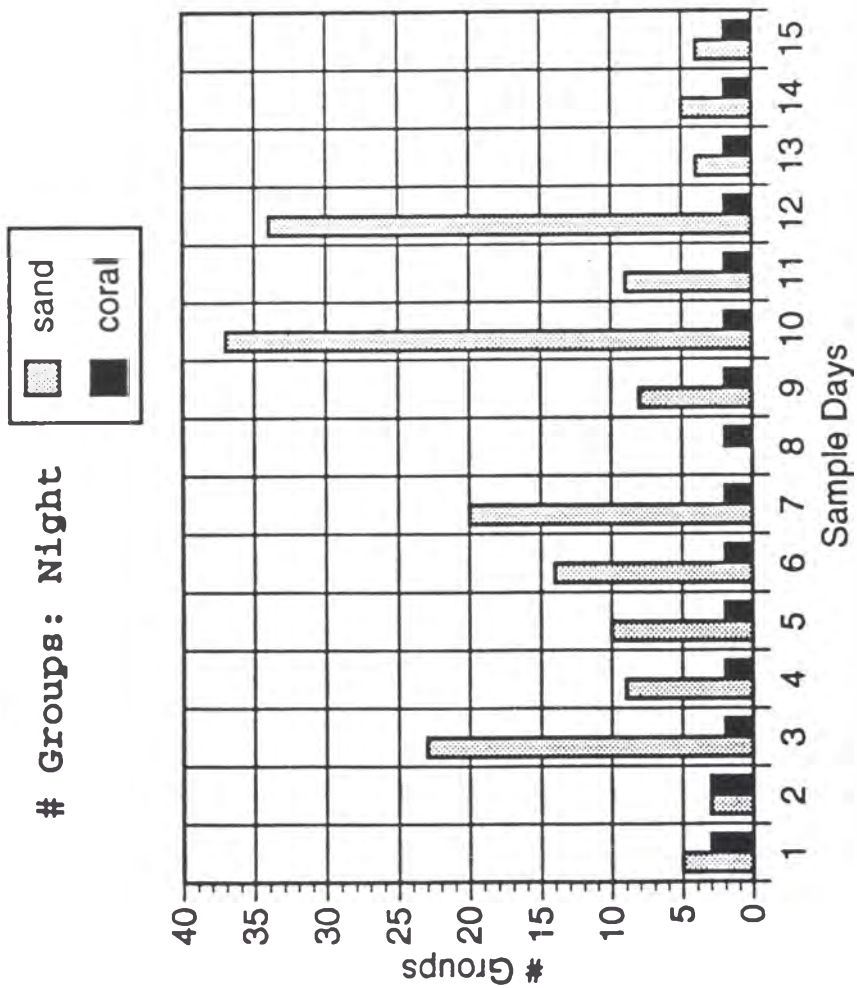
Appendix 3 Total Number of *Diadema savignyi* per Day. Sand vs. Coral



Appendix 4 Total # of *Diadema savignyi* per Night. Sand vs. Coral

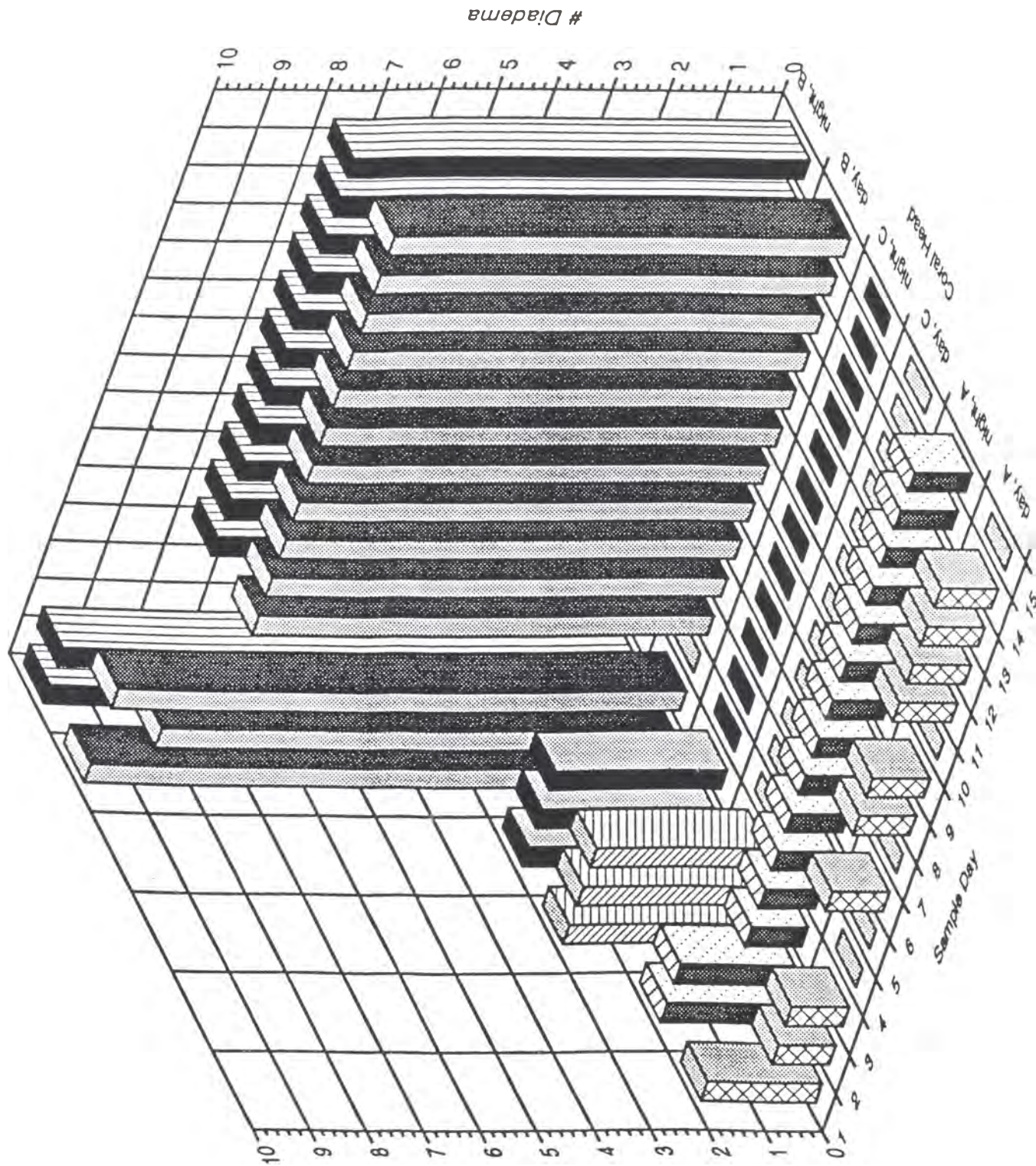


ppendix 5 The number of groups of *Diadema savignyi* per day. Sand vs. coral.



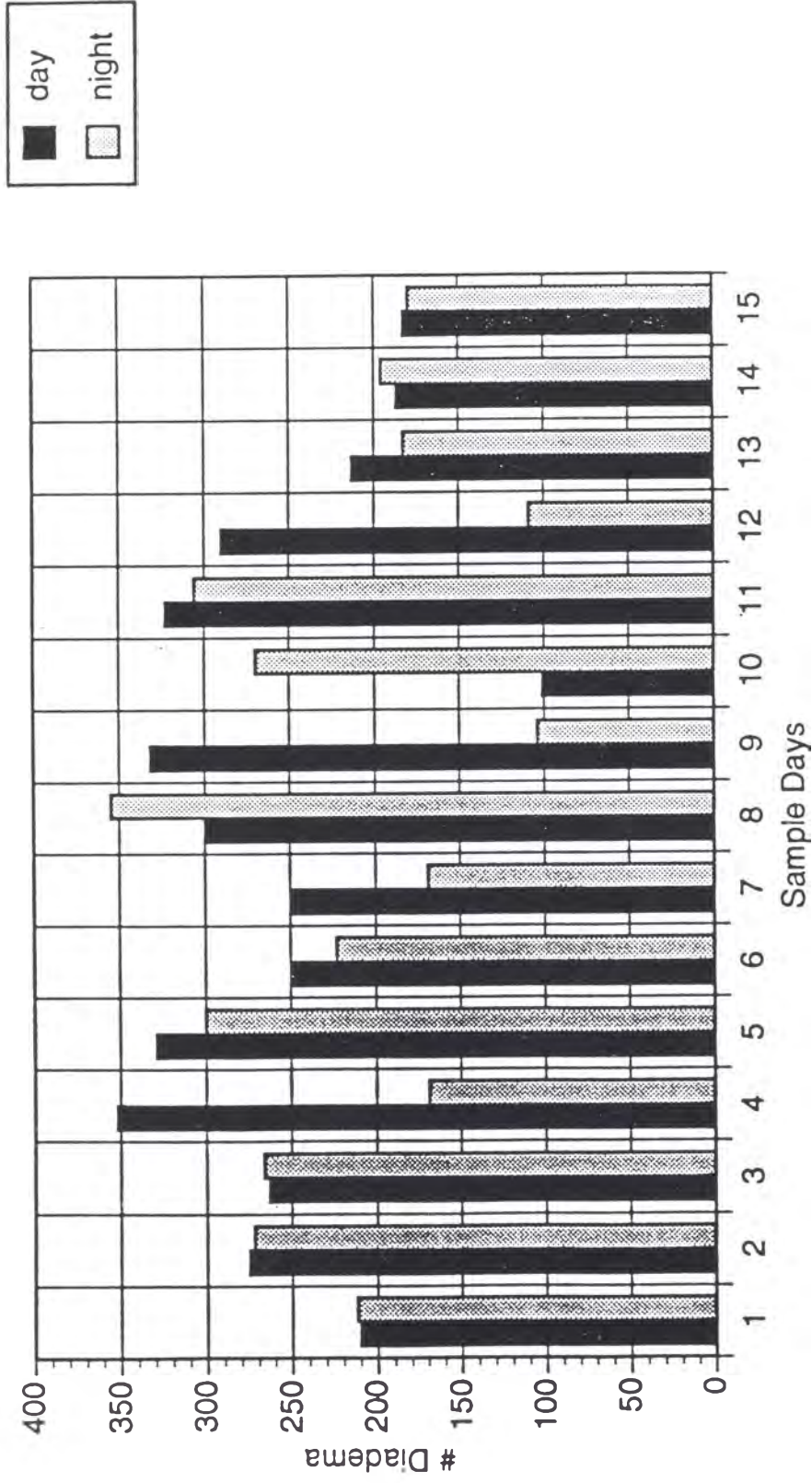
Appendix 6 The number of groups of *Diadema savignyi* per night. Sand vs. Coral.





Appendix 7. The number of individuals of *Diadema* *savini* per sample day in the Coral, Day vs. Night. Note the inconsistency of the first four days from the rest is due to collection of urchins by locals. Heads were recolonized on the 5th day.

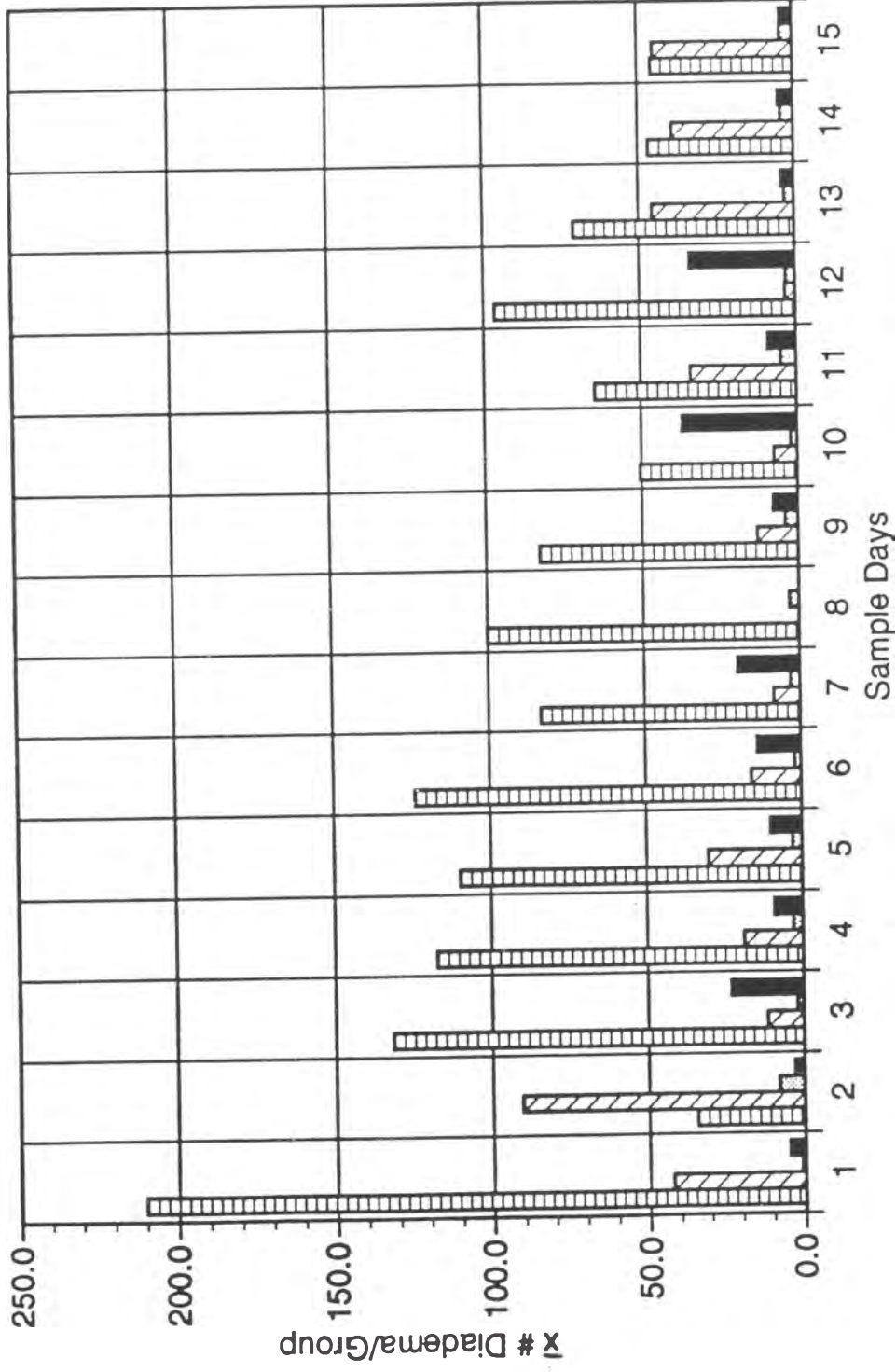
# Total # Diadema: Sand



Appendix 8 The number of groups of *Diadema savignyi* per sample day in the Sand. Day vs. night.

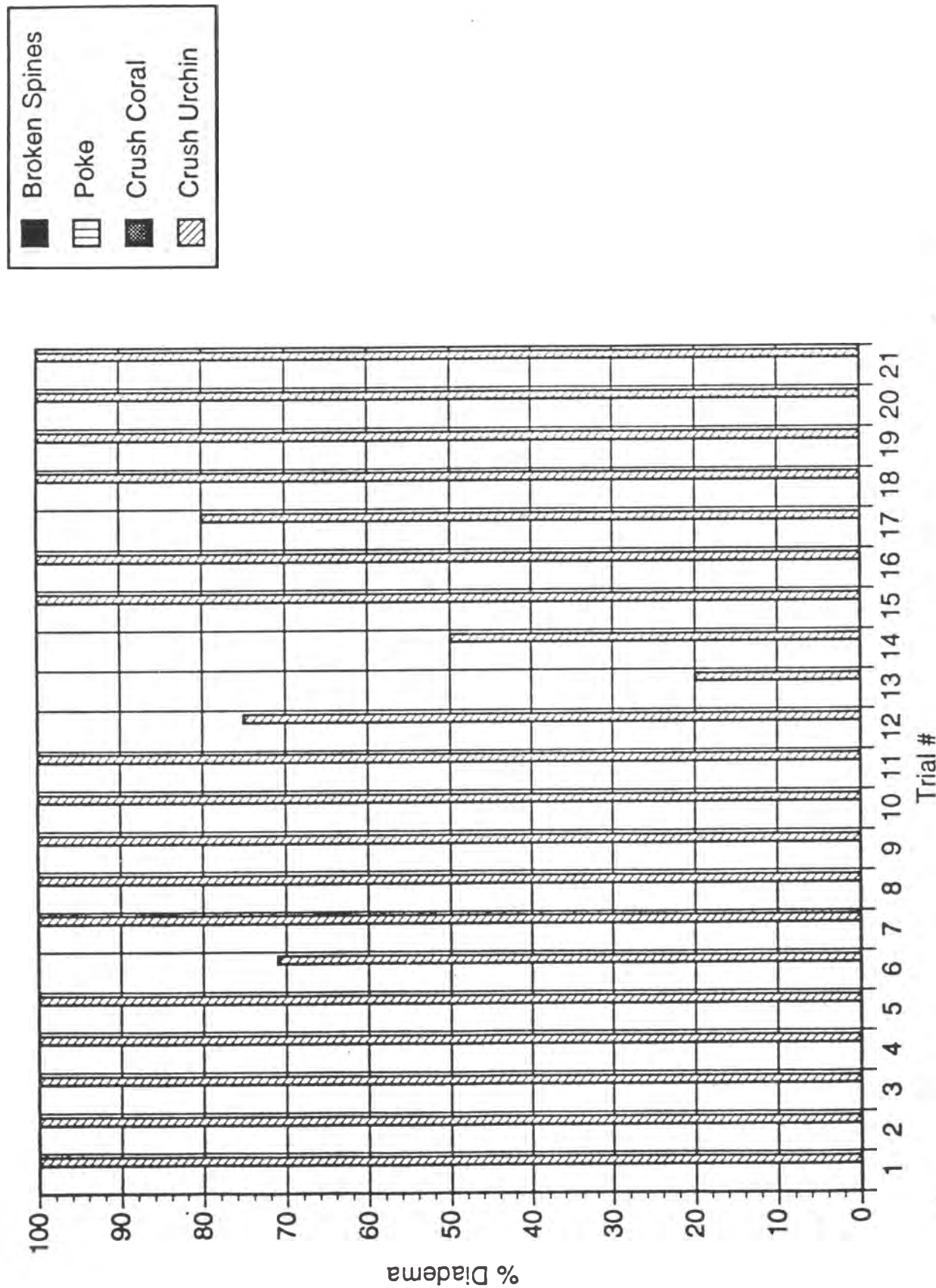


# # Groups and Mean Group Size: Sand



Appendix 9 The # of Groups and Mean Group Size of *Diadema savignyi* in the Sand. The number of groups and mean group size for every sample day.

# Alarm Response: % of *Diadema* that Respond to Different Kinds of Disturbance



Appendix 10 Alarm Response: The % of *Diadema* that Respond to Different kinds of Disturbance. Response to Disturbance is defined as movement of one urchin away from the crushed urchin. Crushing of the urchin is the only

Label	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z	AA	AB	AC	AD	AE	AF	AG	AH	AI	AJ	AK	AL	AM	AN	AO	AP	AQ	AR	AS	AT	AU	AV	AW	AX	AY	AZ	BA	BB	BC	BD	BE	BF	BG	BH	BI	BJ	BK	BL	BM	BN	BO	BP	BQ	BR	BS	BT	BU	BV	BW	BX	BY	BZ	CA	CB	CC	CD	CE	CF	CG	CH	CI	CJ	CK	CL	CM	CN	CO	CP	CQ	CR	CS	CT	CU	CV	CW	CX	CY	CZ	DA	DB	DC	DD	DE	DF	DG	DH	DI	DJ	DK	DL	DM	DN	DO	DP	DQ	DR	DS	DT	DU	DV	DW	DX	DY	DZ	EA	EB	EC	ED	EE	EF	EG	EH	EI	EJ	EK	EL	EM	EN	EO	EP	EQ	ER	ES	ET	EU	EV	EW	EX	EY	EZ	FA	FB	FC	FD	FE	FF	FG	FH	FI	FJ	FK	FL	FM	FN	FO	FP	FQ	FR	FS	FT	FU	FV	FW	FX	FY	FZ	GA	GB	GC	GD	GE	GF	GG	GH	GI	GJ	GK	GL	GM	GN	GO	GP	GQ	GR	GS	GT	GU	GV	GW	GX	GY	GZ	HA	HB	HC	HD	HE	HF	HG	HH	HI	HJ	HK	HL	HM	HN	HO	HP	HQ	HR	HS	HT	HU	HV	HW	HX	HY	HZ	IA	IB	IC	ID	IE	IF	IG	IH	II	IJ	IK	IL	IM	IN	IO	IP	IQ	IR	IS	IT	IU	IV	IW	IX	IY	IZ	JA	JB	JC	JD	JE	JF	JG	JH	JI	JJ	JK	JL	JM	JN	JO	JP	JQ	JR	JS	JT	JU	JV	JW	JX	JY	JZ	KA	KB	KC	KD	KE	KF	KG	KH	KI	KJ	KL	KM	KN	KO	KP	KQ	KR	KS	KT	KU	KV	KW	KX	KY	KZ	LA	LB	LC	LD	LE	LF	LG	LH	LI	LJ	LK	LM	LN	LO	LP	LQ	LR	LS	LT	LU	LV	LW	LX	LY	LZ	MA	MB	MC	MD	ME	MF	MG	MH	MI	MJ	MK	ML	MM	MN	MO	MP	MQ	MR	MS	MT	MU	MV	MW	MX	MY	MZ	NA	NB	NC	ND	NE	NF	NG	NH	NI	NJ	NK	NL	NM	NN	NO	NP	NQ	NR	NS	NT	NU	NV	NW	NX	NY	NZ	OA	OB	OC	OD	OE	OF	OG	OH	OI	OJ	OK	OL	OM	ON	OO	OP	OQ	OR	OS	OT	OU	OV	OW	OX	OY	OZ	PA	PB	PC	PD	PE	PF	PG	PH	PI	PJ	PK	PL	PM	PN	PO	PP	PQ	PR	PS	PT	PU	PV	PW	PX	PY	PZ	QA	QB	QC	QD	QE	QF	QG	QH	QI	QJ	QK	QL	QM	QN	QO	QP	QQ	QR	QS	QT	QU	QV	QW	QX	QY	QZ	RA	RB	RC	RD	RE	RF	RG	RH	RI	RJ	RK	RL	RM	RN	RO	RP	RQ	RR	RS	RT	RU	RV	RW	RX	RY	RZ	SA	SB	SC	SD	SE	SF	SG	SH	SI	SJ	SK	SL	SM	SN	SO	SP	SQ	SR	SS	ST	SU	SV	SW	SX	SY	SZ	TA	TB	TC	TD	TE	TF	TG	TH	TI	TJ	TK	TL	TM	TN	TO	TP	TQ	TR	TS	TT	TU	TV	TW	TX	TY	TZ	UA	UB	UC	UD	UE	UF	UG	UH	UI	UJ	UK	UL	UM	UN	UO	UP	UQ	UR	US	UT	UU	UV	UW	UX	UY	UZ	VA	VB	VC	VD	VE	VF	VG	VH	VI	VJ	VK	VL	VM	VN	VO	VP	VQ	VR	VS	VT	VU	VV	VW	VX	VY	VZ	WA	WB	WC	WD	WE	WF	WG	WH	WI	WJ	WK	WL	WM	WN	WO	WP	WQ	WR	WS	WT	WU	WV	WW	WX	WY	WZ	XA	XB	XC	XD	XE	XF	YG	YH	YI	YJ	YK	YL	YM	YN	YO	YP	YQ	YR	YS	YT	YU	YV	YW	YX	YY	YZ	ZA	ZB	ZC	ZD	ZE	ZF	ZG	ZH	ZI	ZJ	ZK	ZL	ZM	ZN	ZO	ZP	ZQ	ZR	ZS	ZT	ZU	ZV	ZW	ZX	ZY	ZZ	AA	AB	AC	AD	AE	AF	AG	AH	AI	AJ	AK	AL	AM	AN	AO	AP	AQ	AR	AS	AT	AU	AV	AW	AX	AY	AZ	BA	BB	BC	BD	BE	BF	BG	BH	BI	BJ	BK	BL	BM	BN	BO	BP	BQ	BR	BS	BT	BU	BV	BW	BX	BY	BZ	CA	CB	CC	CD	CE	CF	CG	CH	CI	CJ	CK	CL	CM	CN	CO	CP	CQ	CR	CS	CT	CU	CV	CW	CX	CY	CZ	DA	DB	DC	DD	DE	DF	DG	DH	DI	DJ	DK	DL	DM	DN	DO	DP	DQ	DR	DS	DT	DU	DV	DW	DX	DY	DZ	EA	EB	EC	ED	EE	EF	EG	EH	EI	EJ	EK	EL	EM	EN	EO	EP	EQ	ER	ES	ET	EU	EV	EW	EX	EY	EZ	FA	FB	FC	FD	FE	FF	FG	FH	FI	FJ	FK	FL	FM	FN	FO	FP	FQ	FR	FS	FT	FU	FV	FW	FX	FY	FZ	GA	GB	GC	GD	GE	GF	GG	GH	GI	GJ	GK	GL	GM	GN	GO	GP	GQ	GR	GS	GT	GU	GV	GW	GX	GY	GZ	HA	HB	HC	HD	HE	HF	HG	HH	HI	HJ	HK	HL	HM	HN	HO	HP	HQ	HR	HS	HT	HU	HV	HW	HX	HY	HZ	IA	IB	IC	ID	IE	IF	IG	IH	II	IJ	IK	IL	IM	IN	IO	IP	IQ	IR	IS	IT	IU	IV	IW	IX	IY	IZ	JA	JB	JC	JD	JE	JF	JG	JH	JI	JJ	JK	JL	JM	JN	JO	JP	JQ	JR	JS	JT	JU	JV	JW	JX	JY	JZ	KA	KB	KC	KD	KE	KF	KG	KH	KI	KJ	KL	KM	KN	KO	KP	KQ	KR	KS	KT	KU	KV	KW	KX	KY	KZ	LA	LB	LC	LD	LE	LF	LG	LH	LI	LJ	LK	LM	LN	LO	LP	LQ	LR	LS	LT	LU	LV	LW	LX	LY	LZ	MA	MB	MC	MD	ME	MF	MG	MH	MI	MJ	MK	ML	MM	MN	MO	MP	MQ	MR	MS	MT	MU	MV	MW	MX	MY	MZ	NA	NB	NC	ND	NE	NF	NG	NH	NI	NJ	NK	NL	NM	NN	NO	NP	NQ	NR	NS	NT	NU	NV	NW	NX	NY	NZ	OA	OB	OC	OD	OE	OF	OG	OH	OI	OJ	OK	OL	OM	ON	OO	OP	OQ	OR	OS	OT	OU	OV	OW	OX	OY	OZ	PA	PB	PC	PD	PE	PF	PG	PH	PI	PJ	PK	PL	PM	PN	PO	PP	PQ	PR	PS	PT	PU	PV	PW	PX	PY	PZ	QA	QB	QC	QD	QE	QF	QG	QH	QI	QJ	QK	QL	QM	QN	QO	QP	QQ	QR	QS	QT	QU	QV	QW	QX	QY	QZ	RA	RB	RC	RD	RE	RF	RG	RH	RI	RJ	RK	RL	RM	RN	RO	RP	RQ	RR	RS	RT	RU	RV	RW	RX	RY	RZ	SA	SB	SC	SD	SE	SF	SG	SH	SI	SJ	SK	SL	SM	SN	SO	SP	SQ	SR	SS	ST	SU	SV	SW	SX	SY	SZ	TA	TB	TC	TD	TE	TF	TG	TH	TI	TJ	TK	TL	TM	TN	TO	TP	TQ	TR	TS	TT	TU	TV	TW	TX	TY	TZ	UA	UB	UC	UD	UE	UF	UG	UH	UI	UJ	UK	UL	UM	UN	UO	UP	UQ	UR	US	UT	UU	UV	UW	UX	UY	UZ	VA	VB	VC	VD	VE	VF	VG	VH	VI	VJ	VK	VL	VM	VN	VO	VP	VQ	VR	VS	VT	VU	VV	VW	VX	VY	VZ	WA	WB	WC	WD	WE	WF	WG	WH	WI	WJ	WK	WL	WM	WN	WO	WP	WQ	WR	WS	WT	WU	WV	WW	WX	WY	WZ	XA	XB	XC	XD	XE	XF	YG	YH	YI	YJ	YK	YL	YM	YN	YO	YP	YQ	YR	YS	YT	YU	YV	YW	YX	YY	YZ	ZA	ZB	ZC	ZD	ZE	ZF	ZG	ZH	ZI	ZJ	ZK	ZL	ZM	ZN	ZO	ZP	ZQ	ZR	ZS	ZT	ZU	ZV	ZW	ZX	ZY	ZZ
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Label	A	B	C	Break Response	#	Poke Response	%	Poke Response	#	Crush Coral Res	%	Crush Urchin Res	#	Crush Urchin Res	%
1	trial	grp total		Break Response		Break Response		Poke Response		Crush Coral Res		Crush Urchin Res		Crush Urchin Res	
2	1	3		0	0	0	0	0	0	0	0	2	0	2	100
3	2	3		0	0	0	0	0	0	0	0	2	0	2	100
4	3	0		0	0	0	0	0	0	0	0	2	0	2	100
5	4	3		0	0	0	0	0	0	0	0	2	0	2	100
6	5	5	2 mv spines	0	0	0	0	0	0	0	0	4	0	4	100
7	6	15	4mv spines	0	0	0	0	0	0	0	0	10	0	10	71
8	7	10	0	0	0	0	0	0	0	0	0	9	0	9	100
9	8	3	0	0	0	0	0	0	0	0	0	2	0	2	100
10	9	4	0	0	0	0	0	0	0	0	0	3	0	3	100
11	10	4	0	0	0	0	0	0	0	0	0	3	0	3	100
12	11	2	0	0	0	0	0	0	0	0	0	1	0	1	100
13	12	5	2 mv spines	0	0	0	0	0	0	0	0	3	0	3	75
14	13	6	0	0	0	0	0	0	0	0	0	1	0	1	20
15	14	7	0	0	0	0	0	0	0	0	0	3	0	3	50
16	15	7	0	0	0	0	0	0	0	0	0	6	0	6	100
17	16	3	2 mv spines	0	0	0	0	0	0	0	0	2	0	2	100
18	17	6	3mv spines	0	0	0	0	0	0	0	0	4	0	4	80
19	18	5	0	0	0	0	0	0	0	0	0	4	0	4	100
20	19	10	2 mv spines	0	0	0	0	0	0	0	0	9	0	9	100
21	20	3	0	0	0	0	0	0	0	0	0	2	0	2	100
22	21	99	4 mv spines	0	0	0	0	0	0	0	0	98	0	98	100

Table 1. Alarm Response in *D. savignyi*. Response is measured in terms of movement of one urchin away from the body fluids of a crushed conspecific. Column B illustrates the movement of spines by Diadema touching the urchin getting its spines broken off. However, it does not count as an actual alarm response and thus the % break response = 0. The % Response to the crushed urchin was found by subtracting 1 from the group total (the number of urchins that could respond since one urchin in the group was subjected to the various treatments) and dividing by the number of urchins that showed a response.



# Moorea, French Polynesia

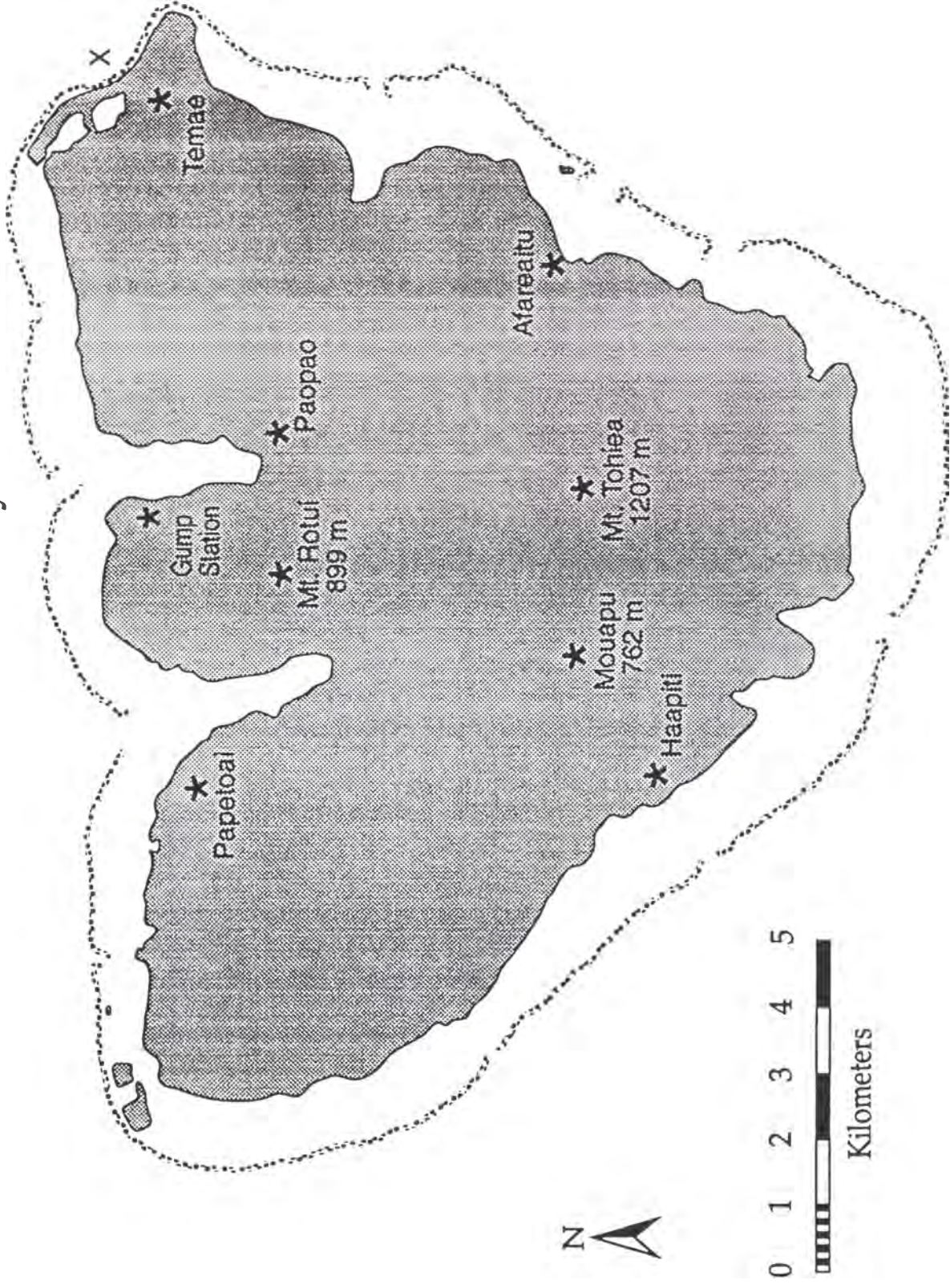


Figure X. Study Site Location

# Polio and Outcroppings of Man

## and the Social Geography

by J. H. Stoddard

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# Valleys and Outcroppings of Moorea

## A Study of Erosional Geomorphology

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Geography 142 (I.D.S. 158)  
Fall 1992





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## Abstract

Some aspects of the erosional geomorphology of the island Moorea in French Polynesia (longitude: 149° 50' W, latitude: 17° 32' S) were examined in the field during October-November 1992. Valleys were categorized into five types and mapped. Outcroppings (including cliffs) were categorized into four types. Both the valleys and outcroppings were then mapped along with other landforms. Valleys areas were calculated and the valley categorizations were quantified and compared with the results, revealing a hierarchy of area associated with valley categories. Cliffs and valleys were spatially correlated and larger valleys were found to contain larger outcroppings. Precipitation data was analyzed and converted into a map. Comparisons between precipitation, geology, and valley forms were made revealing some relationships. Cliffs were examined in detail in the field and data was found suggesting active parallel retreat.

## Introduction

The physical landscape of Moorea is striking. With broad valleys separated by knife edged ridges and tall horn-shaped mountains, the landscape is similar in form to the glaciated mountain landscapes of the temperate zones. In many places, high cliffs fringe the ridges, forming terminal walls to the edges of the smoothly sloping valley floors. The island is ringed by a coral reef interrupted by 12 passes and dotted with four islets (or motu). It is a remarkable landscape which has been described by various authors including geomorphologists such as W. M. Davis (1928) who examined the island as an example of a middle stage in Darwin's island subsidence and atoll formation theory and by Frank Murphy and Professor David Stoddard of U.C. Berkeley who are presently studying the coastal, depositional landforms of the island. Other authors have examined the mountains and knife edged ridges according to Davis (1928). This study is not concerned with depositional features or the mountains, but is an examination of what lies between them, the erosional features of the valleys and cliffs. Most of the recent work on the erosional geomorphology of tropical volcanic islands has been conducted on the Hawaiian islands by authors such as Stearns (1985) and Macdonald and Abbott (1970) who examined some valley forms and cliffs. Little work of this nature has been conducted on Moorea and this study represents an initial systematic examination of the valleys and cliffs of the island.

The valleys vary in form greatly around the island in terms of area, cross sectional profiles, and long profiles. It is desirable to group valleys with common morphologies together into categories in order to study their spatial distributions. Five categories of valleys are proposed to encompass all of the 88 valleys of the island, four of which are also noted by Ollier (1969). The spatial distribution of these categories is then examined by means of mapping and two factors influencing these distributions are hypothesized: rainfall patterns on the island govern the development and thus the distribution of valley types, and the location of resistant geologic features govern the distributions of these valley categories. Both of these hypotheses have been suggested before and have been correlated to valley types in Hawaii by Stearns (1985).

The cliffs also vary significantly in form in terms of height, length, and bedding structure. In this study the term "cliffs" is used interchangeably with the term "outcroppings" and is defined as an exposure of rock free of vegetation, a "free face" in the terminology

used by Young (1972), greater than 5 meters high. The cliffs are categorized into three size groups based on height and mapped in order to display length and to correlate their spatial distributions with the distributions of the valley types. Another category is proposed for small scattered cliffs and is also mapped. A correlation between large valleys and cliffs and small valleys and cliffs is hypothesized to exist. The processes which led to the formation of these cliffs is then examined. Hypotheses include: cliffs are resistant features which have been exposed by differential erosion of surrounding weaker rocks, cliffs are formed by a resistant caprock being undercut by basal erosion of underlying weaker rock, and cliffs are formed by multiple beds of resistant rocks overlying beds of weaker rocks which have retreated and coalesced together. All of these hypotheses have been suggested by other authors as well, including Stearns (1985) and Selby (1985).

The objective of this study is to determine where and why these geomorphic features are occurring on Moorea and to evaluate the importance or validity of the hypotheses previously suggested.

## Methods

The first step in investigating these questions was to describe, classify, and map the valleys and cliffs of the island. The description of the valleys was accomplished by careful examination of the 1:20,000 topographic map of Moorea and the construction of slope profiles from it, and more importantly, by direct field observations from hiking trails, from the sea, and from roads all around the island. The first method was quantitative and the second was qualitative but resulted in a more thorough understanding of the forms of the valleys. A classification scheme for the valleys was developed from these observations and descriptions which grouped valleys with similar forms into five valley categories or types. These categories are: C Valleys or caldera valleys, which are the large, central valleys of the island headed by the heavily eroded remnants of the caldera rim which are also described by Davis (1928), P Valleys or pali valleys, also referred to as amphitheater-headed valleys by Stearns (1985), which are medium sized valleys headed by steep pali slopes which are not quite cliffs because they are vegetated, U Valleys or U-profile valleys which are medium to small in area and have a U-shaped cross profile similar in form to a catenary curve, D Valleys or dissected valleys which tend to be smaller and contain numerous small ridges and valleys within them and which lack the concave

upward slopes of the previous valley types, and V Valleys or V-profile valleys which have V-shaped cross profiles and tend to be long and narrow and smallest in total area of all the valley types. With these categories established, the valleys of the island could be classified and mapped. A map of the valleys was constructed by drawing in drainage divides on the geologic map around the catchments for every stream emptying separately into the surrounding lagoon. Topographic contours were employed to locate the ridges forming the divides and the existence of streams was cross checked on both the geologic map and the topographic map. Then this base map was field checked while the valleys were classified and mapped onto it from observations made from the perimeter road. This process of valley classification was qualitative, based solely on the morphology of the valleys observable from the road, valleys which were not visible from the road (which were very few) were classified by careful examination of the topographic map. In P Valleys, the pali slopes were also mapped from field observations and by examination of the elevation contours on the base map.

The cliffs were also observed and described in the field as well as from both of the maps. The maps, however were of little utility, the topographic map often misplacing or omitting cliffs and the geologic map also omitting cliffs. Again, field observations revealed the most information and yielded a classification system based on cliff height, continuity of length, and bedding structure which was employed in the mapping of these features. The classification scheme is as follows: Small Cliffs are 5 to 10 meters high, Medium Cliffs are 10 to 50 meters high, and Large Cliffs are greater than 50 meters high. An additional classification, Scattered Outcrops, is used to refer to exposures of rock greater than 5 meters high which are not wider than they are high as is the case with the previous cliff types. The continuity of length refers to the degree of connection which the cliffs exhibited, i.e. long cliffs were well connected while scattered, narrow cliffs were not well connected. The bedding structure of the cliffs was also classified according to the degree of separation of the beds of solid basalt by pyroclastic deposits. With this classification scheme established, the cliffs were examined in the field during the valley observations and were mapped along with them. The location and the classifications of the cliffs was recorded directly onto the same base map by direct observation of the cliffs in relation to topographic features of the valleys. This map was then checked against the topographic map to verify the locations of the cliffs. The heights of the cliffs were estimated only to the degree to



fit them into one of the three categories. Binoculars were employed to aid in these classifications.

Once the cliffs and valleys had been mapped, it was possible to construct a master map displaying all of the classified features and other observed features which were neither cliffs nor valleys but which are significant parts of the landscape. This map was produced by computer cartography based on the same working field map mentioned above. Once the valleys were mapped into the computer, an image analysis program was used to calculate their areas and this data was variously manipulated and plotted in graphs. Only the area of the erosional surface of the valley was considered, the area measurements do not include areas of alluvial deposition or marine deposition. Data regarding the correlation between the cliffs and the valleys was also derived from the map and was graphed. In order to spatially correlate rainfall patterns to valley types a rainfall map was constructed from the rainfall data supplied by the Antenne Museum (see Acknowledgments), and other observations regarding precipitation were made around the island.

In addition to these large scale observations, detailed field observations were conducted on the cliffs in order to identify the processes acting to form and maintain them. Cliff faces were viewed from a distance by binoculars during different weather conditions and photographic evidence was collected. The bases of four cliffs of different types and sizes were visited and detailed observations were carried out, the data being collected in the form of notes, sketches, and photographs. The results of these observations are detailed hereafter.

## Results

The examination of the topographic map yielded quantitative descriptions of P Valleys and C Valleys in the form of two long slope profiles graphed in Figure 2(A+B) in which there is no vertical exaggeration. Both profiles cross the caldera rim and are located in Figure 1. Notice the asymmetry of valley size between the left and right sides of the graphs as well as the generally steeper slopes on the right sides of the ridge separating these valleys. The qualitative distinctions between the categories of valleys are exemplified by the photographic examples provided in Plates 1-5. In Plate 2, notice that the pali slopes do not extend all around the valley head and are therefore not exactly amphitheater-headed valleys in the sense of Stearns (1985).



Examples of the four categories of cliffs are shown in Plates 6-9. The degree of connection of the cliffs is reflected on the master map (Figure 3) by the separation between individual cliffs within a valley. The bedding was found to vary between cliffs with even thicknesses of solid basalt and pyroclastic deposits and cliffs composed of only solid basaltic beds. Most of the bedded cliffs were proportionately dominated by solid basalt. In addition, some of the cliffs found in the C Valleys between Mt. Tohivea and Mt. Tearai appeared to be composed of un-bedded solid basalt with a well defined jointing structure (Plate 10).

The results of the classifications and mapping of the valleys and cliffs are shown in Figure 3 which displays these erosional features as well as the triangular facets and remnant planeze surface which eluded the classification scheme for the valleys and cliffs. The depositional features and the location of the eroded caldera rim which are displayed on the map were derived directly from the geologic map. Notice the spatial separation, isolation, and location of the D Valleys and C Valleys and the close correlation of the P Valleys and C Valleys to the eroded caldera rim. A similar correlation also exists between the large cliffs and the caldera rim.

The analysis of the valley areas yielded the data plotted in Figure 4(A+B), Figure 5, and Figure 6. The horizontal axis in Figure 5 and Figure 6 does not have units, the symbols representing the valleys are arranged from largest area to least and are equally spaced. Notice the logarithmic nature of the data in Figure 4A which is also plotted on a logarithmic scale, with an exponential regression line to illustrate linearity, in Figure 4B. In Figure 5, the valley areas have again been plotted as a histogram but have also been grouped by valley categories. The same data has been plotted in Figure 6 as average areas for valley types with standard deviations represented by the error bars. Notice that the valley types have been arranged according to descending average areas.

The results of the analysis of the cliff and valley correlations are graphed in Figure 7 and Figure 8. In Figure 7, notice that there is a generally descending frequency of higher outcroppings going from large valley types to small valley types. In Figure 8 notice that the D Valleys contain a greater proportion small cliffs than might be expected from the general trend of the graph.

Figure 9 displays the precipitation data collected at seven different gauging stations around the island. A table of the values derived from the precipitation data which is mapped is also included in the figure. Notice that average rainfalls are greatest in the central portion of the island, less in the south-western and eastern parts of

the island, and least in the north-west. Notice also that these precipitation values were not recorded during the same span of years. SPOT satellite imagery of the island (Plate 11), aerial photos, and the topographic map show that many of the ridges are dominated by grasses along the northern shore of the island, especially in the north-west and north east, and to a lesser degree on the southern end of the island. Field observations of the vegetation indicate that the north-eastern end of the island is dominated by shrubby trees in the valleys and shrubs and grasses on the ridges, and that the north-western end is dominated by the same vegetation types as well as two species of introduced pines. This in contrast to the rest of the island in which the valleys are mostly dominated by forests of Tahitian chestnut and hibiscus trees and the ridges are populated mostly by shrubby trees or pali vegetation at higher altitudes.

The smaller scale cliff observations produced many descriptive results. Most of the cliffs composed of bedded lava and pyroclasts have an S-shaped profile with upper half convex and the lower half concave, often producing a smoothly curving overhang. The detachment scars found on some of the cliffs were located within the middle third of the cliff's height. Other cliffs were rectilinear in form (mostly the large cliffs) or irregular. Plate 12 is a photograph of the face of a typical medium height cliff, Plate 13 is a photograph of the same cliff during a heavy rainfall event which lasted for two days. Notice that the locations of the waterfalls contain the least amount of tan colored material. The closer observations of the bases of the cliffs revealed a sharp break between the rock of the cliff and the scree deposits of the cliff, Plate 14 shows this at Site 1 in Figure 1 and Plate 15 shows this at Site 2. In all cases, vegetation of different types were found growing thickly on the scree slopes. Root systems were exposed at the surface near and on the rock of the cliffs, with density and size of roots decreasing away from the cliff (Plates 15 and 16). The pyroclastic layers were colored orange and white in many places and were always concave with the maximum concavity located just under the overlying solid basalt layer (Plate 15). The solid lava beds were flat on their exposed edges and were covered with a blue-black casing. The bedded cliffs were scalloped by vertical indentations about 4-10 meters wide in which water was often flowing (during dry weather). Gullies existed in the scree slopes just below these indentations with convex interfluves between them.

## Discussion

The valley classification scheme accounts for all of the valleys of the island as defined in this study. Except for the D Valleys, these classifications are supported by the work of many geomorphologists summarized by Ollier (1969). However, in a few cases the valleys did not fit neatly into the categories, such as the largest U Valley which had elements of D Valleys as well, and a decision had to be made based on which aspects of the categories were dominant. The fact that there are valleys containing characteristics of two different types suggests that they may be evolutionarily (in the geomorphological sense) linked.

The analysis of the valley areas reveals some interesting relationships. The logarithmic spread of all the valley areas might be a consequence of the pre-eroded geometry of the island, or perhaps a consequence of erosion on the particular geology of a volcano. If this is true, this might be worth further investigation so that a similar inventory on other volcanoes could reveal these initial factors. The breakdown of the areas by valley type shows that area is an important factor in the distinctions between certain valley types. The fact that U Valleys contain both the largest range of valley areas and the largest number of individual valleys (2.875 times the number of P or D Valleys) hints that these forms are favored by the erosive processes acting on the entire island. This, in conjunction with the previous observation of valleys containing features of two valley types and the theories of valley evolution summarized by Selby (1985) and Ollier (1969), supports the hypothesis that all the valleys are becoming U valleys. This hypothesis will only remain valid if sea level does not drop, for in this case renewed incision will begin the process of evolution again. If sea level rose, filling by streams would occur and incision would not be initiated.

The maps of valley types and rainfall are useful in answering the question of what factors are dominant in determining the distribution of valley forms. The effects of resistant geology, e.g. the caldera rim, are very important in determining the location of P Valleys and C Valleys, and this makes sense since the steep slopes which partially define them could only be developed in areas of sufficient available relief. However, the U Valleys and V Valleys have a much more scattered distribution on the map and do not seem to be correlated with any type of geological formation. The D Valleys are not associated with a geologic formation, but show a strong localization on the most leeward area of the island. The precipitation map and the vegetation differences both show that this



is the driest part of the island and this supports the rainfall dominated hypothesis. High rainfall is also correlated with the central portion of the island which is dominated by the C Valleys but their large areas are due not only to greater amounts of erosion but also to the location of the caldera rim. The conclusion is that geological features dominate the formation of the C and P Valleys, which is supported by the observations of Stearns (1985) and others, but that precipitation is more important in determining the form of the D Valleys. This implies that the D Valleys should be found on other islands, and that they should be located in areas of sufficiently low rainfalls. Of course, there may be some unknown geologic reason for the form of the D Valleys, and further study in the details of the geology of the area would be illuminating.

As for the cliff and valley correlations, Figure 7 shows that the initial hypothesis about the correlation of large cliffs and valleys seems to be true, but that the correlation of small cliffs to small valleys is not apparent. A more general conclusion is that larger valleys contain more cliffs. The reason that there are no medium or small cliffs or scattered outcroppings in the C Valleys is that the method of recording cliff types of valleys gave only the dominant type of feature for each valley. This poses a problem for the C Valleys because there are only three of them and there is no chance for a statistical expression of the other types of outcroppings. The previous conclusion is also reflected in Figure 8 where larger valleys types contain a greater proportion of valleys with cliffs. The large proportion of small cliffs apparent in the D Valleys is due to a fault that runs along the western side of the D Valleys' area which results in an unusually large proportion of small cliffs since most of the other cliffs of the island are not fault related (according to the geologic map). Perhaps most interesting is the fact that even though U Valleys are the most numerous, the proportion of them containing outcroppings is comparatively low. This might be an indicator that these valleys have reached a stable state of form if cliffs represent some change in conditions such as lower sea level causing river incision leading to cliff cutting and retreat or higher sea level leading to wave cutting and again leading to cliff cutting. If this is true, then the low proportion of cliffs in U Valleys compared with C Valleys and P Valleys supports the hypothesis that they are evolving into U Valleys because the effects of the change of conditions will fade due to the effects of erosion. All of these points are tenuous for the sample size is small, and the data is only suggestive not conclusive. More work needs to be done on the relationships between cliffs and these valley types on other islands before a strong pattern can

emerge. One way to improve the sampling method would be to record every outcropping totally independently from the valleys and to categorize it separately, but of course this would be a great deal of work.

An interpretation of the data concerning the processes acting on the cliffs is now presented. The overall S-form of the bedded cliffs along with the location of the detachments does not support the hypothesis of undercutting of the entire cliff because in such a case one would expect a large overhang near the base of the cliff. The orange and white coloring of the pyroclasts appears to be evidence of weathering and the fact that the coloration is missing from where the waterfalls run suggests that erosion due to the waterfalls is occurring there. Thus the pyroclastic layers in the bedded cliffs are being weathered and eroded away faster than the lava beds, undercutting them and causing cliff formation and maintenance by accretion of separately retreating layers. This is in agreement with the findings of Stearns (1985) for similar cliffs in Hawaii. The large cliffs composed of massive basalt do not have the same S-form and lack bedding so that they cannot be maintained by the same process. The hypothesis of exposure of resistant rock is supported here. In both cliff types, erosion at the base of the cliff seems to be occurring due to the exposure of the roots near the cliffs. It is hypothesized that erosion is occurring at the base of the cliff and that the cliffs are presently being exposed. This in combination with the erosion occurring mid way up the slope probably due to the waterfalls would result in near parallel retreat and thus maintain the existence of the cliff until the top of the ridge was reached. But of course much more work on the cliffs would have to be performed in order to come to a definite conclusion about this. It would be useful to measure the amount of rock removal off the surface of the cliffs in some way.

All of these conclusions are really only hints at the truth and this study does not profess to have attained that truth, but it does represent a first look at some of the most interesting erosional features of Moorea. Its purpose will be complete if it helps other researchers to learn more about the island and perhaps other islands as well.

## Acknowledgments

I would like to thank all of the faculty for giving me the opportunity to pretend to be scientist and showing me how to do



it: Werner, David, Carla, Jere, Mary, Roy, Carole, George, Lary and Stuart. Thank you all, it was excellent! I'd also like to thank Professor Oberlander and Bill Deitrich for their hints on how to be a geomorphologist. And finally I'd like to thank all of my friends for putting up with me while I figured this report out.

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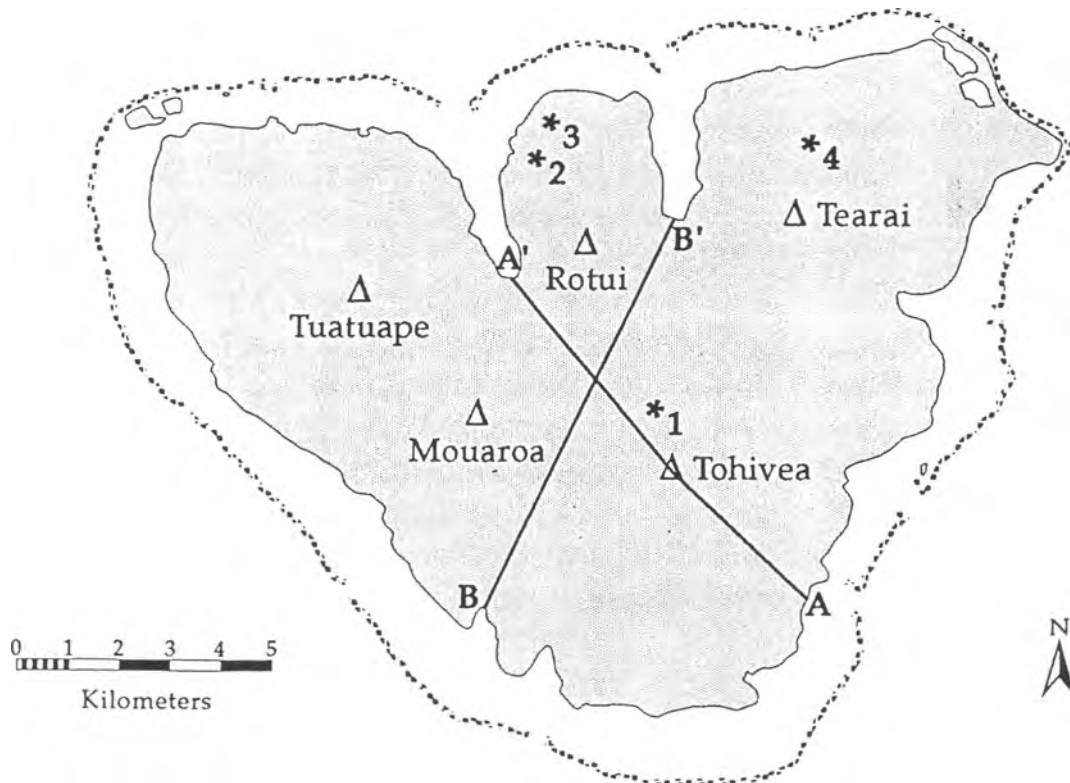
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# Moorea, French Polynesia



△ Prominent mountain

\* Study site (by number)

A—A' Slope profile from Humai to Oponuhu Bay

B—B' Slope profile from Vaianae to Cook's Bay



Land



Water



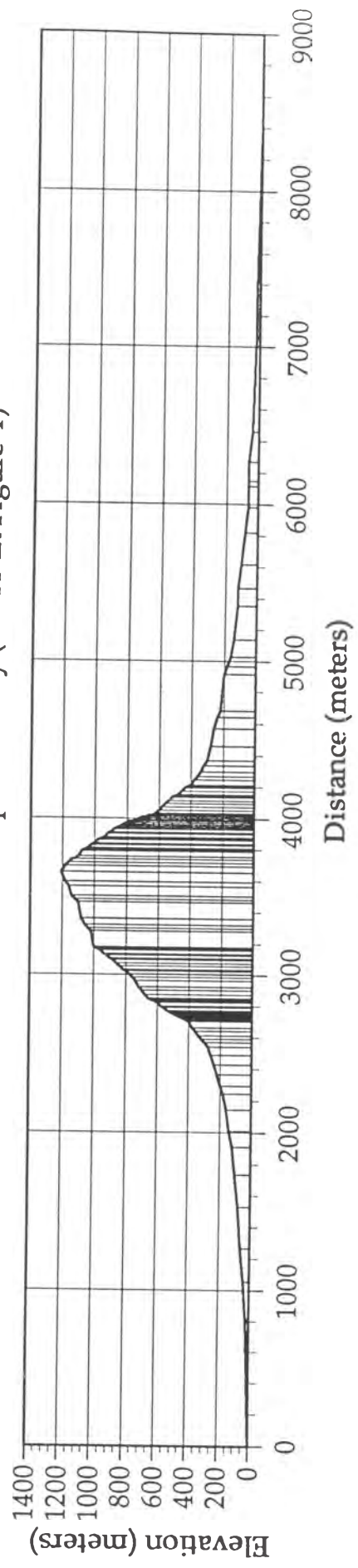
Reef



Profile line

**Figure 1:** Map of the island of Moorea displaying locations of some of the mountains, the cliff study sites, and the slope profiles in Figure Y.

A. Profile from Humai to Oponuhu Bay (A—A' in Figure Y)



B. Profile from Vaianae Bay to Cook's Bay (B—B' in Figure Y)

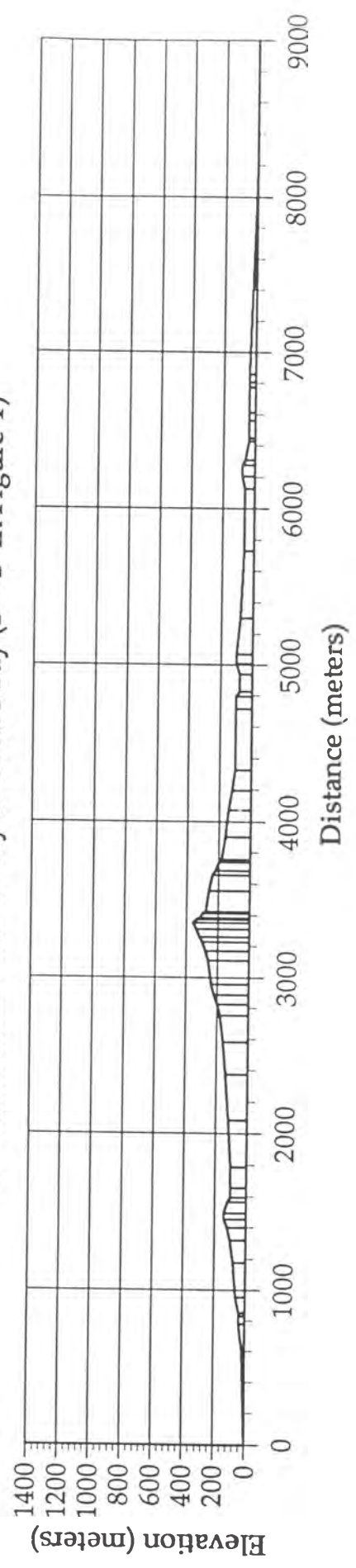


Figure 2(A+B): Long slope profiles running from P Valleys in the left through different parts of the caldera ridge into C Valleys on the right. Vertical lines under the curve mark data points of distance values taken at twenty meter intervals in elevation.





# Valleys and Outcroppings of Moorea

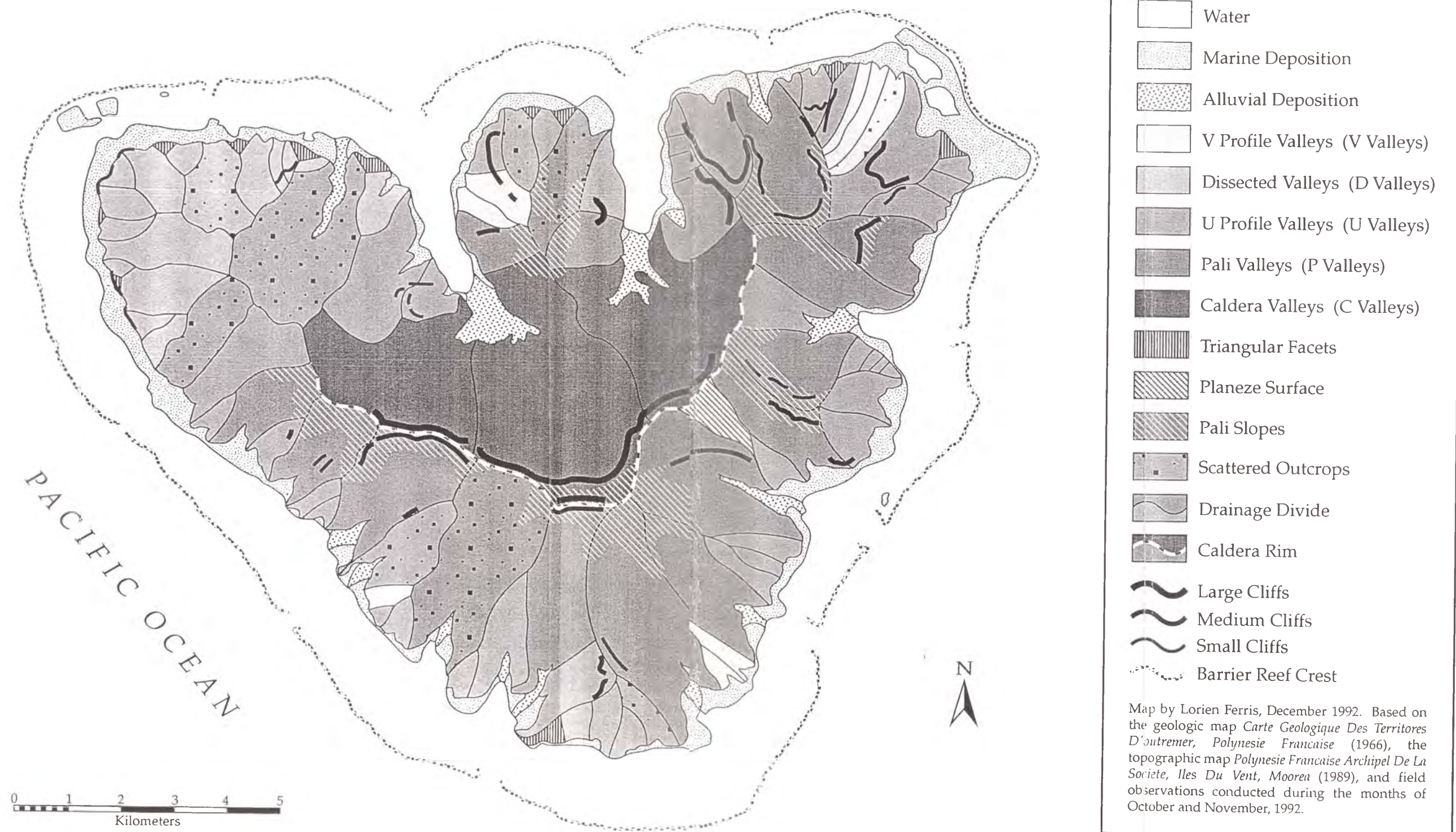


Figure 3: Master map.





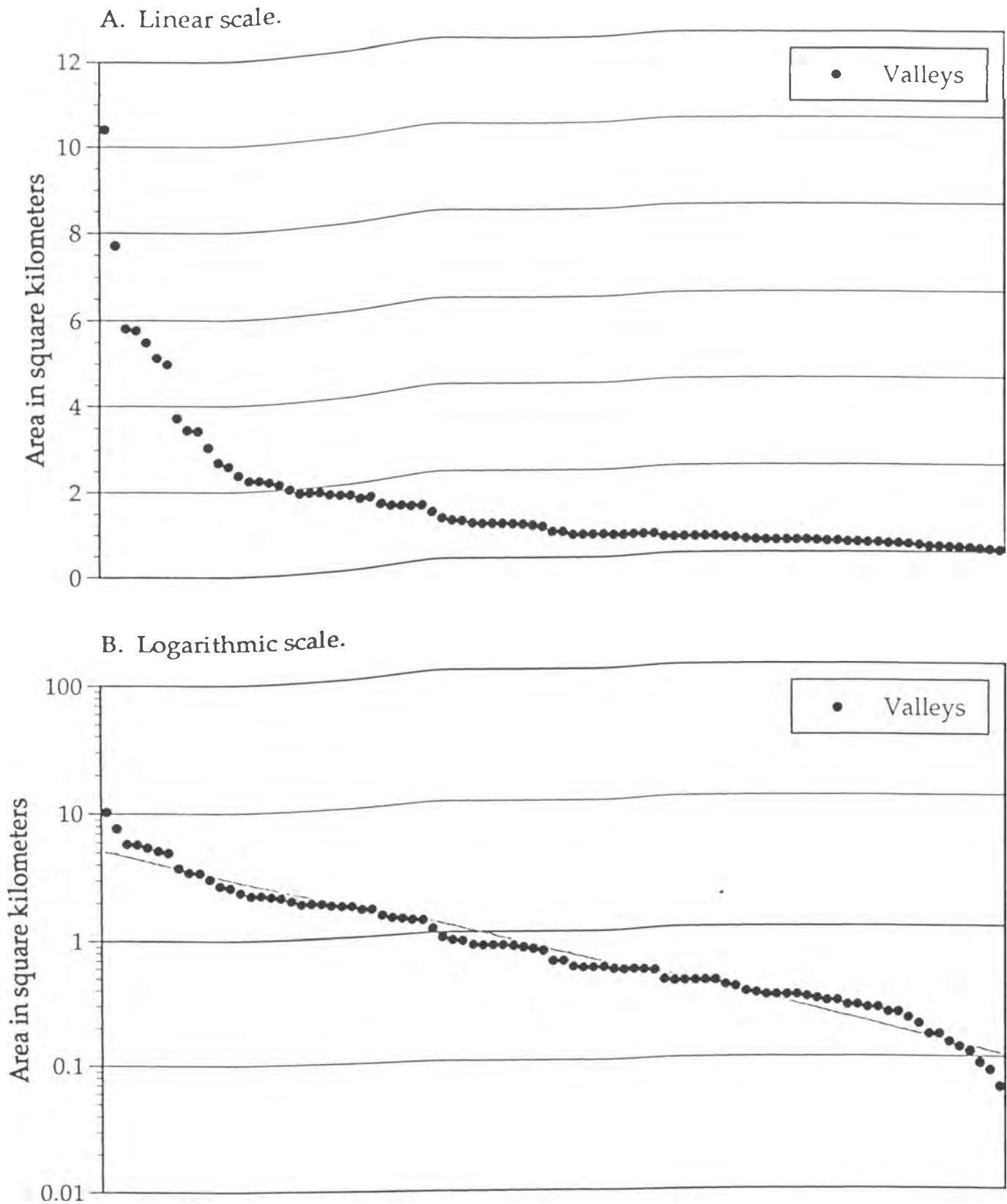


Figure 4(A+B): Histogram of the areas of all of the 88 valleys of Moorea with a regression line to show the linearity of the data which is arranged from greatest to least in area. The vertical axis is plotted in two scales: linear and logarithmic.

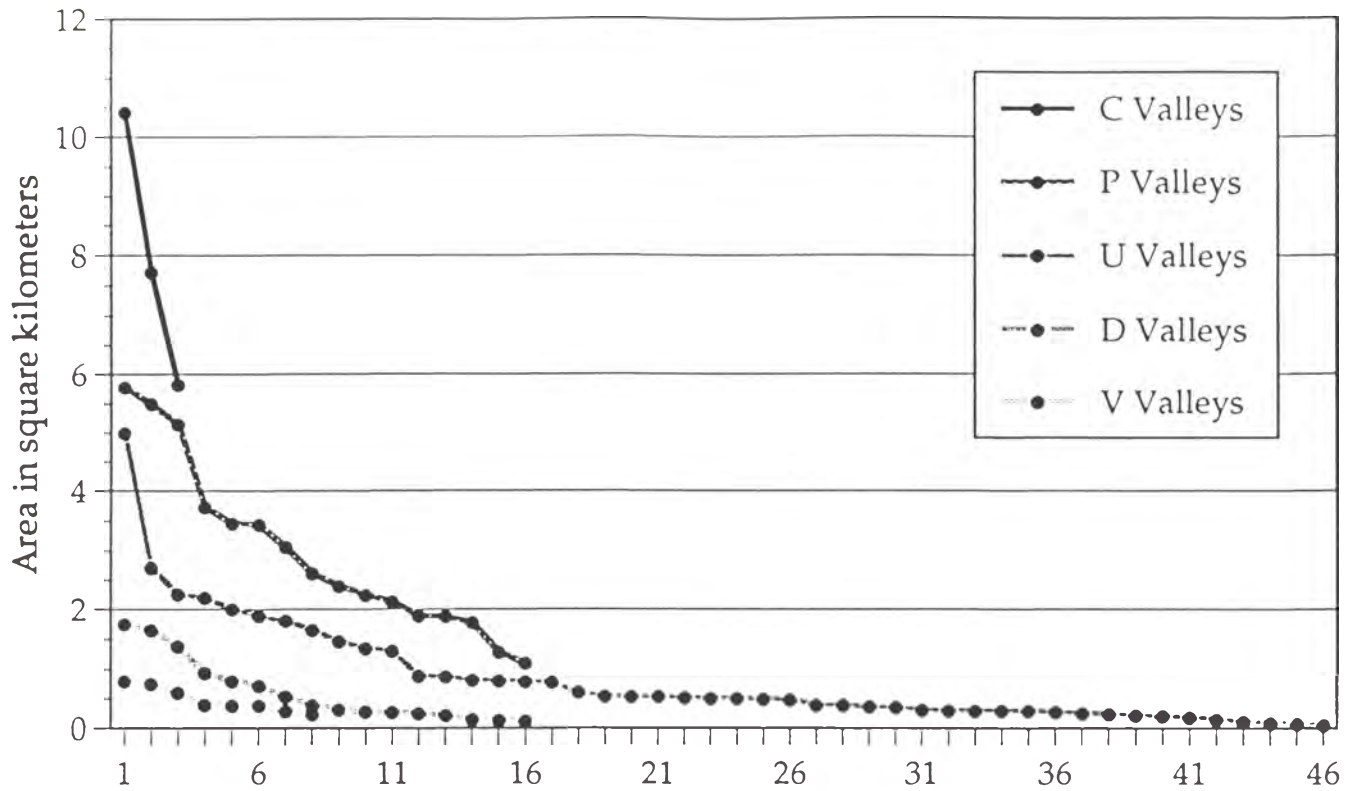


Figure 5: A histogram of different categories of valleys (represented by shaded lines) composed of individual valleys (represented by dots) arranged from largest to least in area. The bottom axis indicates the total number of valleys in each category.

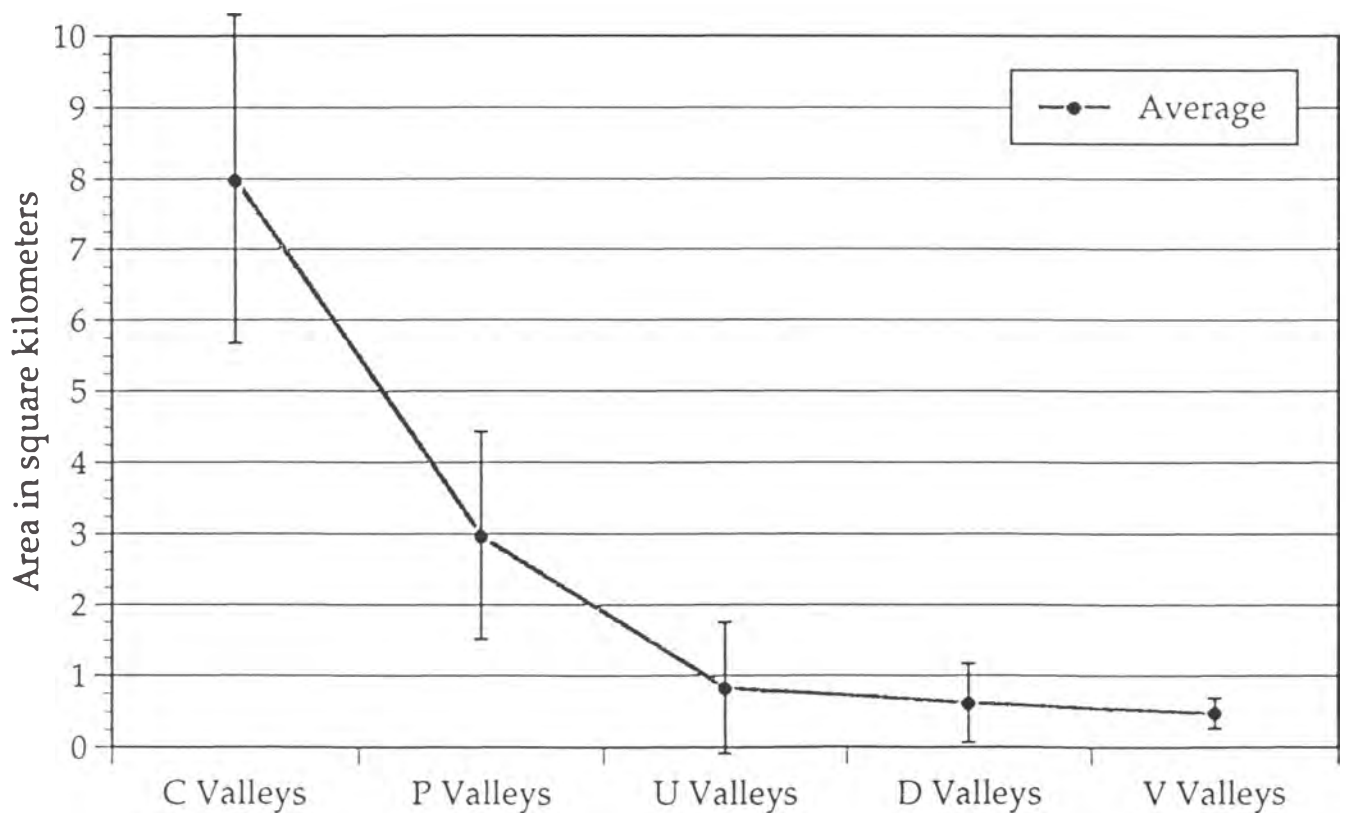
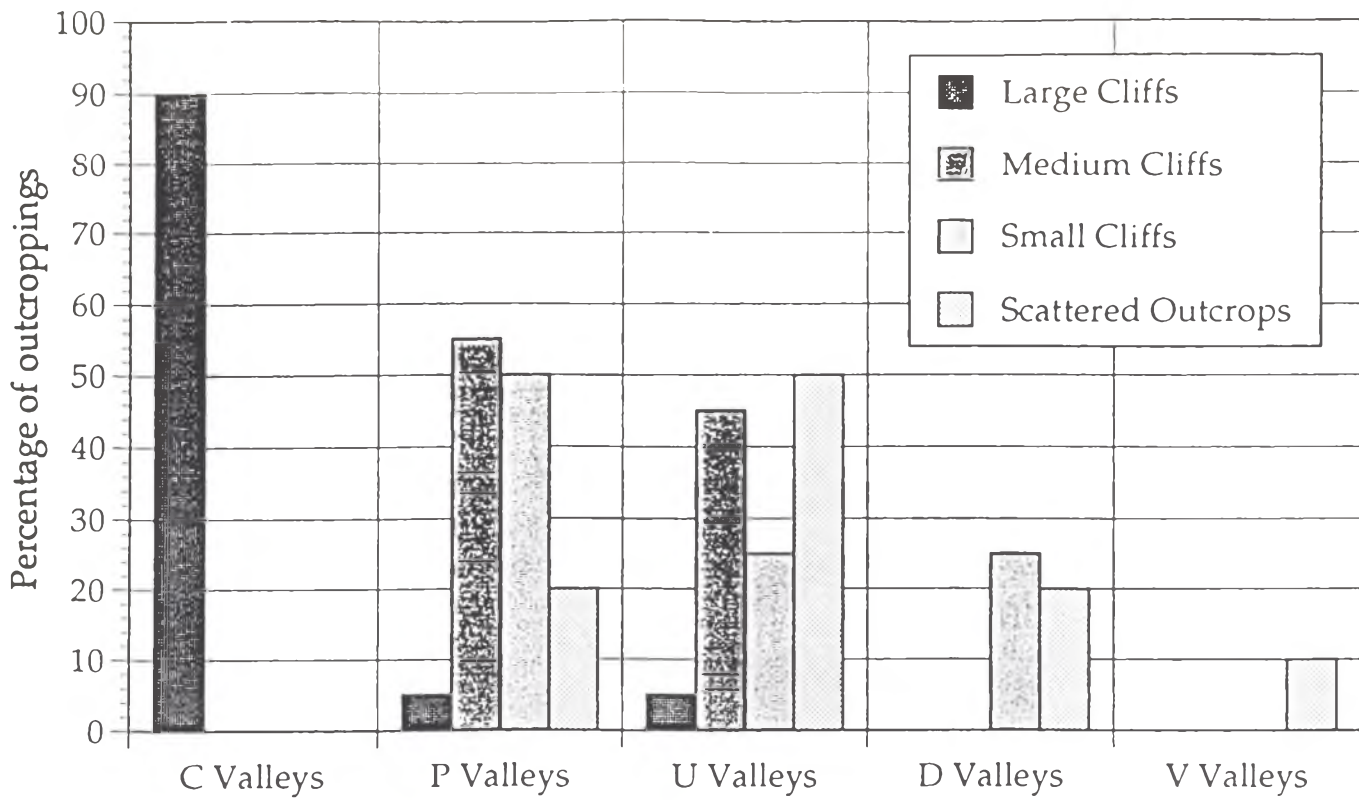
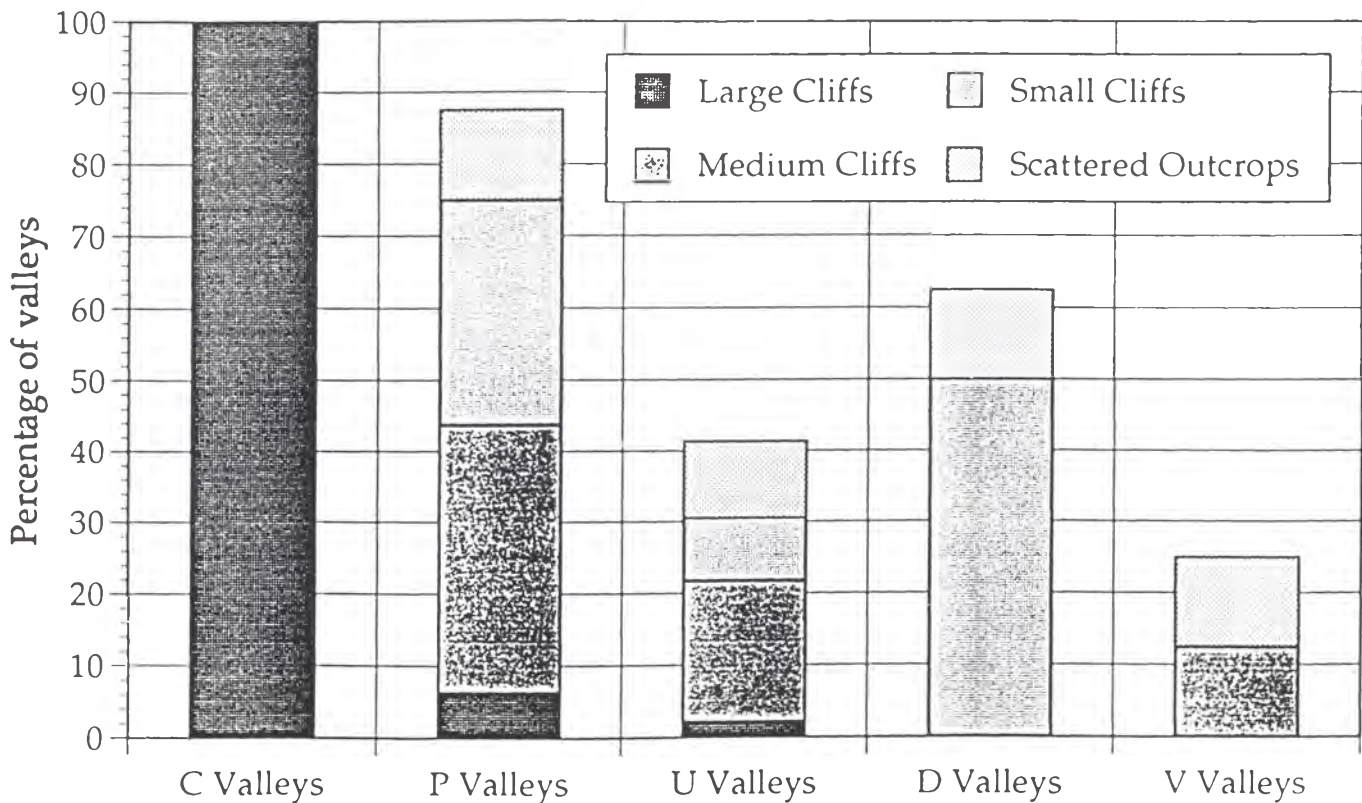


Figure 6: The same data as Figure X but plotted as averages and standard deviations. The line connecting the average values displays the slope trend in the data.

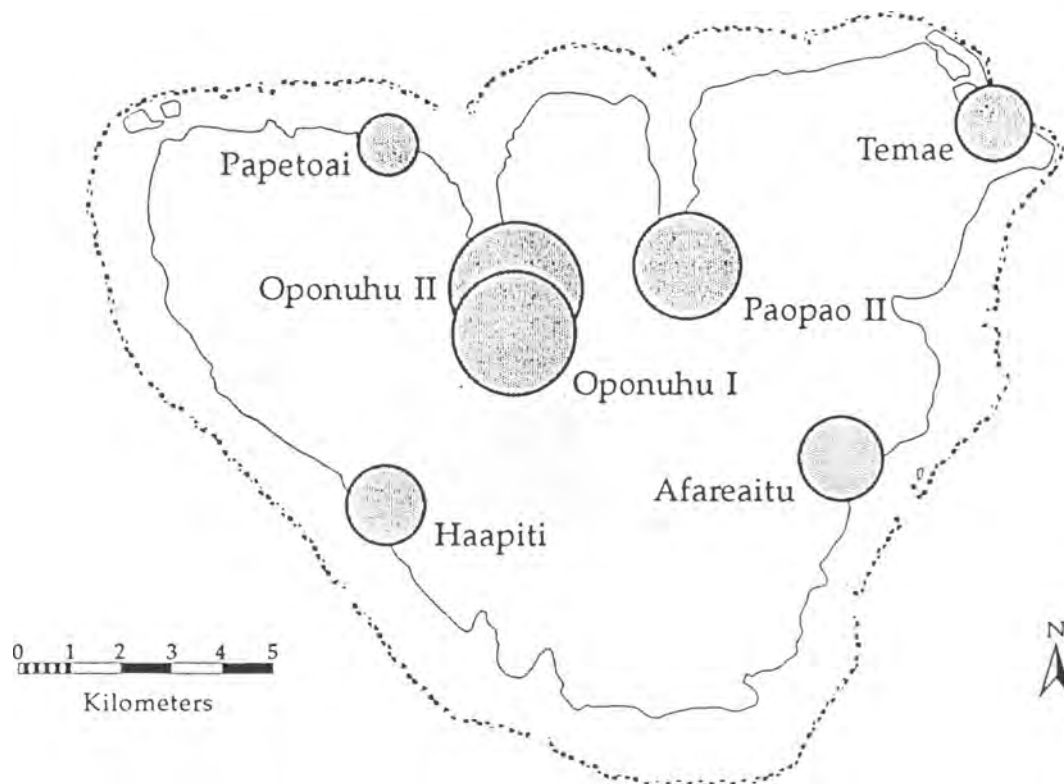


**Figure 7:** Graph showing the percentages of outcroppings found in each of the five valley types. Values for the cliffs were assessed according to the length of the cliffs.



**Figure 8:** Graph of the percentage of valleys containing outcroppings by valley type. Shading represents outcropping type.

## Average Annual Precipitation



	Average*	Min*	Max*	Total
Afareaitu (61-88)	1898	0	11939	637742
Haapiti (70-90)	1711	22	11000	431237
Oponuhu I (70-88)	2707	200	13262	617285
Oponuhu II (79-90)	2940	265	12411	423297
Paopao II (60-90)	2357	13	15247	876953
Papetoai (60-77)	1328	0	7720	286759
Temae (80-90)	1634	58	7367	221559

\* Annual precipitation in millimeters.

**Figure 9:** Circles on this map are scaled to the average annual precipitation during the span of years indicated after the name of the gauging station. Minimum and maximum values are also yearly averages.



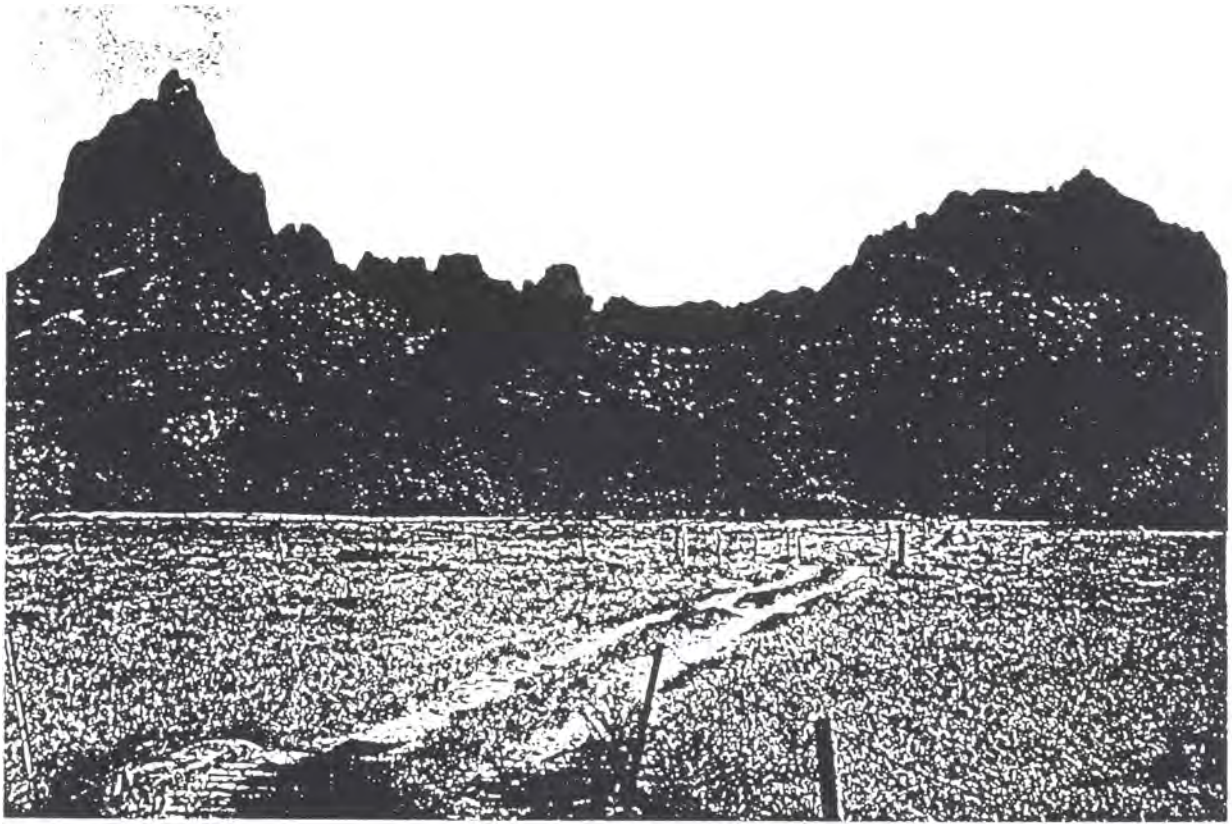


Plate 1: C Valley with large cliffs at the valley head.

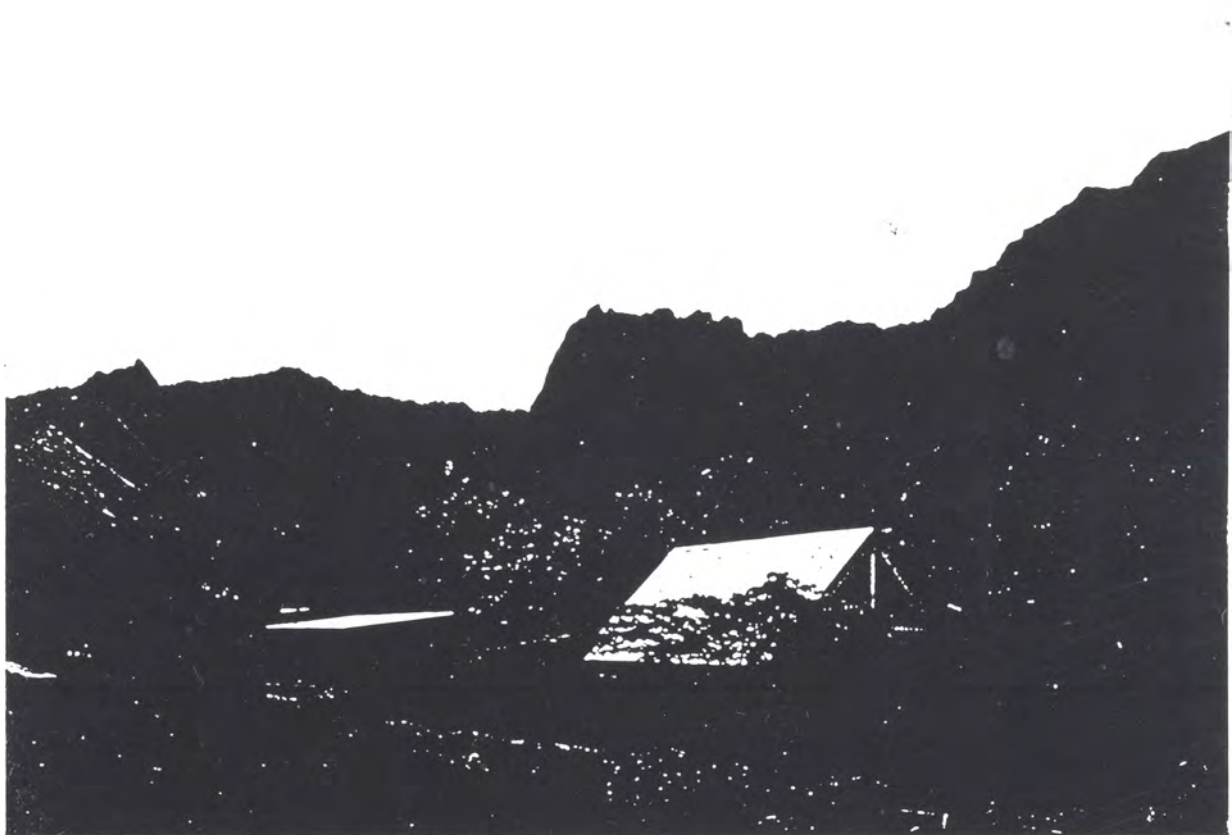


Plate 2: P Valley with pali slopes on the right side.



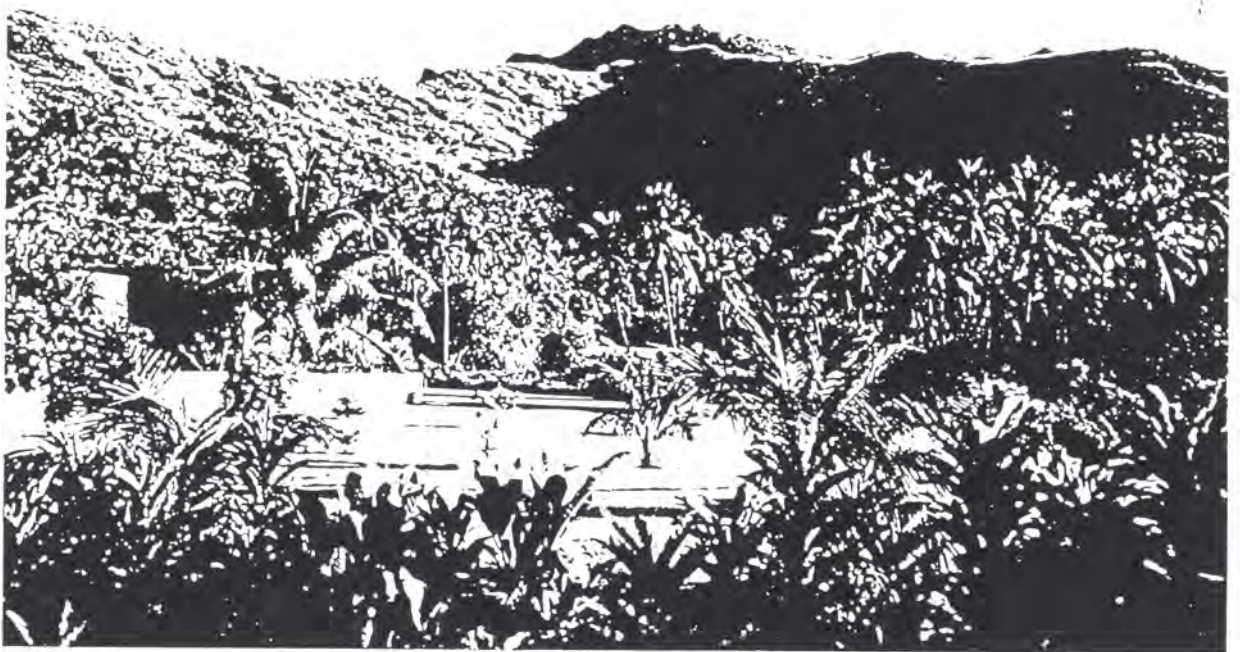


Plate 3: U Valley.



Plate 4: D Valley.



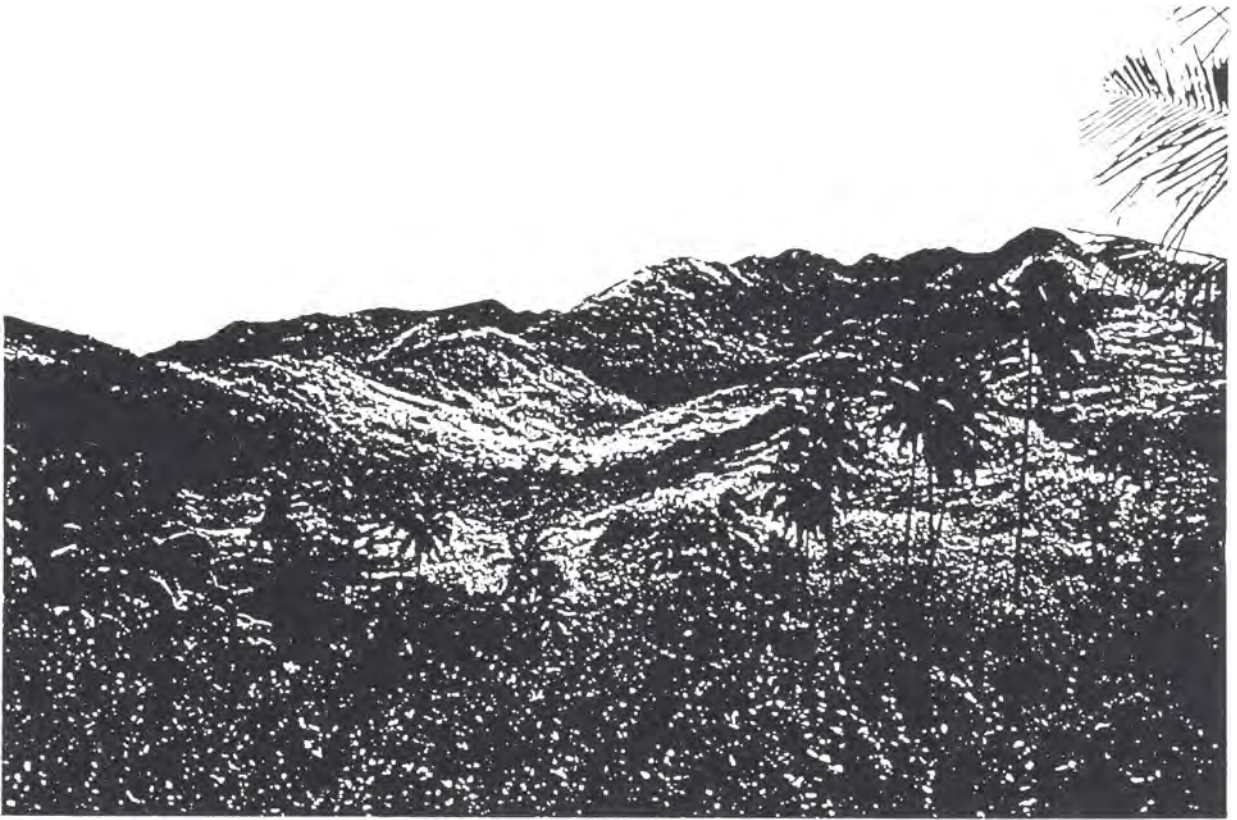


Plate 5: V Valley.



Plate 6: Small Cliffs.





Plate 7: Medium Cliffs.

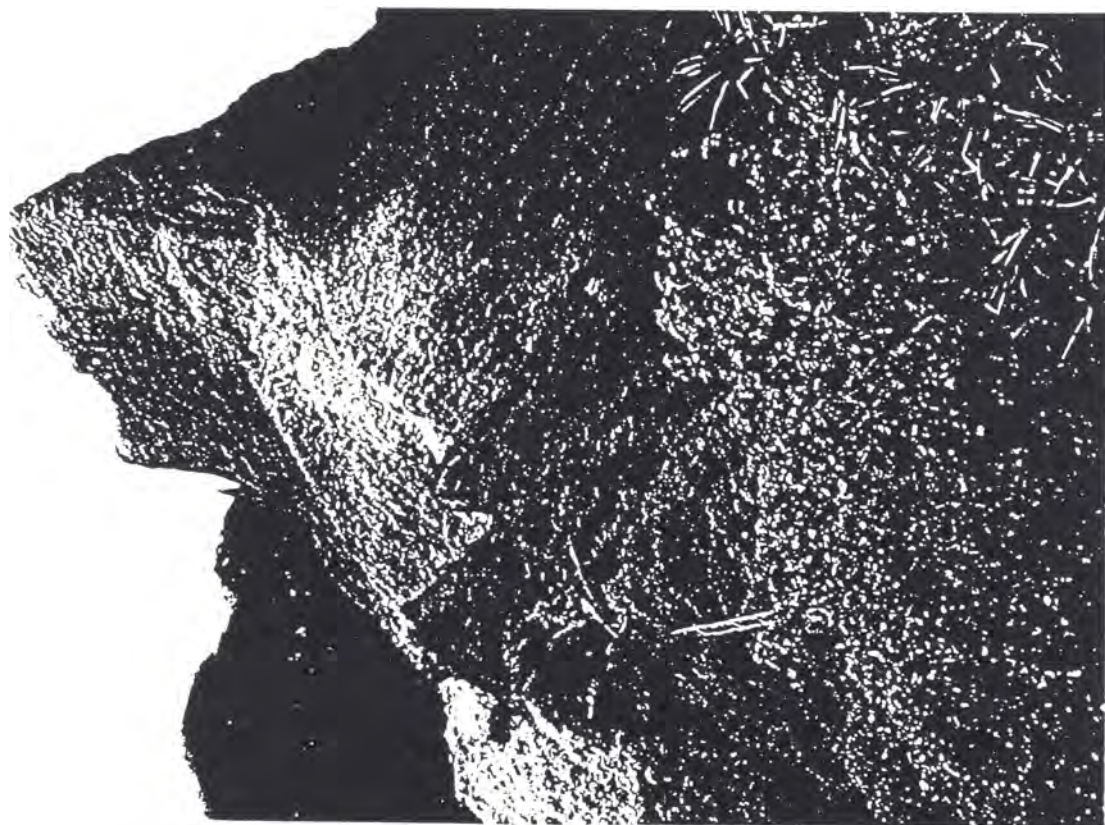


Plate 8: Large Cliffs.





Plate 9: Scattered Outcrops.

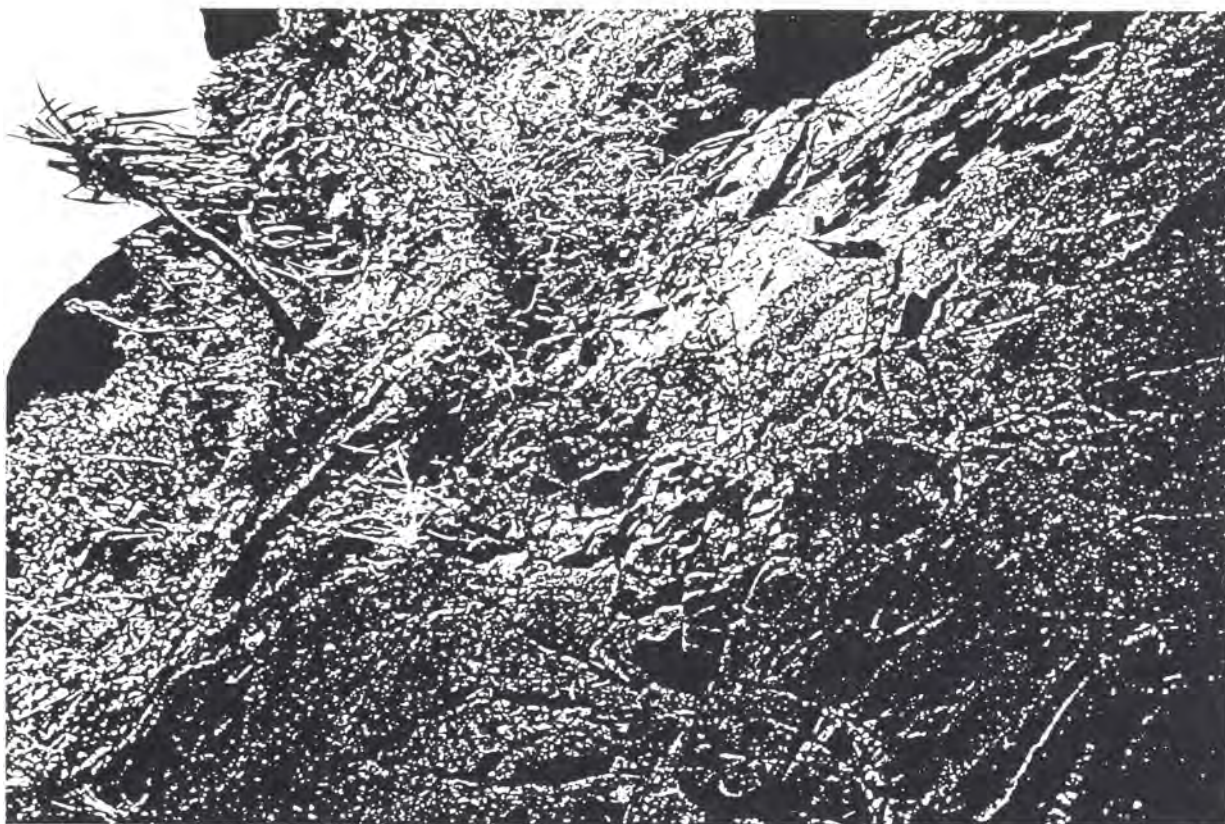


Plate 10: Un-bedded basalt cliff face (Site 1).





Plate 11: SPOT satellite image of Moorea.

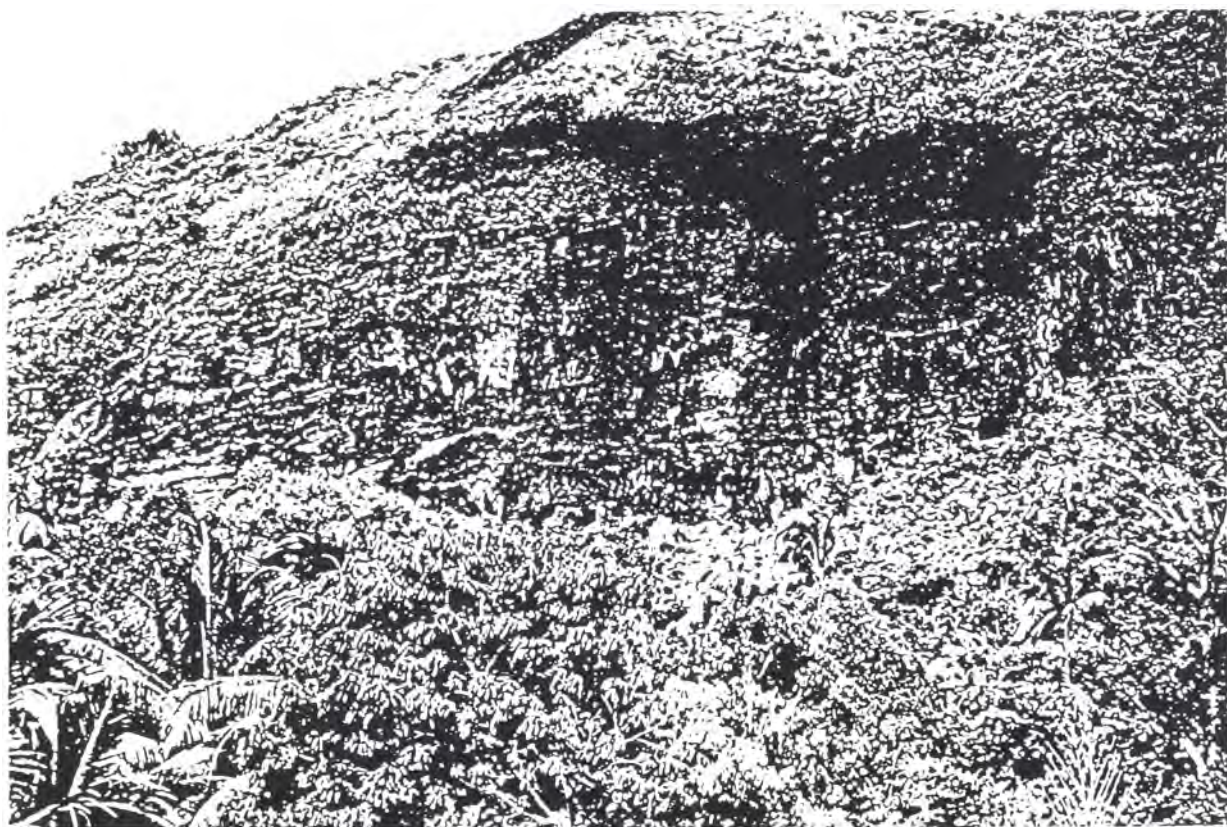


Plate 12: Bedded cliff face (Site 2).



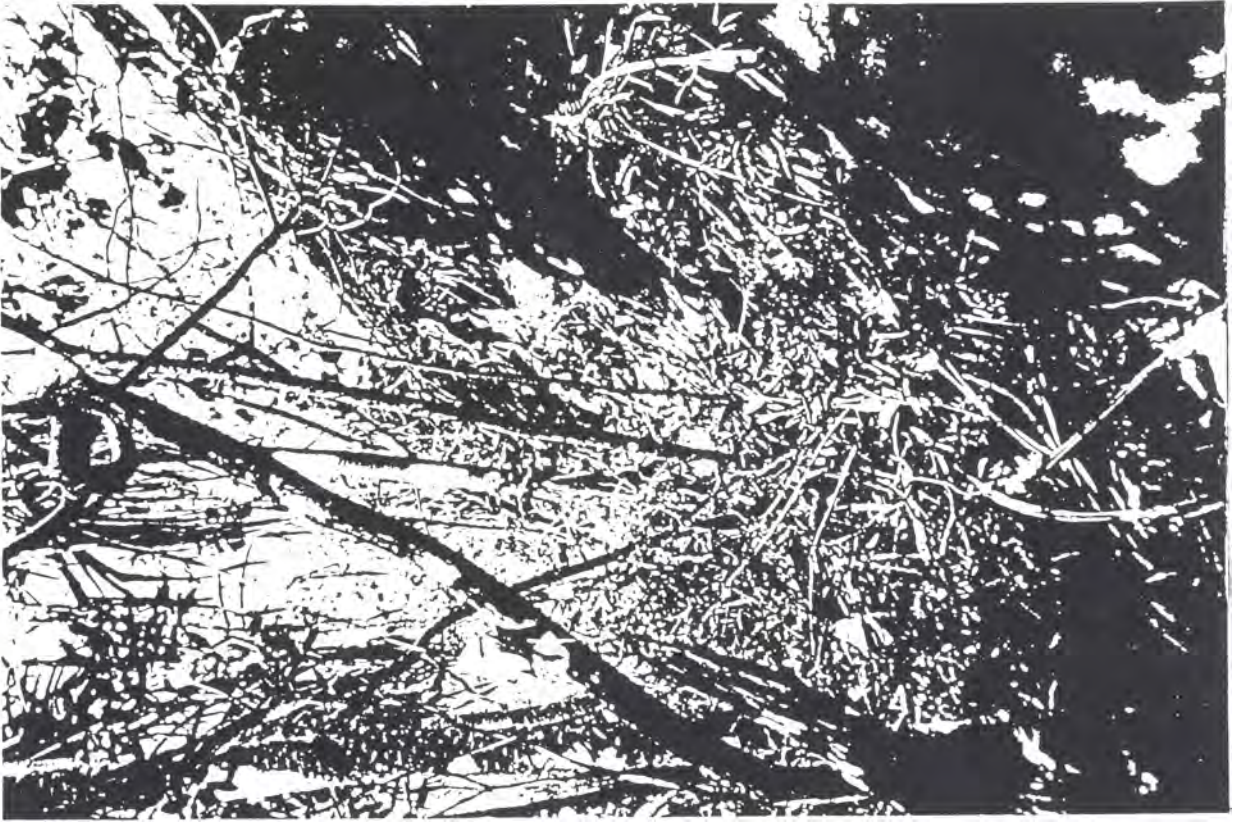


Plate 14: Contact of cliff face and scree slope (Site 1).

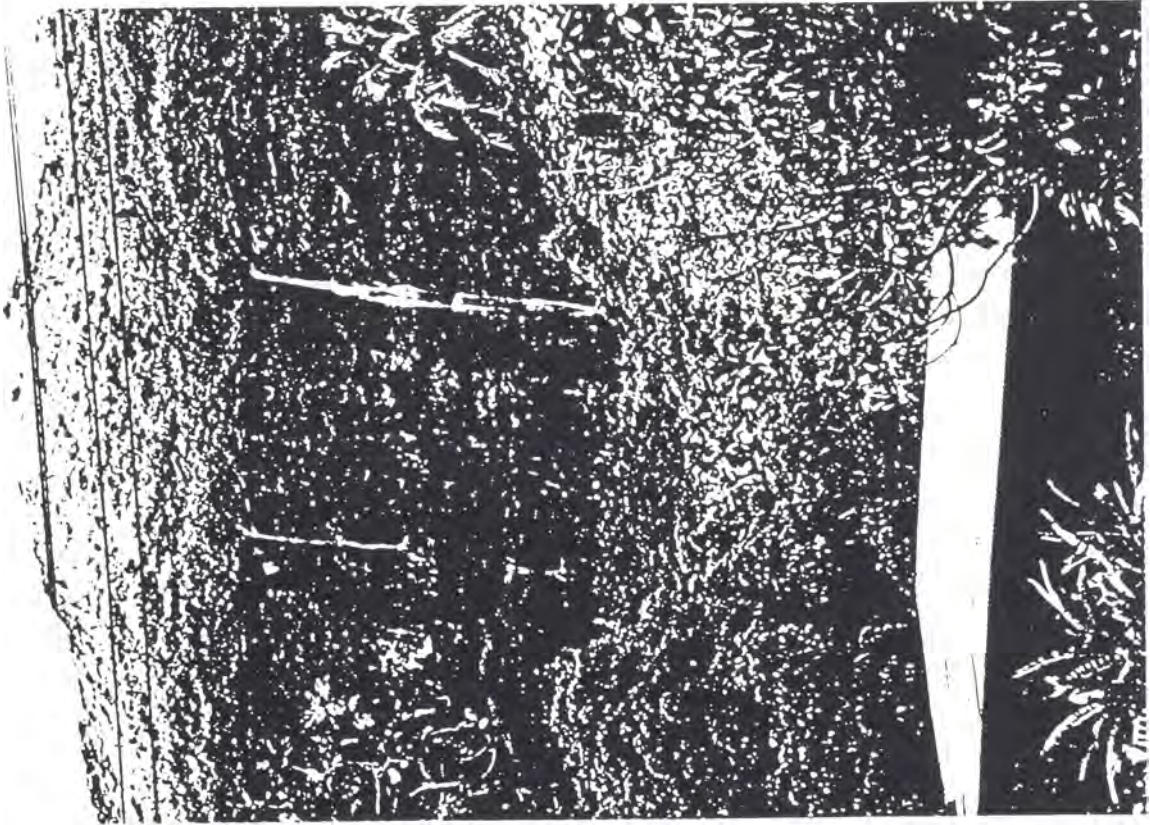


Plate 13: Same cliff in Plate 12 during heavy rain.



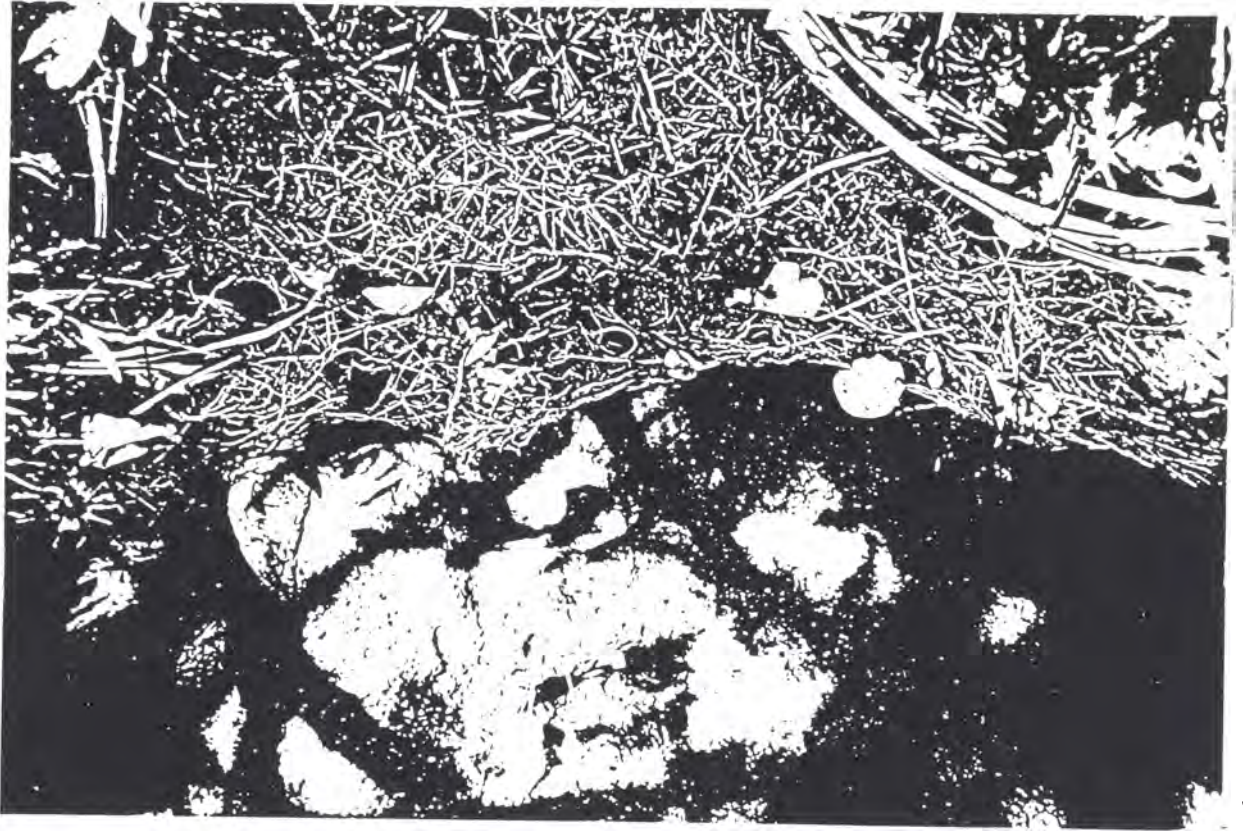


Plate 16: Root exposure at Site 1.

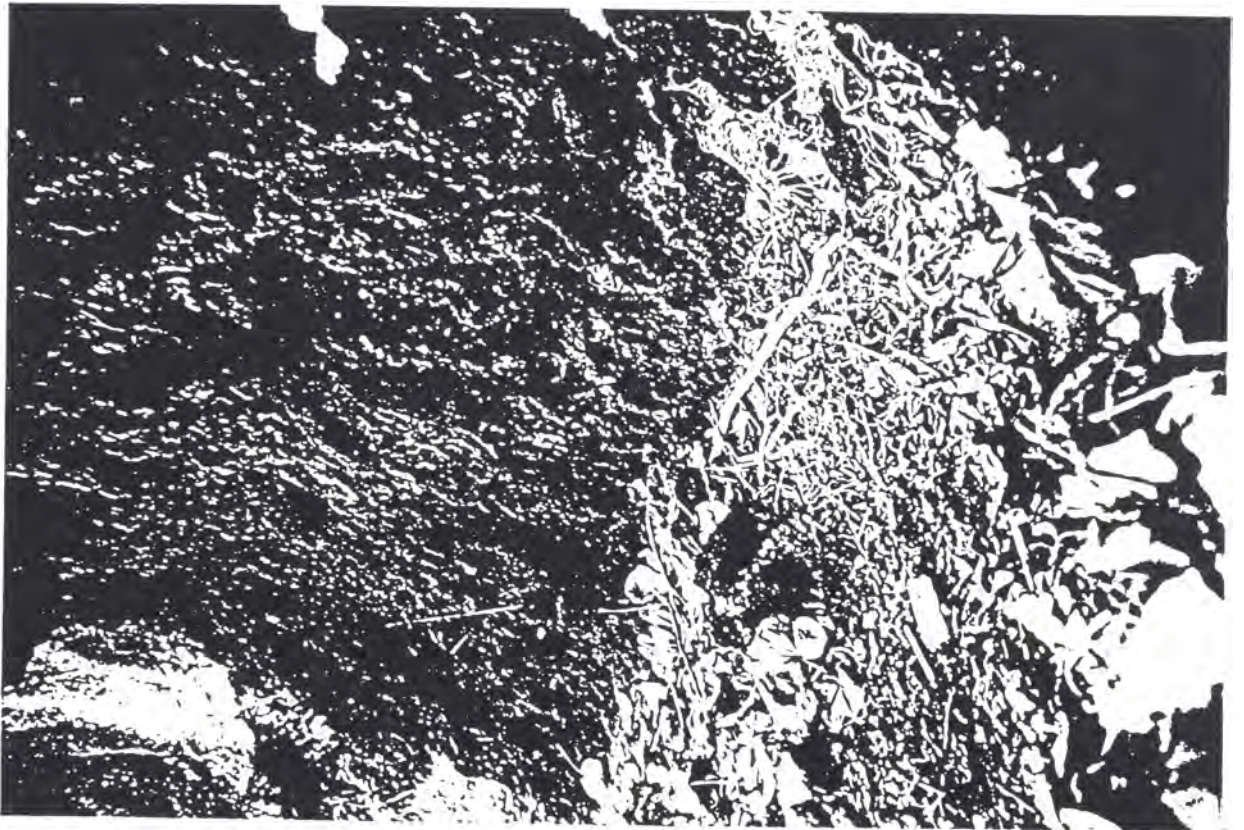


Plate 15: Eroded pyroclastic layer and root exposure at Site 2.

**Evidence for Nocturnal Migration Amongst the Five Symbionts of**  
*Pocillopora verrucosa*

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University of California, Berkeley, IB158 Fall 1992







## ABSTRACT

Twenty eight heads of *Pocillopora verrucosa* were defaunated and placed in the back reef area of Moorea., French Polynesia. The corals were separated into three different treatments, Day, Night, and Constant Exposure. Strong evidence for night recolonization by the five most common recolonizers was obtained by looking at replacement community sizes with in the treatments. The noticeable exception being postlarvae and juvenile *Alpheus lottini*. These shrimp appear to be settling out of the plankton layer during the day and night. A significant drop in overall population size and species richness was also observed. Finally, a new method of defaunating *Pocillopora* corals was developed that allows coral heads of any size to be completely defaunated without breaking them apart.

## Introduction

The decapod symbionts of *Pocillopora* corals were first described by J. Crane in 1937. Since then, numerous studies have evaluated the size, composition, structure, and nature of these coral communities (see Abele, 1984; Austin, et al 1980; Gotelli and Abele, 1983; Odinietz and Collart 1985). In 1984 Abele looked at reassembly of symbiont communities on defaunated coral heads of *P. damsicornis* and suggested that recolonization was taking place at night. To test the hypothesis that the decapod symbionts migrate at night an experiment was designed that would limit the times of potential recolonization of defaunated heads. If the hypothesis is true then population sizes of the recolonizing decapods of *P. verrucosa* that are only available for recolonization at night should be significantly greater than population sizes of *P. verrucosa* that are only available for recolonization during the day. Furthermore, one would expect to find no significant difference between population sizes of *P. verrucosa* with night exposure and *P. verrucosa* with constant exposure.

## Materials and Methods

The twenty seven *P. verrucosa* used in this experiment were removed from three different sites in the back reef area between Cooks and Opunohu bays (Map 1). The corals were covered with a plastic bag and then detached from the substrate using a hammer and chisel. The coral heads were brought to the surface and placed in a large bucket and were not removed from the bags until they were to be defaunated. Initially the coral heads were defaunated in the laboratory at the Richard Gump South Pacific Biological Field Station in aquariums which had access to running

sea water. Later, defaunation was done in the field due to the high mortality rate of the corals brought back to the laboratory. This high mortality rate was probably due to the use of plastic bags in transporting the corals from the reef to the lab.

The heads were defaunated by spraying them with a household insecticide, BAYGON (1% Propoxur, .5% Dichlorvos, and .04% Cyfluthin from Bayer Co., France) while they were still submerged in sea water. In the laboratory this was done in an aquarium, in the field this was done in a bucket. Corals remained in the insecticide saturated water for a minimum of five minutes after which the dead decapods were shaken and rinsed off. When defaunation was done in the lab, the original decapod populations were removed from the aquarium with a siphon that flowed to a sieve (.77 mm mesh). The decapods were then picked out of the sieve and preserved in 70% ethanol.

In order to promote recolonization defaunated coral heads were placed in the back reef amongst stretches of damselfish territories where *Pocillopora verrucosa* densities were high and where it was the predominate coral species. All corals except the Distance Control were set within one foot of two other sizable colonies (diameter > 20 cm) of *P. verrucosa*. The three different treatments were: 1) Day Exposure, 2) Night Exposure, and 3) Constant Exposure. For the Day Exposure and the Night Exposure treatments mesh bags (hole size approx. 1 mm x 1 mm) were used to limit the time of possible recolonization. The Day Exposure treatment consisted of covering the coral heads with mesh bags from approximately 6:00 pm to 5:15 am, a half an hour before dusk and a half an hour after dawn, in order to prevent colonization during the night. The covering of the Night Exposure treatment was the opposite of that for the Day Exposure. Night exposure corals were covered from 5:15 am to 6:00 pm in order to prevent day time colonization. The constant exposure treatment were exposed 24 hours a day. In order to simulate the effect of the bagging and unbagging procedure, the constant exposure heads were lifted off the substrate and turned around once or twice before being set back down. During the bagging and unbagging the mesh bags were inspected for holes and were replaced if any existed.

One coral head was continuously bagged (Bag Control) in order to test the effectiveness of the bags in keeping organisms from colonizing. Only two decapods, one *Trapezia* spp. post larvae and one *A. lottini* post larvae, were found on this head after nine days in the field this recolonization most likely occurred due to a large hole

discovered during evening bag inspection, the bag was subsequently replaced. Despite this hole and the two crustaceans on the coral head the Bag Control demonstrated that overall the bags were effective in preventing recolonization since its total number of individuals was less than any treatment's population mean or any individual head's population total. With the exception of the bag control, all coral heads were visually examined twice a day, during the bagging and unbagging procedure, in order to gauge recolonization. It is important to note that visual inspection can only give partial positive evidence of recolonization because it is only effective with the adult *Trapezia* spp. crabs. Each coral head was exposed in the field for a period of nine days. The entire experiment was carried out over a 17 day period in November 1992. After their nine day period of exposure the corals were brought back into the lab. In the lab, the corals were defaunated and decapods were collected with the previously described method. The collected decapods were first soaked in 10% formalin before being preserved in 70% ethanol.

The decapods removed after the recolonization experiment were sorted and catalogued. The *Trapezia* spp. crabs were divided into three categories, *Trapezia* Postlarvae, (Carapace Width {CpW} < 3 mm), *Trapezia* Juveniles (3 mm < CpW < 8 mm), and *Trapezia* Adults (CpW > 8 mm), based on carapace width (after Gotelli and Abele, 1983). For all statistical analysis, species populations of the genus *Trapezia* (*T. serenei*, *T. reticulata*, and *T. tigrina*, identified from Odinetz's 1983 descriptions) were considered to be one type of recolonizer and their populations were combined in each size category and for the total *Trapezia* population (*Trapezia* Total). *Alpheus lottini* was also subdivided into two categories based on rostrum and carapace length. Those with a combined rostrum and carapace length less than 3.50 mm were considered to be *A. lottini* Juveniles & Postlarvae, those with a combined rostrum and carapace length larger than 3.5 mm were considered to be *A. lottini* Adults. All other decapods were simply counted and their populations tabulated for each coral head. For summary statistics the data from one head (Head HHH) was randomly selected from the night treatments and ignored due to the uneven treatment sizes. These specimen along with most of the ones from initial defaunation are in the author's possession.

The insecticide itself seemed to have no adverse effect on the corals since there was no mortality of those coral heads defaunated in the field. Furthermore, the insecticide did not seem to leave any



long-lasting residue on the corals that might prevent or deter recolonization since evidence of recolonization by *Trapezia* crabs was observed within three days after treatment with the insecticide. The procedure seems to be 100% effective in killing or removing the decapod symbionts since trial runs in the lab where defaunated coral were broken apart revealed no living decapods on the coral heads.

This new method of defaunation is in some ways superior to other methods used by researchers which required breaking up the larger coral heads in order to remove all the symbionts. The necessity of breaking up of the larger coral heads limits the size of heads usable in recolonization experiments. This new method allows the use of any size heads in such experiments. However, there are three major draw backs to this new method, first off the use of insecticides has a detrimental effect on the environment. This effect appeared to be insignificant in this experiment because of its small scale, but on a larger scale or with more replications the effect of the insecticide on the reef via the outflow from the aquariums or the bucket in the field could be cause for concern. Therefore, care should be exercised in deciding where and when it is appropriate to use this method. Secondly, the insecticide itself tended to cause the decapods to selfdestruct to some degree, the loss of a cheliped or leg for a *Trapezia* crab was more common than not. Finally, although the insecticide method is rather selective in ensuring the demise of any decapod on the heads and yet having no noticeable effect on fish, there is no guarantee that this decapods can be easily removed. The larger *Trapezia* Spp. tended to get stuck amongst the branches of the corals and were only dislodged after mutilating the crab. This was not much of a problem in the recolonized heads because of lower number of individuals and the overall smaller size of these individuals.

## Results

For statistical testing the five most common recolonizers following defaunation were used. These recolonizers included three species of *Trapezia* crabs (*T. serenei*, *T. reticulata*, and *T. tigrina*) which were considered to be one type of recolonizer, *Alpheus lottini*, a *Phymodius* crab (Crab B), a crab of an unknown genus (Crab A), and a shrimp of an unknown genus (Shrimp A). The *Trapezia* group was further broken down into three main categories

( Postlarvae, Juvenile, and Adult), while the *A. lottini* was broken down into two (Juvenile & Postlarvae, and Adult).

To test the statistical significance of the differences in recolonization patterns amongst treatments Kruskal-Wallis ANOVA and Chi-Squared Random Distribution Tests were employed (Tables 1 and 2). Kruskal-Wallis ANOVA only detected a statistical significance (i.e.  $p < .05$ ) in three cases, *Trapezia* Adult (test = 6.052,  $p < 0.05$ ), *Trapezia* Total (test = 7.161,  $p < 0.03$ ), and Shrimp A (test = 6.79,  $p < 0.04$ ). Looking at the population sums for each treatment (Chart 1) it appears that in all cases but the *A. lottini* post larvae/juvenile, the rather high p values obtained from Kruskal-Wallis ANOVA are probably due to the relatively small sample size. The small sample size makes it difficult to detect significance with of non parametric tests such as Kruskal-Wallis. In light of this, the population were summed by treatment and evaluated with a Chi-Squared Random Distribution Test. Expected values were taken from the constant exposure sums. Significant differences between populations sums for the three treatments were found in *Trapezia* Adult, *Trapezia* Total, *A. lottini* Juvenile & Postlarvae, *A. lottini* Adult, *A. lottini* Total, Shrimp A, and Crab A (see Table A below and Table 2).

	<i>Trapezia</i> Postlarvae	<i>Trapezia</i> Juvenile	<i>Trapezia</i> Adult	<i>Trapezia</i> Total	<i>A. lottini</i> Juvenile & Postlarvae
$\chi^2$	2.90909091	1.625	7	8.923077	30.03333
p values	0.23350648	0.44374731	0.030197	0.011545	3.01E-07

	<i>A. lottini</i> Adult	<i>A. lottini</i> Total	Shrimp A	Crab A	Crab B
$\chi^2$	6.166667	16.11111	24.2963	18.77778	2
p values	0.045806	0.000317	5.3E-06	8.36E-05	0.36787944

Table A:  $\chi^2$  distribution test sums and p values for Constant, Day, and Night Exposure population sums. Findings of significant differences highlighted in bold face (degrees of freedom = 2).

Further Chi-Squared testing between Constant and Night Exposure, and Constant and Day Exposure (Table 2) reveal that the significant distributional differences in all cases but *A. lottini*



Juvenile & Postlarvae, Shrimp A and Crab A, are between the Day Exposure populations and the Night and Constant Exposure populations. In the case of Crab A the significant difference lies between the Night Exposure heads and the Constant and Day Exposures. The difference between Shrimp A distributions appears to be an anomaly that can not be readily explained.

The overall structure of the reassembled decapod communities differed greatly from the community structures of *P. verrucosa* found in the back reef area of Moorea as described by Kropp and Birkehard (1981). For the same sample size, the Constant Exposure plus the distance coral heads had overall 30.8% fewer individuals (153 vs. 221) and less than one third of the species richness (12 spp vs. 40 spp) when compared to Kropp's initial defaunation data.

## Discussion

Despite the small sample size, significant distributional differences ( $p < .050$ ) between the treatments were detectable in three cases, *Trapezia* Adult, *Trapezia* Total, and Shrimp A, using Kruskal-Wallis ANOVA. This data indicates that overall recolonization by the *Trapezia* Adults and *Trapezia* Total groups are nocturnal. These findings were reconfirmed by a Chi-Squared Random Distributional Test. Using this test the list of nocturnal migrators was expanded to include: *Trapezia* Adult, *Trapezia* Total, *A. lottini* Adult.

In contrast to these night migrators, overall population sums for *A. lottini* Juvenile & Postlarvae (Constant = 36, Day = 60, and Night Exposure = 38) indicated that this group is migrating during the day and night. The large population of *Alpheus lottini* post larvae on Head I I which served as an indicator of distant migration since it was more than 5 m from any species pool indicates that *A. lottini* is settling out of the plankton layer. The statistical differences found between the Night and Constant Exposures and the Day Exposures is probably due to competitive exclusion between the nocturnally migrating *A. lottini* Adults and the settling *A. lottini* Juvenile & Postlarvae.

Evidence of intraspecific competition can be seen by the negative correlation of -0.5099824 between *A. lottini* Adults and *A. lottini* Juveniles & Postlarvae and, more convincingly by the fact that the population mean of *A. lottini* Juvenile & Postlarvae are 6.2 times greater in cases where *A. lottini* Adults are absent than when

they are present. Previous studies of *Pocillopora* Spp. show that *Alpheus lottini* is usually found in single adult pairs on 70-80% of *Pocillopora* spp. coral heads (Glynn, 1976; Abele, 1984; and Gotelli et al., 1985). The highest incidence previously observed of non adult *A. lottini* was 13% of all *A. lottini* encountered (Gotelli et al. 1985); yet juveniles and post larvae made up more than 90% of the total observed recolonizing *A. lottini* in my experiment. It is interesting to note that in Abele's 1984 recolonization study he saw no evidence of recolonization by any *A. lottini*.

Looking at population sums for 8 replicates of each treatment (Figure 1) one sees that in all cases but the *A. lottini* Juvenile and Postlarvae and *A. lottini* Total the sum of recolonizers for each category was at least 2.43 times greater in the night exposure group versus the day exposure group. The control group also had higher recolonization sums than the day exposure group, except in the aforementioned cases and Crab A where its recolonization was equal to the day group. Crab A appears to be migrating mostly at night in light of the differences in population sums and the  $\chi^2$  values obtained from comparing the Night Exposure and the Day Exposure ( $\chi^2 = 18.7777$ ,  $p < 0.01$ ). More evidence of night migration by Crab B can be found in the differences of population sums of each of the treatments. The verification of night migration, however, was not detectable with any of the statistical tests employed when looking at all three treatments.

The discrepancy in recruitment sums between Night and Constant Exposure, however, cannot be readily explained. With the exception of Shrimp A, the Night Exposure recruitment totals were consistently higher than the Constant Exposure totals. The best hypothesis I can come up with to explain this discrepancy is that crabs move from coral head to coral head through the visual cue of a coral head other than the one they presently occupy. If this is true, covered coral heads would not provide such a cue and the decapods would make no attempts to move on to the coral head. Preston (1973) has suggested that fish predation of these symbiont crabs is highest during the day. Therefore, crabs attempting to recolonize the controls during the day have a greater chance of mortality than those moving at night. Furthermore, it is assumed that the overall pool of potential recolonizers is limited in each of the coral head's micro environment to that of adjacent corals.

If the following three conditions are true-- visual cues for migration, higher rates of fish predation during the day, and a

limited colonist pool- then the discrepancy between the two treatments can be explained as follows. Because decapods recolonizing on night exposure corals will not attempt to recolonize during the day, this colonist pool will have a higher overall success rate since they are only moving at night when the risk of predation is lowest. Thus, the higher recolonization success rate is reflected in the higher population sums for the Night Exposure versus the Constant Exposure treatment. This explanation, along with the evidence that some migration occurs during the day, stipulates that most of these symbionts are attempting to recolonize, not necessarily in even numbers, during both the day and night; yet the success rate of those attempting to migrate at night must be significantly higher than those attempting to migrate during the day.

## Conclusion

If one looks at the replacement community structure of defaunated *Pocillopora verrucosa* two things stand out. First, overall population size and species richness are drastically reduced. Second, recolonization of is dominated by five types of recolonizers, *Trapezia* Spp. crabs, *Alpheus lottini*, a species of *Phymodius* crabs (Crab B), an unknown Crab A, and an unknown Shrimp A. Although *Trapezia* Adults, *Trapezia* Total, *A. lottini* Adults, Shrimp A, Crab A, and Crab B all appear to be doing the majority of their successful recolonization at night.; clear statistical differences exist only for the *Trapezia* Adults, *Trapezia* Totals and the *A. lottini* Adults. The data collected from this experiment also illustrates that successful migration by juvenile and postlarva *A. lottini* occurs during both night and day periods and that there is strong intraspecific competition keeping these individuals from settling out of the plankton layer on to corals occupied by adult *A. lottini*.

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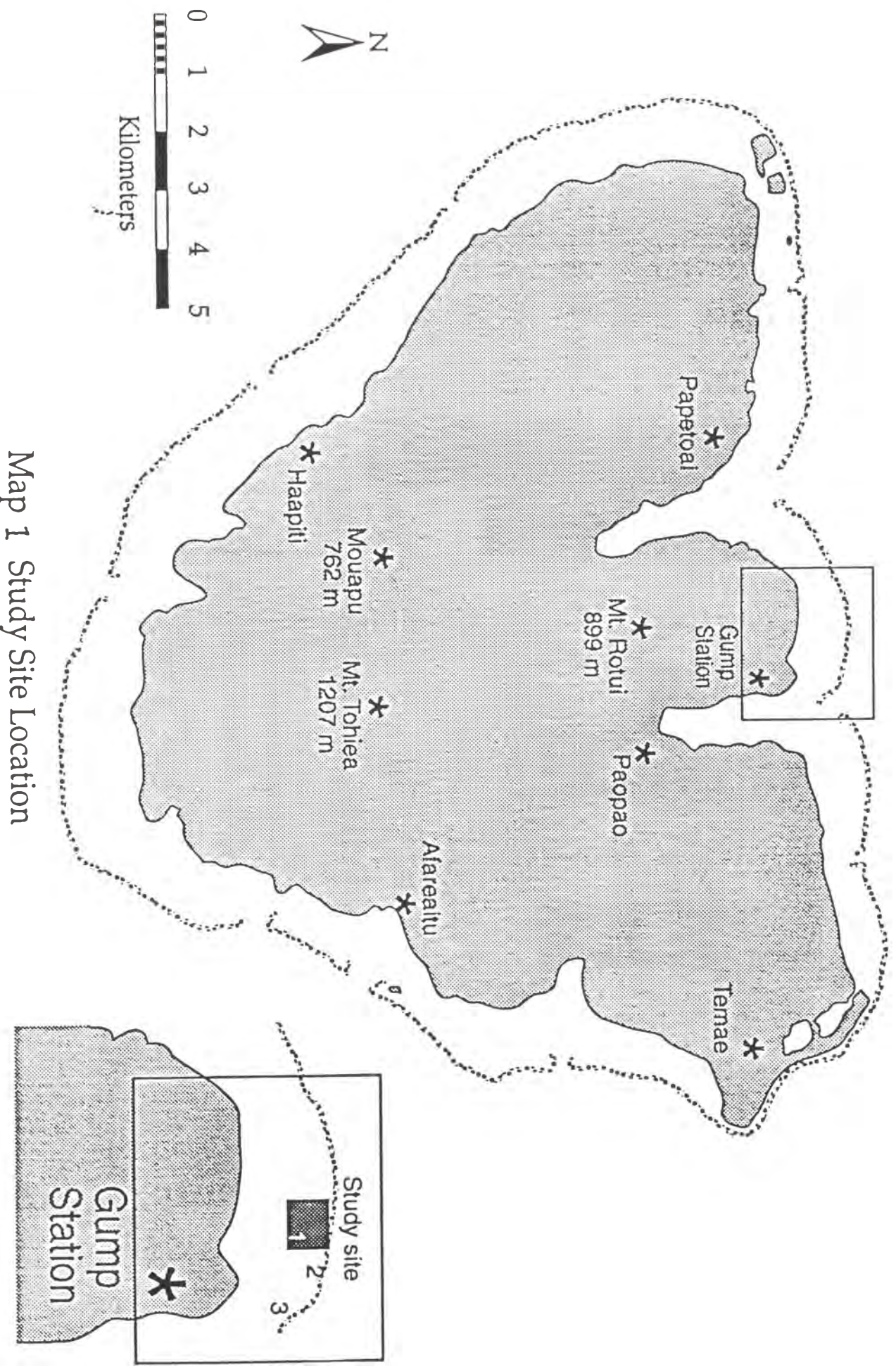
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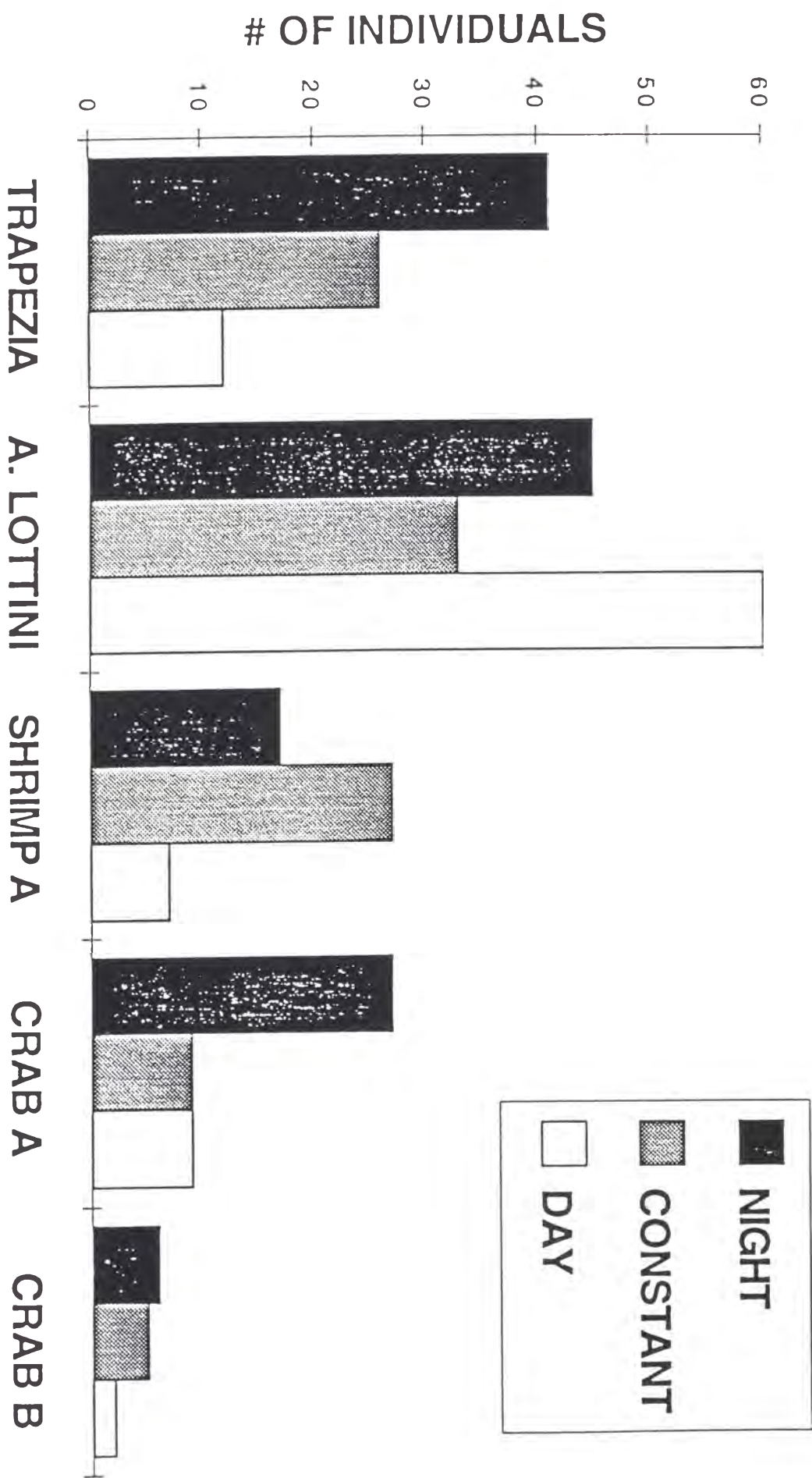
# Moorea, French Polynesia



Map 1 Study Site Location



SUM OF RECOLONIZERS SEPARATED BY TREATMENT



EXPOSURE SUMS	<i>Trapa</i> Postlarvae	<i>Trapa</i> Juvenile	<i>Trapa</i> Adult	<i>Trapa</i> Total	<i>A. lottini</i> Juvenile & Postlarvae	<i>A. lottini</i> Adult	<i>A. lottini</i> Total	Shrimp A	Crab A	Crab B
Constant (C)	11	8	7	26	30	6	36	27	9	5
Day (D)	7	5	0	12	60	0	60	7	9	2
Night (N)	15	10	7	32	31	7	38	11	22	6
Total for all treatments	33	23	14	70	121	13	134	45	40	13
Expected Sums	11	8	7	26	30	6	36	27	9	5

$\chi^2$ for C,D,&N	2.90909091	1.625	7	8.92307692	30.03333333	6.16666667	16.11111111	24.2962963	18.77777778	2
p values	0.23350648	0.44374731	0.03019738	0.01154459	3.0085E-07	0.04580631	0.00031733	5.2982E-06	8.3648E-05	0.36787944
$\chi^2$ for C & N	1.45454545	0.5	0	1.38461538	0.03333333	0.16666667	0.11111111	9.48148148	16.77777776	0.2
p values	0.22780011	0.47950012	1	0.23931667	0.85513214	0.6830914	0.73888268	0.00207556	1.4687E-05	0.65472085
$\chi^2$ for C & D	1.45454545	1.125	7	7.53846154	30	6	16	14.8148148	0	1.8
p values	0.22780011	0.28884457	0.00815097	0.00603956	4.3205E-08	0.01430588	6.3342E-05	0.0001186	1	0.17971259
$\chi^2$ for D & N	2.90909091	1.625	7	8.92307692	30.03333333	6.16666667	16.11111111	24.2962963	18.77777778	2
p values	0.08808153	0.20239611	0.00815097	0.0028159	4.2468E-08	0.01301797	5.9733E-05	8.2598E-07	1.4687E-05	0.15729926

Table 2:  $\chi^2$  and p values from Chi Squared Random Distribution Test of the population sums of each category of recolonizers from Constant (C), Day (D), and Night Exposures(N). Expected sums derived from Constant Exposure population sums. Significant differences, where  $p < 0.05$ , are highlighted in bold.



All Recolonizers

	<i>Trapezia</i>	<i>A. lottini</i>	Shrimp A	Crab A	Crab B
KRUSKAL WALLIS	7.161	1.585	6.79	3.71	2.679
PROBABILITY	0.028	0.453	0.034	0.156	0.262

*Trapezia*

	Postlarvae	Juvenile	Adult	Total
KRUSKAL WALLIS	1.647	3.629	6.052	7.161
PROBABILITY	0.439	0.163	0.049	0.028

*Alpheus lottini*

	Juvenile & Postlarvae	Adult	Total
KRUSKAL WALLIS	2.424	5.652	1.585
PROBABILITY	0.298	0.059	0.453

Table 1: Results from Kruska-Wallis ANOVA for all categories. Significant differences of  $p < 0.05$  are highlighted in bold.

Data Table

HEAD	Exposure	<i>Trapezia</i> Postlarvae	<i>Trapezia</i> Juvenile	<i>Trapezia</i> Adult	<i>Trapezia</i> Total	<i>A. latini</i> Juvenile & Postlarvae	<i>A. latini</i> Adult	<i>A. latini</i> Total	Shrimp A	Crab A	Crab B
LL	Constant	3	3	0	6	1	4	5	6	2	0
K	Constant	2	2	2	6	4	0	4	6	1	1
N	Constant	0	0	1	1	7	0	7	4	1	2
M	Constant	2	0	0	2	10	0	10	1	4	1
UKC	Constant	2	0	0	2	0	1	1	4	0	0
RR	Constant	2	1	2	5	0	0	2	2	0	0
JJJ	Constant	0	0	2	2	4	0	4	3	1	1
BBB	Constant	0	2	0	2	2	1	0	1	0	0
SS	Day	0	0	0	0	18	0	18	4	0	1
P	Day	1	0	0	1	2	0	2	0	2	1
O	Day	2	0	0	2	11	0	11	0	1	0
D	Day	2	0	0	2	3	0	3	1	3	0
EEE	Day	0	0	0	0	4	0	4	2	3	0
GGG	Day	0	3	0	3	3	0	3	0	0	0
QQ	Day	0	2	0	2	5	0	5	0	0	0
JJ	Day	2	0	0	2	14	0	14	0	0	0
FF	Night	0	0	1	1	9	0	9	0	0	1
KK	Night	5	2	1	8	8	0	8	3	2	0
H	Night	1	1	2	4	8	0	8	0	6	1
PP	Night	1	1	0	2	0	2	2	1	0	1
L	Night	0	1	2	3	0	2	2	2	2	1
HHH	Night	3	6	0	9	7	0	7	6	5	0
UKN	Night	5	1	0	6	1	1	2	1	7	1
R	Night	2	3	0	5	1	1	2	0	3	1
CCC	Night	1	1	1	3	4	1	5	4	2	0
II	Distant	1	2	0	3	21	0	21	11	0	0
FFF	Bag Control	1	0	0	1	1	0	1	0	0	0

Table 3: Data sheet of all corals used in experiment.



Ecology and Thermal Correlations of the Nocturnal Activity Cycle  
of a Tropical Gecko, *Gehyra oceanica*

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## Abstract

*Gehyra oceanica*, a nocturnal, arboreal gekkonid lizard, continues to be active throughout the night in the equitable, tropical habitat. In temperate zones, nocturnal ectotherms have a much more distinct activity pattern which decreases as the temperatures drop below the minimum foraging temperature. The ambient temperature does not drop below this minimum, and hence, activity can continue throughout the night. Both warmer ambient and substrate temperatures promote a greater number of geckos to be active in the *G. oceanica* of a study site on Moorea, French Polynesia. This correlation supports the hypothesis that minimum foraging temperatures are a limiting factor in the movement of nocturnal ectotherms into higher latitudes (Bustard, 1967). A high amount of predation or intra-specific aggression is indicated by the high incidence of tail regeneration within the population. The sex ratio is male-biased, with three times as many males as females. This may be due to a variation in the catchability of the different sexes. Males are larger in snout-vent length than females within the studied population. This is different than data of other populations of *G. oceanica* of various Pacific islands. The reason for this difference is not evident in the data collected.

## Introduction

Ectotherms are dependent upon the environment for promotion of body heat in the form of solar radiation and conduction from the substrate. Lab and field studies have found that reptiles have preferred body temperatures presumably for optimum metabolic functions (Bogert, 1949; Bustard, 1967). Both diurnal and nocturnal lizards behaviorally thermoregulate within small, species-specific temperature ranges, generally between 30-40°C (Bogert, 1949, 1959; Huey et al, 1989). Diurnal reptiles thermoregulate by basking, burrowing, and seeking shade (Bogert, 1949, 1959; Cowles et al, 1944; Heath, 1965). Nocturnal ectotherms are dependent upon the substrate they are surrounded by during the day to absorb enough heat to obtain their specific thermal optimum (Bogert, 1949; Bustard, 1967; Huey, 1989).

It is generally thought that the activity cycles of nocturnal reptiles is strongly correlated with the temperature range of the habitat in which the organism is active. Nocturnality, hypothesized to be a strategy for predator avoidance (see Bustard, 1967), places their active phase in a lower temperature regime than their thermal optimum. Temperate zone temperatures vary in daily and yearly cycles much more substantially than those of the more equitable tropical zone (Bogert, 1949; Bustard, 1967). Since the capacity to cope with low temperatures seems to be the limiting factor in the distribution of nocturnal ectotherms to higher latitudes (Bustard, 1967), behavioral and physiological adaptations to nocturnal activity have been studied mainly in temperate zone reptiles (Cowles, et al, 1944). Few studies on the activity patterns of the reptiles of tropical habitats have been done to substantiate the assumption that the active phase of nocturnal ectotherms are not affected by the temperature regime (but see Park, 1938; Ruibal, 1961).

Although nocturnal lizards of temperate habitats have been seen foraging at temperatures as low as 7°C (Cowles et al, 1944), the general activity pattern is an initial burst of activity early in the evening, tapering off and almost stopping completely after 12:00 a.m., or as the temperature drops below a tolerable level (Bustard, 1967; Park, 1938). The amount of activity of *Gehyra variegata*, an arid, temperate zone gecko, was affected by the temperatures of the night and early morning hours (Bustard, 1967; Henle, 1990). However, a quiescent phase, a period of no activity, was

characteristic even on warm nights (Bustard, 1967).

In this paper, the thermal ecology of a tropical gecko, *Gehyra oceanica* will be examined. The activity pattern of *Gehyra oceanica* will be compared to that of *G. variegata*, a related species in the temperate zone, to examine the assumptions involved in the effects of temperature on tropical ectotherms. Specifically, the relationship between ambient temperatures and the number of active individuals in the study population, as well as measuring the relationship between cloacal temperatures and ambient and substrate temperatures will be examined. In addition, body size, tail condition, and sex ratios of the population will be described.



## Methods and Materials

The study population was in a coconut grove at sea level. This particular grove has discrete boundaries of a fence on the west side, a paved road on the north side, dense understory on the south side, and a ditch and banana trees on the east side. The understory is mown grass and the relatively low density of trees reduces the movement of geckos between trees across overlapping fronds. It is 3.5 kilometers to the west of the Richard Gump Biological Research Station on Moorea, French Polynesia. The accessibility of the grove and the discrete nature of the habitat enhanced the feasibility of catching many individuals and decreased the likelihood of immigration and emigration.

Data collection was conducted from October 23, 1992 through November 24, 1992, between 6:00p.m. to 5:00a.m.; the majority between 8:00 and 11:00p.m. The rainy season begins in October, and several heavy storms occurred during the collection period. I observed geckos active in all weather conditions, except in high winds. No data was collected in extremely windy or rainy conditions. Geckos were breeding throughout the duration of the study.

Geckos were spotted with a headlamp and caught by hand if on the lowest 2 meters of the trees. A tool of two 3-meter long sticks, connected at one end by a 15-centimeter long piece of rubber tubing, was used to force geckos down the tree to within catching distance. The sticks were held at the free ends with the tubing placed against the trunk of the tree above the retreating lizard. The sticks were then lowered, while keeping the tubing against the trunk. This caused the gecko to turn and run down the trunk. The gecko was then caught by hand.

Snout-vent length was measured with an aluminum ruler from the anterior end of the lizard to the vent opening, down the midline of the ventral surface. Tail lengths were not measured due to the high number of partially to completely damaged and regenerated tails (86%), which would not be an accurate representation of size. Amount of tail loss and regeneration were visually assessed. The presence and number of eggs in female specimens was also visually recorded. Cloacal temperature was taken within 15 seconds of capture. The specimens were held by the head and a back leg to reduce conduction of heat. Temperatures were recorded to the nearest tenth of a

degree celcius. Males were identified both by swollen tail base and presence of enlarged femoral pores. Individuals were considered juvenile if femoral pores and hemipene were not developed. The number and location of mites was noted by visual counts.

Individuals were marked with liquid paper on the dorsal surface between the front legs, on the tail base and on the tail tip. The last few caught were also marked with permanent ink on the base of the tail. To evaluate the fidelity of lizards to individual trees, each tree was tagged with a uniquely numbered disk. A marked lizard which was sighted after one capture was noted for being on the same tree or a different tree.

All-night surveys were conducted four times. The grove was scanned at approximately two-hour intervals between 6:30 p.m. and 4:30 a.m. The number of active lizards was recorded during each scan. A gecko is considered active if it is in view of the observer (see discussion). The temperatures of the air and a representative tree were taken at the start of each scan. Tree temperatures were taken by sliding the tip of the thermometer underneath a piece of loose bark 1.5-meters above the ground. Air temperatures were also taken at 1.5-meters above the ground. Cloud cover was also noted (cloudy, partly cloudy, clear).

Correlations between the number of active individuals to ambient and substrate temperatures were measured using the Spearman Correlation Coefficient,  $r_s$  (Siegel, 1956). The correlation coefficient ranges from -1 to +1; a value of 1 suggesting the greatest correlation, 0 suggesting the least. Un-paired, two-tailed t-tests were used to compare male and female characteristics including snout-vent length, tail condition, number of mites, and cloacal temperatures. The Contingency Coefficient,  $C$ , was used to compare the number of individuals active during cloudy, partly cloudy and clear survey periods (Siegel, 1956).

## Results

A dramatic shift in the number of active geckos right after sunset and right before sunrise was observed. Before sunset, the 6:30 census, geckos would be seen poking their heads out from under the rat guards and fronds on the trees. Immediately after sunset, the geckos would venture from cover. At sunrise, the 4:30 census, the opposite would occur- the geckos would all retreat to cover. On night three, there was a negative correlation between the time of night censused and the number of active geckos. That is, as the night progressed, and the temperature dropped, the number of active geckos decreased (Figure 2C and Figures 8A,B). The activity pattern on night two and all nights combined, however, are the opposite of that on the third night; the number of active geckos increases as the night progressed (Figure 2B, 3). This pattern of increased activity also suggests a dependence upon temperature, since the air temperature increased throughout the second night (Figure 8A). There is no correlation between the time period and the number of active individuals on nights one or four, however (Figures 2A, D). The cloacal temperatures are positively correlated with the tree temperatures, but not with the air temperatures (Figure 5A and 4A, respectively). The activity patterns suggest that both the air and tree temperatures influence the activity of the geckos in the grove, however (Figures 4B and 5B). There was no statistical association between the cloud cover and the number of lizards active in the grove ( $C=.226$ ,  $X^2 > 1.29$ ,  $DF = 2$ ,  $p < .7$ ). The lack of influence of sky conditions on the activity of the geckos may be due to the limited parameters used. The sky was classified as cloudy, partly cloudy or clear, but other parameters such as wind, rain, and moon phase may need to be considered (see discussion).

The ratio of the population is male-biased at 21:14:4 (male:female:juvenile). Males are significantly larger than females ( $t\text{-value} = -5.1$ ,  $DF = 76$ ,  $p < .0001$ , range = 50-89mm, Table 1). There is a strong correlation between snout-vent length and the temperature of the individual (Figure 6) but there is not a significant difference between the temperatures of males and females in the population ( $t\text{-value} = .9$ ,  $DF = 43$ ,  $p < .367$ ). Smaller geckos tend to harbor a greater number of mites than larger geckos (Figure 7) but the  $t$ -test did not reveal a significant difference in the

number of mites on males verses females (Table 1). This greater number of mites on the smaller individuals may be skewed by the fact that fewer small geckos were sampled. There is no significant difference in the tail condition between the males and females of the population.

Of the 78 lizards captured and marked, 16 were positively identified a second time, and two a third time. 80 percent were seen on the tree where they were first captured. Two of the 16 were found on a tree adjacent to the tree where the gecko was originally caught. The average time between capture and re-capture was 5.9 days, with a range of 1 to 16 days.



## Discussion

The geckos in the study population began to forage immediately following sunset, just as the temperate zone nocturnal geckos, *G. variegata* do (Bustard, 1967; Henle, 1990). The activity pattern of *Gehyra oceanica* for the duration of the night is only similar to its temperate zone relative, *G. variegata*, when the temperatures decrease during the night. In the cooler nights of the temperate habitat, *G. variegata* usually peaks in activity within the first three hours following sunset, tapering off and eventually entering a quiescent phase in the late night and early morning hours (Bustard, 1967). *G. oceanica*, also has a pattern of decreasing activity throughout the night, when the temperatures decrease. A quiescent phase is not observed in *G. oceanica*, however; the grove population continued to be active throughout all four of the nights surveyed (Figure 2A-D). This could be due to the lack of ambient and substrate cooling in the tropical habitat. The greatest change in substrate temperature throughout any of the four nights was only 2.8 degrees, from 27.2 to 24.4°C. The range of cloacal temperatures among all nights was only 25.25 to 28.75°C. Neither a temperature as high as that reported in the studies on *G. variegata* (44°C), nor as low as that reported (7.5°C) was experienced by an oceanic gecko on the nights this study was conducted (Bustard, 1967; Henle, 1990). According to Bustard, the minimum foraging temperature for *G. variegata* is 18°C (1967). A body temperature this low was not recorded in the tropical zone geckos.

There was a trend of a greater number of active geckos during the warmer census periods in the coconut grove, even though a period of quiescence does not occur. The number of active geckos on the third night of the census decreased as the night progressed. The substrate temperature, to which activity tends to correlate ( $r_s=.5$ , Figure 5B), also decreased (Figure 8B). If the geckos are dependent upon the temperatures of the surroundings for activity, as temperate species are, the trend should be an increase in the number of active geckos as the temperature increases. Night two and all nights combined reveal exactly that. The ambient temperature increased on the second night, and so did the number of active geckos. This suggests a strong dependence of nocturnal ectotherms on the substrate and ambient temperatures for activity in the

tropical habitat.

Sky condition data did not correlate with the activity levels of the geckos. A significant number of geckos near the base of the palms on a night prior to the quantitative data collection when the moon was almost full and the sky clear was observed. The grove was well lit which may have encouraged the geckos to venture farther from the cover spots. The four nights of activity data collection had variable sky conditions and little or no moon shine. This may explain the lack of a trend in the data. Surveys which include the phase of the moon, spanning several lunar cycles may reveal the amount of influence, if any, the moon has on the activity of geckos.

The extremely male-biased sex ratio of the population (3:2) is most likely due to sampling error or unequal catchability of males and females. Such a large difference in the number of males and females has not been found in other lizard populations (see Ruby, 1984; Henle, 1990- both report 1:1 ratios). The males of the sampled population are longer from snout to vent than the females. Other sources differ from this trend. Zug, for example, reported equal snout-vent length between males and females in Fijian populations (1991). Adults were between 59 and 84 millimeters- females 64-84, males 59-82. Beckon found a wider range of lengths, between 27 and 102 millimeters (1992; see also Crombie, 1986 and King et al, 1989). The extremely high incidence of tail regeneration of 80 percent is much greater than the reported incidence of 68 percent in the Fijian populations (Zug, 1991). This may indicate a higher level of escapes from predation, or a higher amount of predation on the Moorean population. Or, it may indicate higher intra-specific aggression within this population (Busack et al, 1982; Zug, 1991). Indian Mynahs, an abundant scavenger and predator on Moorea, have been observed carrying away *Gehyra oceanica* in their bills (personal obs.; Stuart Siegel, personal comm.).

The marking technique and unequal catchability from initial capture to re-capture may account for the low number of re-citing of geckos. To have a more thorough mark-recapture study of fidelity to trees, a more effective marking technique is necessary. A gecko kept in captivity maintained liquid paper marks for nearly three weeks. In the field, a significant number of geckos the day after initial capture had very little of the mark left on their backs. The fragility of their skin

and the humid weather conditions in the field are most likely the reasons for premature loss of the marks. Permanent ink worked well but is difficult to see from a short distance away. It was found that they do move around the grove, but with such low numbers of sightings of marked individuals, the extent of movement cannot be estimated.

## Acknowledgments

The support and assistance of Carla D'Antonio, Larry Vaughan, Raj Denhoy, and Frank Murphy during the fieldwork is gratefully acknowledged. Preparation for field work was greatly enhanced by the input of Kellar Autumn and Dale DeNardo. This paper was read and improved by Carla D'Antonio, Kerin Lau, and Susan Yamanishi. Susan's generosity in access to her computer must also be gratefully acknowledged.



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Table 1. Physical characteristics of a population of *Gehyra oceanica* in a coconut grove on Moorea, French Polynesia. Juvenile values have been combined with male and female values due to small juvenile sample size; Snout-vent length measured to nearest .5mm; Cloacal temperature to the nearest .5 degrees celcius; \*Tail condition was visually measured: 1= total tail lost and regenerated, .5= half tail lost and regenerated, 0= no tail loss; \*\*Numbers of mites not calculated by location on body due to small number of mites found on any one part of body; t-tests were conducted between male and female mean values.

	<u>n</u>	<u><math>\bar{x}</math></u>	<u>SD</u>	<u>SE</u>	<u>Range</u>
Snout- vent Length: All	78	72.9	9.3	1.1	50-89
Male	45	76.9	6.7	1	58-89
Female	28	69.3	9.6	1.7	50-85
	t-value= -5.1 DF= 76 p<.0001				
Cloacal Temperature: All	45	28	1.2	.2	25.2-30.8
Male	24	27.8	1	.2	25.2-29.5
Female	21	28.1	1.3	.3	26.2-30.8
	t-value= .9 DF= 43 p: not significant				
Tail Condition*: All	36	.6	.4	.1	0-1
Male	24	.6	.3	.1	0-1
Female	12	.4	.3	.1	0-1
	t-value= -1.5 DF= 34 p: not significant				
Number of Mites**: All	43	6.1	1	43.7	0-30
Male	22	4.6	5.5	1.2	0-21
Female	21	7.6	7.4	1.6	0-30
	t-value= 1.5 DF= 41 p: not significant				

## Figure Legend

Figure 1. Location of the coconut grove study site, on Moorea, French Polynesia.

Figure 2. Number of active geckos during each census period, night by night; Census period1= 6:30 p.m., 3= 8:00, 5= 10:00, 7= 12:00, 9=2:00, and 11= 4:30. A= night 1:  $r_s = -.5$ ,  $p > .05$ ; B= night 2:  $r_s = 1$ ,  $p < .01$ ; C= night 3:  $r_s = -.8$ ,  $p < .025$ ; D= night 4:  $r_s = .1$ ,  $p > .05$ . Numbers of active geckos in night 2 increase as the night progresses, whereas the numbers in night 3 decrease from 6:30 p.m. to 4:30 a.m.

Figure 3. Number of active individuals throughout the night, all survey nights combined; There is a negative correlation between the number of active lizards throughout the night,  $r_s = -1$ ,  $p < .01$ . The trend complies with the trend of temperate zone nocturnal ectotherms in which the number of active lizards will decrease as the night progresses.

Figure 4. A comparison between the influence of air temperature on cloacal temperature (A.) and on the number of active geckos (B.). There is no correlation between cloacal and air temperatures:  $n = 45$ ,  $r_s = .1$ ,  $p > .05$ . There is a correlation between the air temperature and the number of active geckos:  $n = 24$ ,  $r_s = .6$ ,  $p < .005$ .

Figure 5. A comparison between the influence of substrate temperature (coconut tree) on cloacal temperature (A.) and on the number of active geckos (B.). There is a correlation between both the tree and the cloacal temperatures:  $n = 16$ ,  $r_s = .6$ ,  $p < .01$ , as well as the tree temperature and the number of active geckos:  $n = 24$ ,  $r_s = .6$ ,  $p < .005$ .

Figure 6. The cloacal temperatures of the geckos decreases as the snout-vent length increases:  $n = 45$ ,  $r_s = -.3$ ,  $p < .025$ .

Figure 7. The number of mites decreases as the gecko size increases:  $n = 43$ ,  $r_s = -.4$ ,  $p < .005$ .

Figure 8. Trends of ambient and substrate temperature for each night of surveys; the air (A.) and tree (B.) temperatures of each survey night are separated by time period; 1= 6:30 p.m., 3= 8:00, 5= 10:00, 7= 12:00 a.m., 9= 2:00, 11= 4:30.

# Moorea, French Polynesia

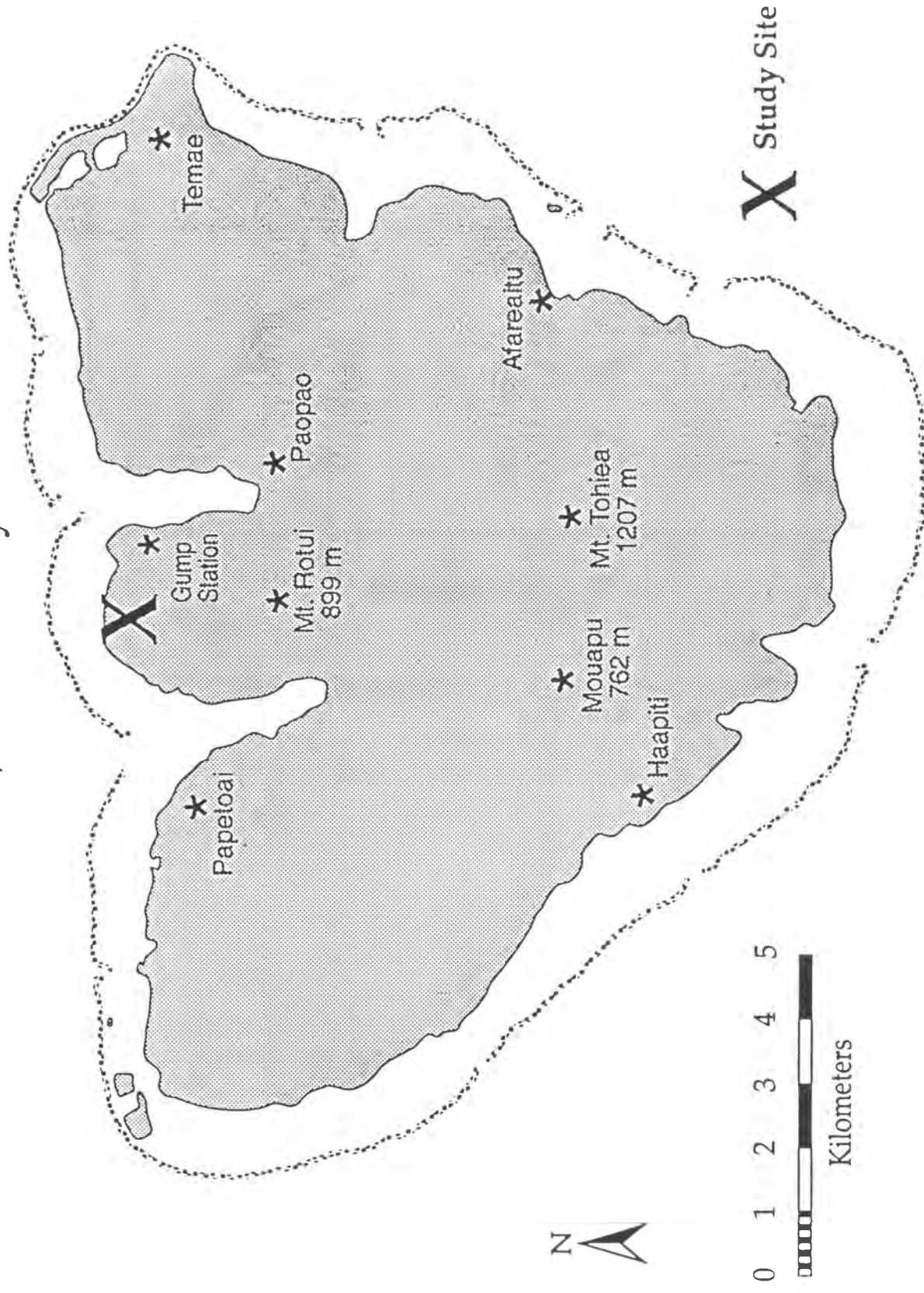


Figure 1. Study Site Location



Figure 2A.

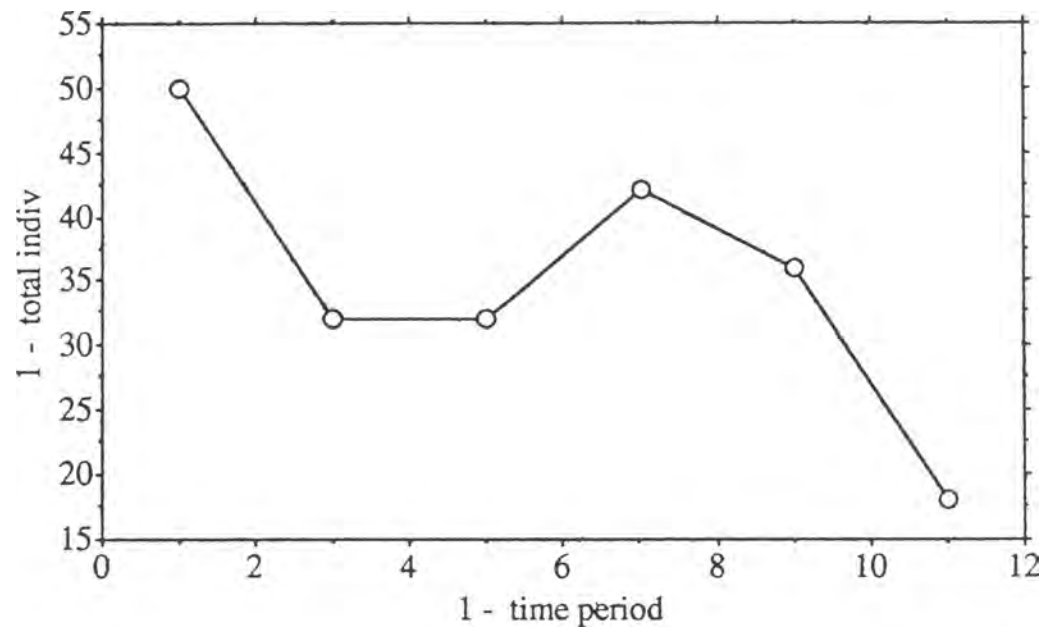


Figure 2B.

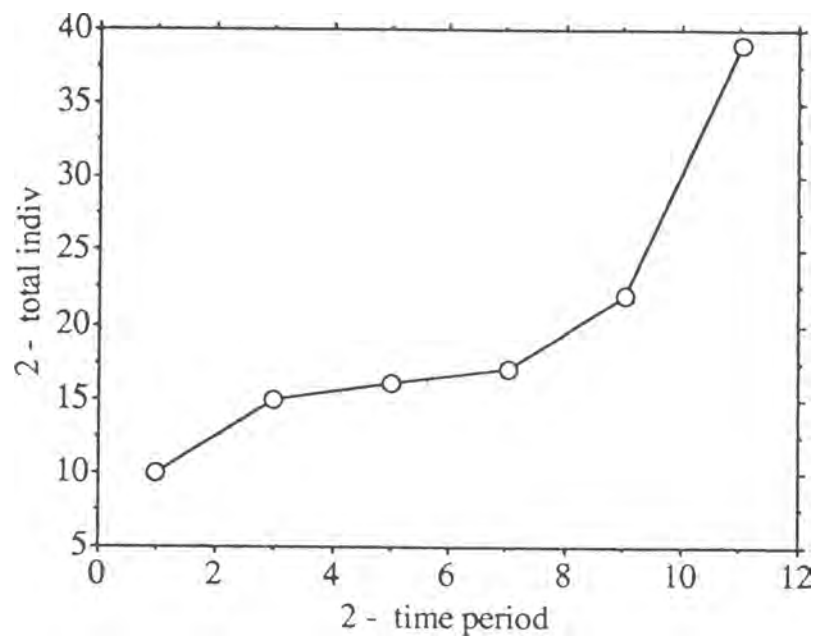


Figure 2C.

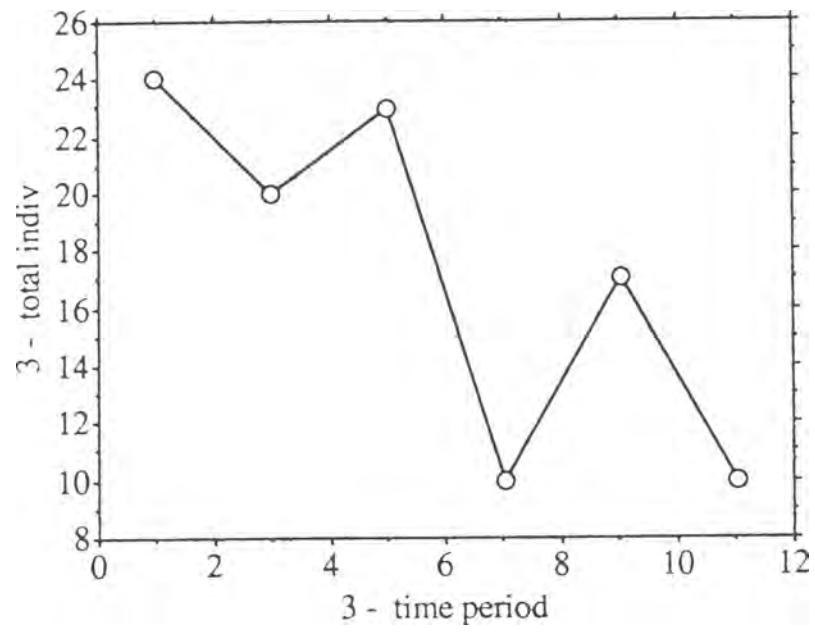


Figure 2D.

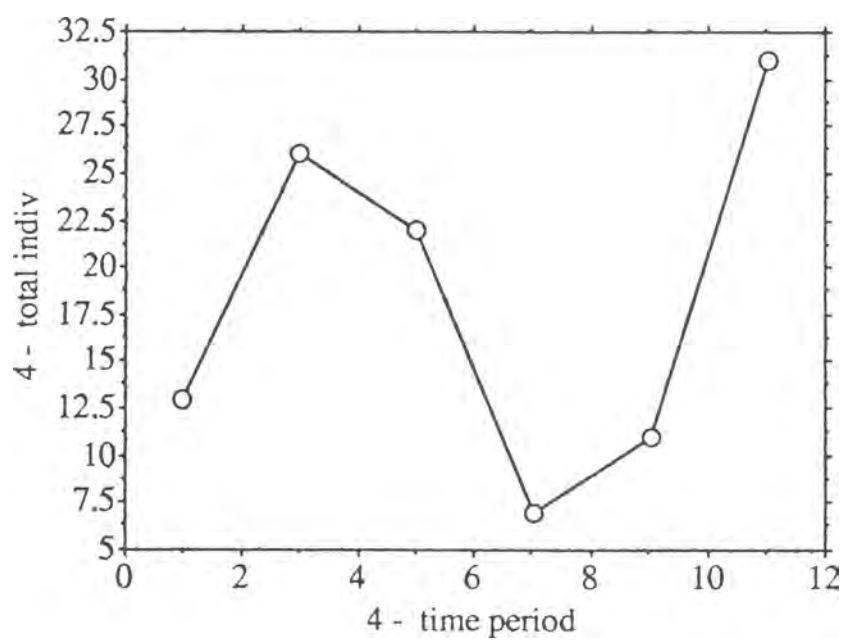




Figure 3.

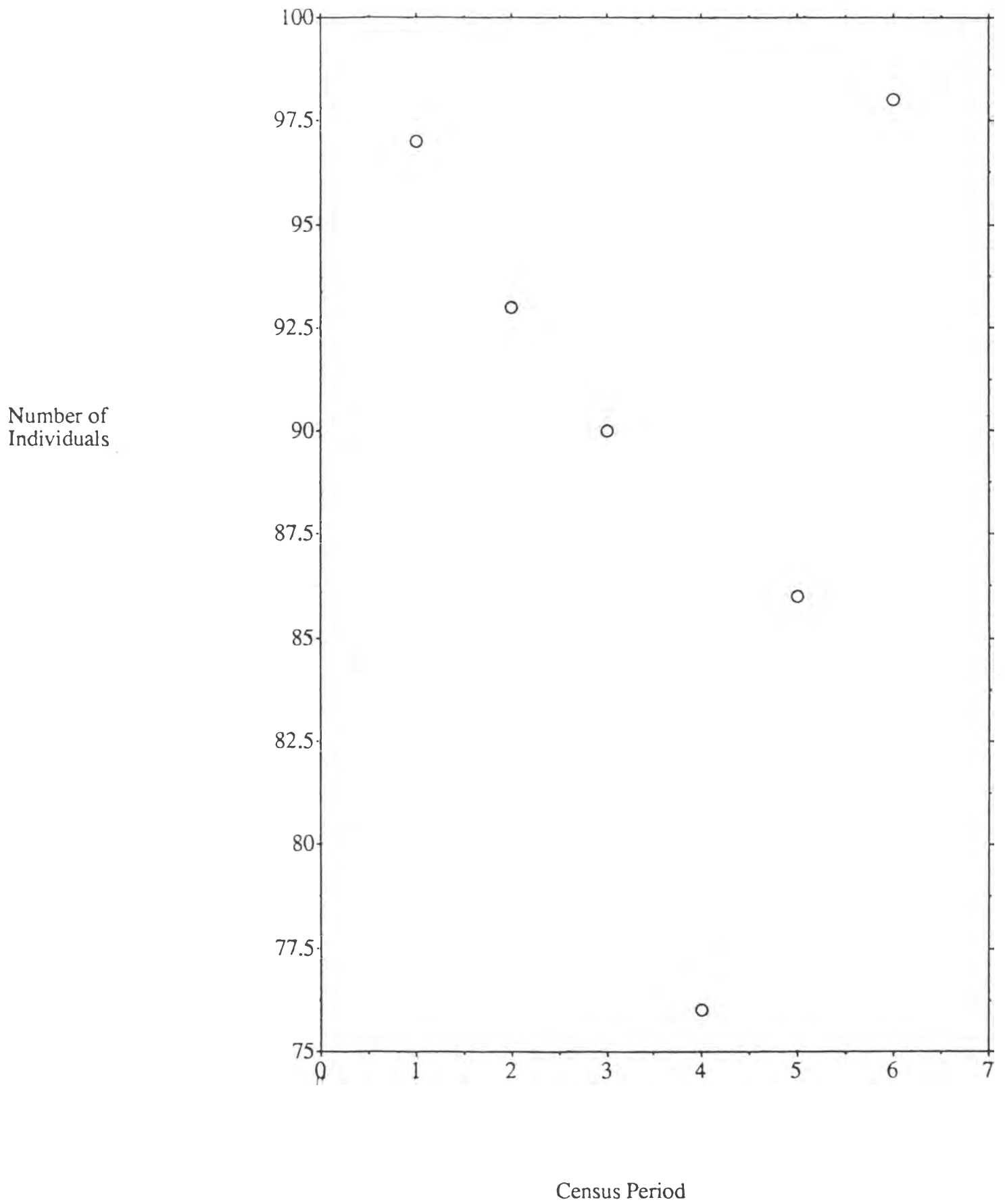


Figure 4A.

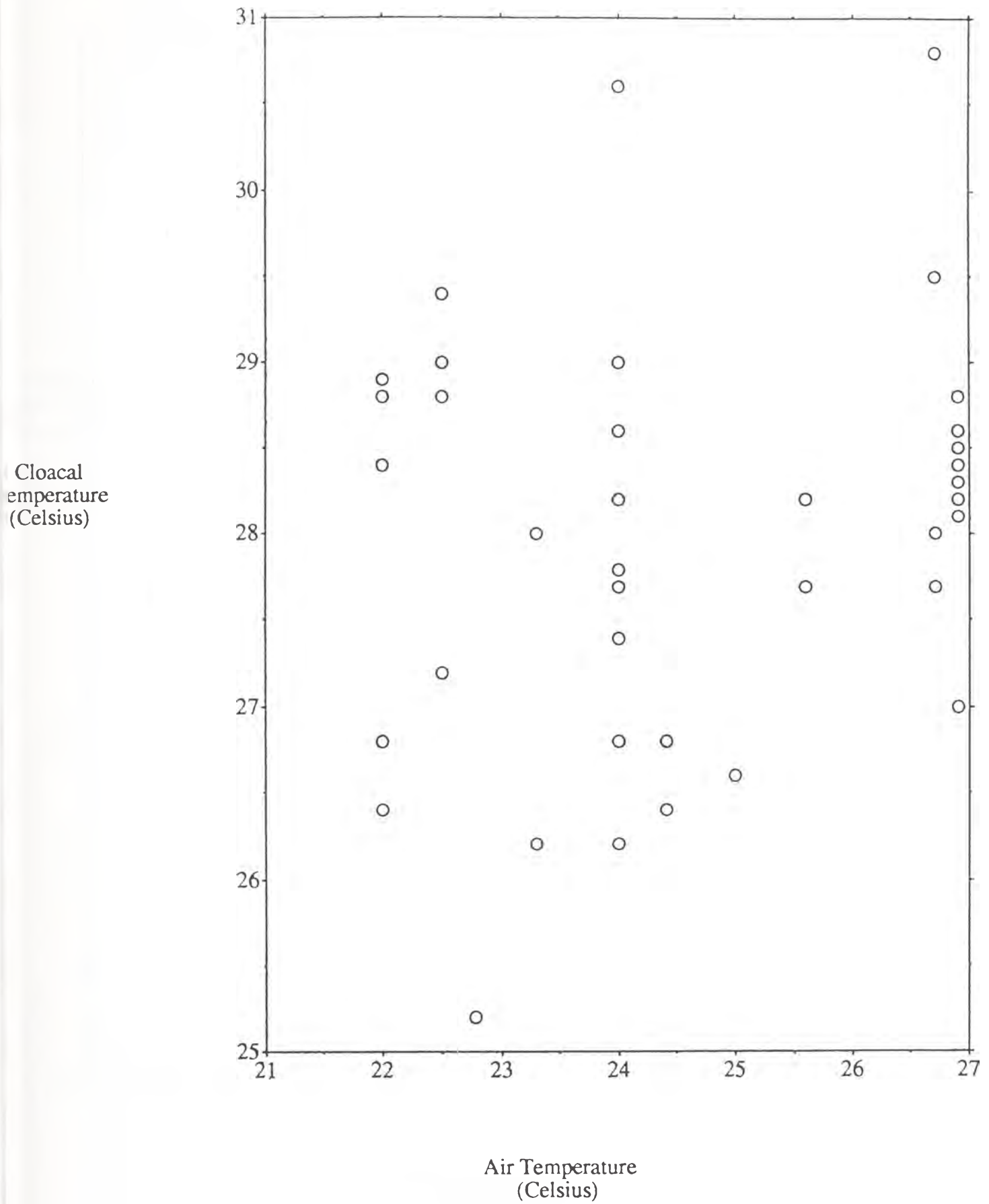


Figure 4B.

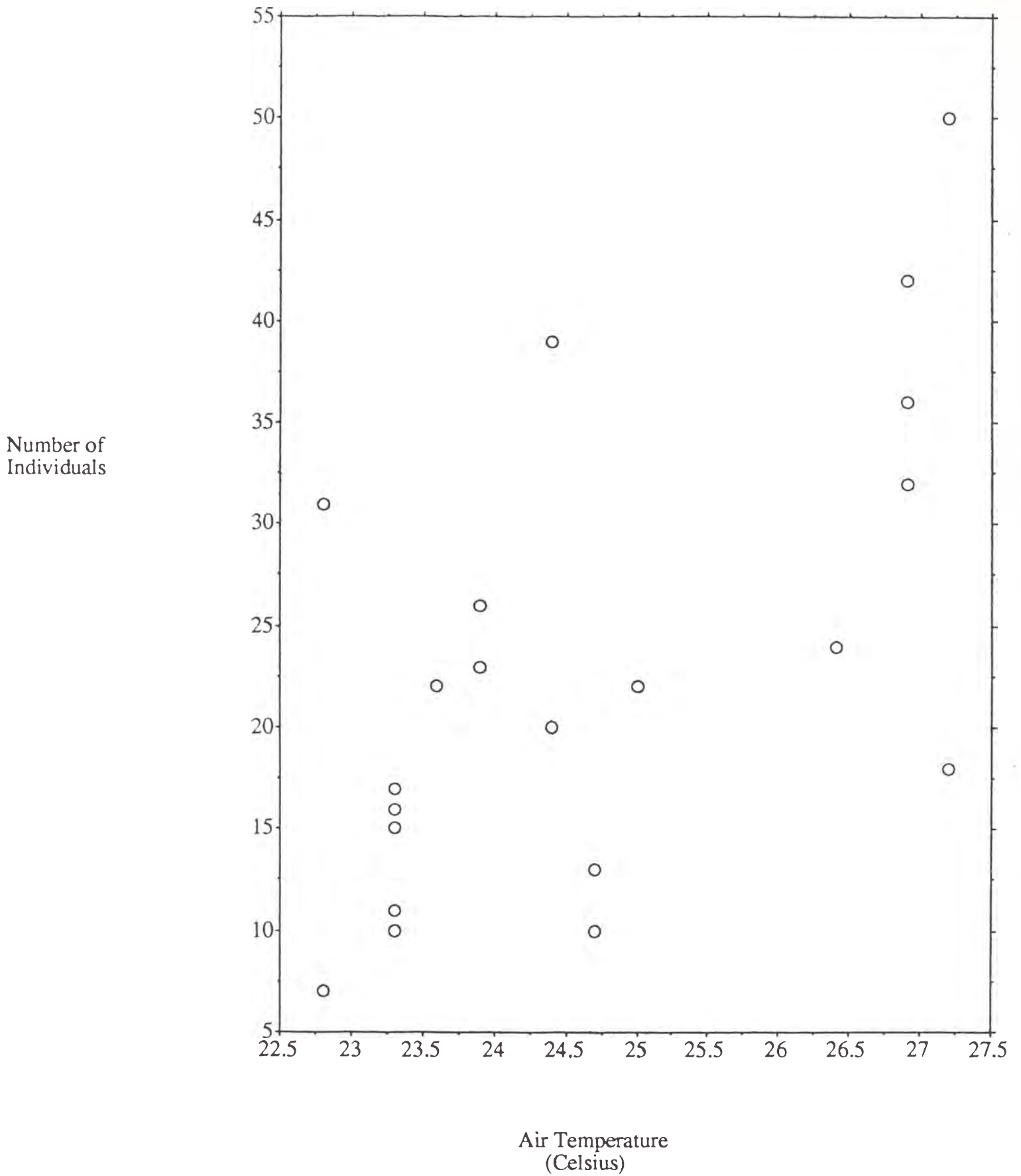


Figure 5A.

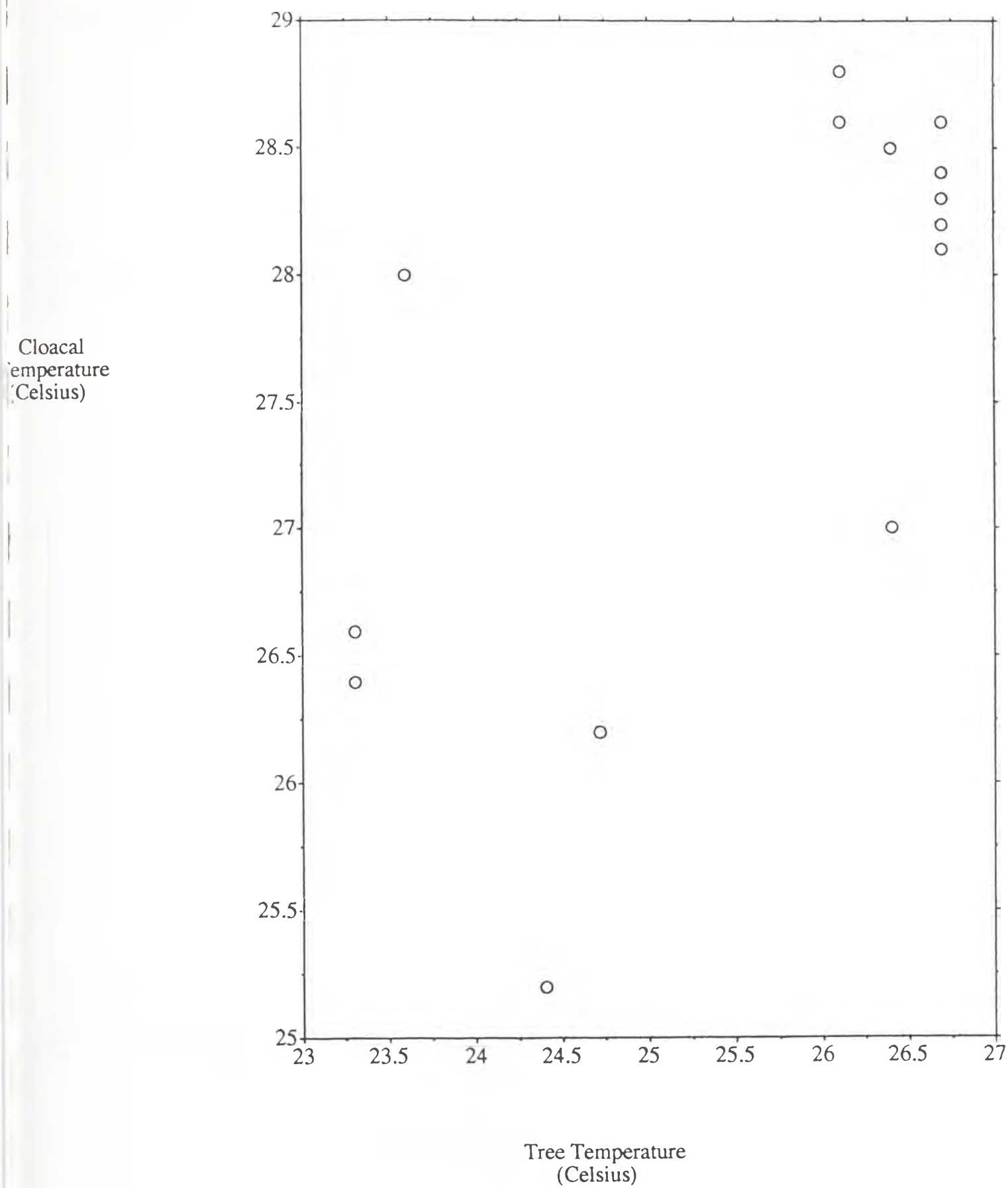




Figure 5B.

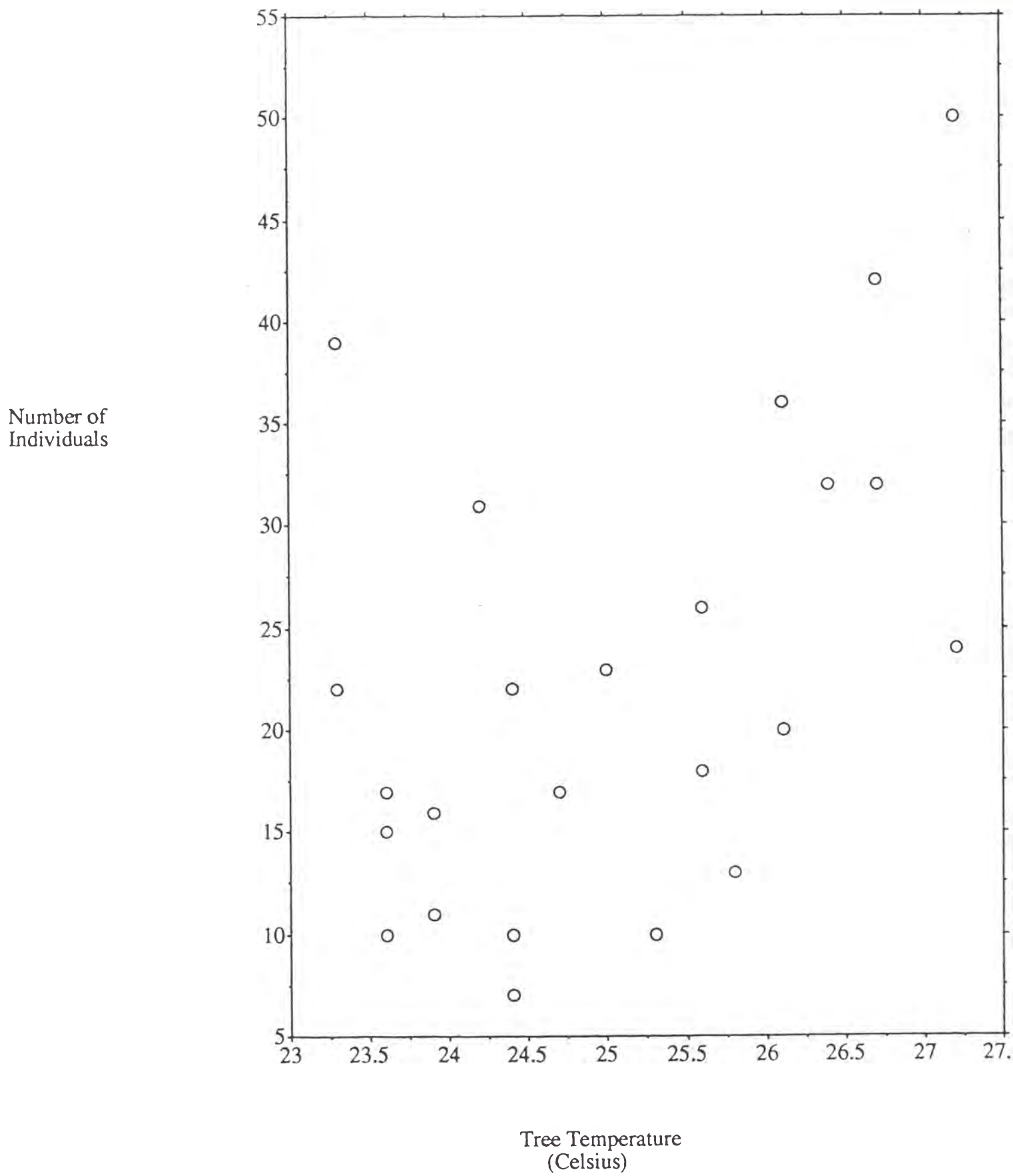


Figure 6.

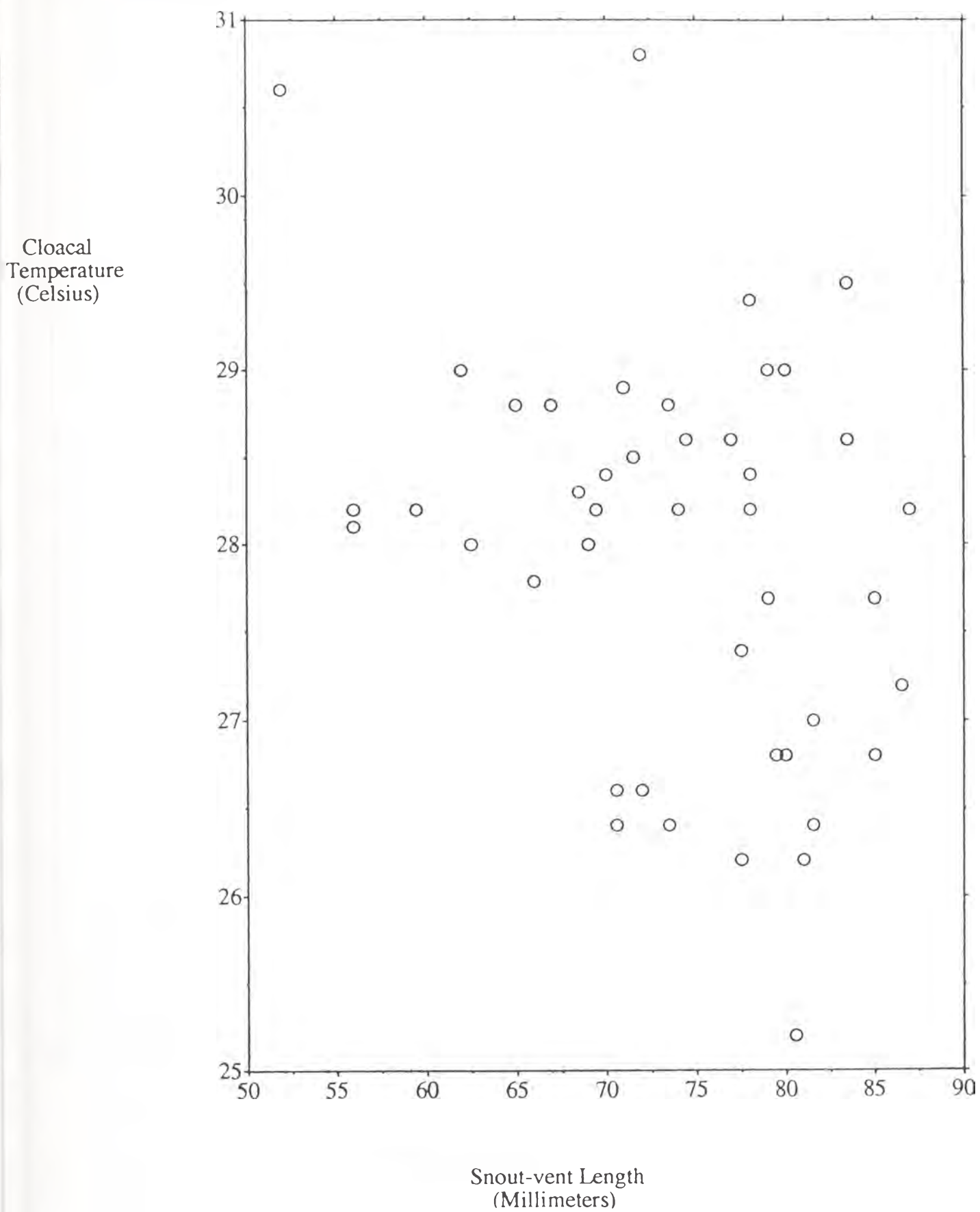


Figure 7.

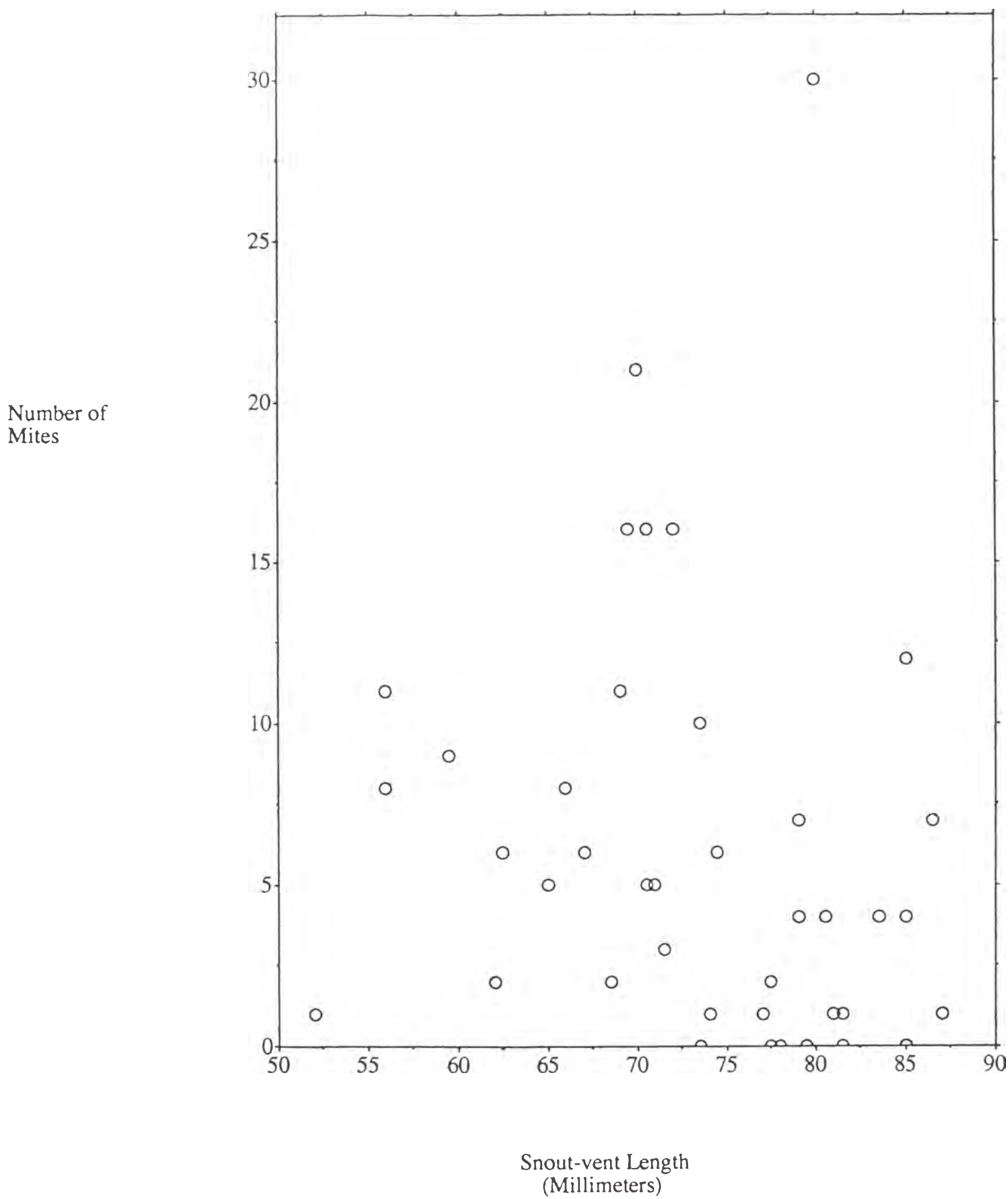


Figure 8A.

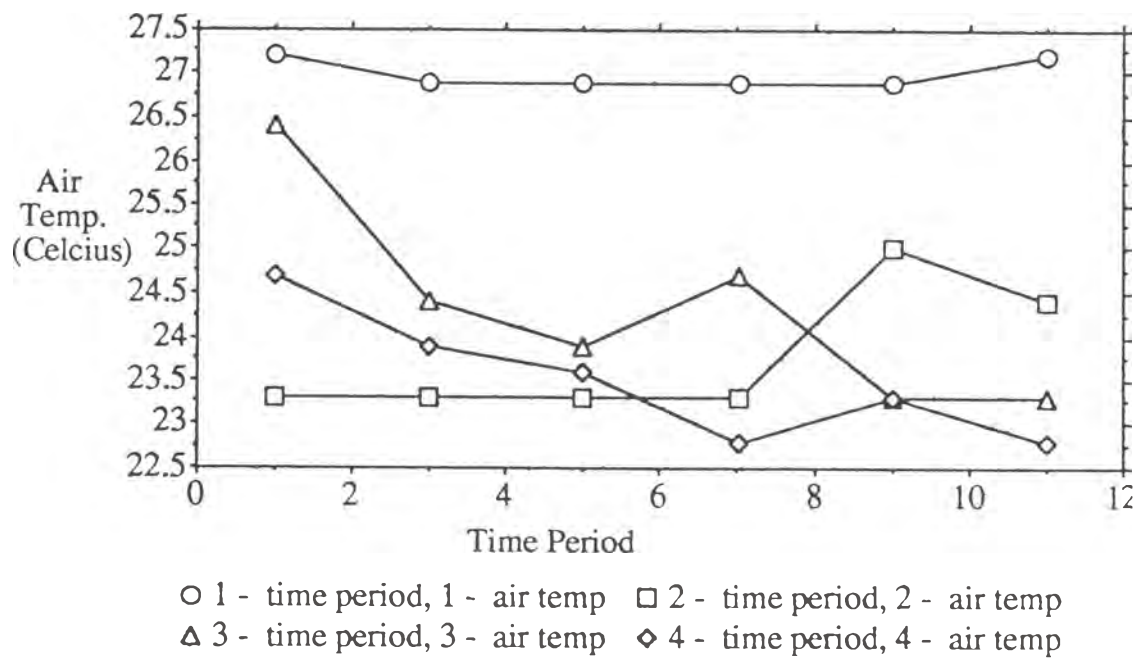
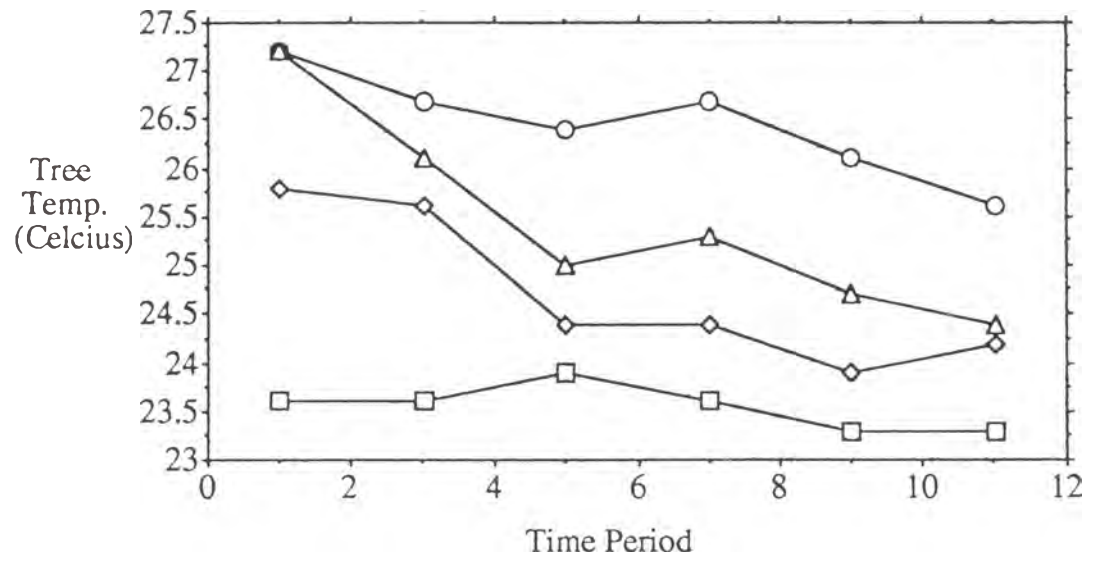




Figure 8B.



# Mangrove colonization on the island of Moorea, French Polynesia

IB 158

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## Abstract

Transplants in a potential habitat indicate that herbivory is keeping *Rhizophora stylosa*, from establishing in many parts of the island, Moorea French Polynesia. All of the areas in which mangrove colonization has taken place had *Paspalum vaginitum* in or near the colonized site (Cavaloc 1987). A bare patch in this perennial innertidal grass occurred beneath colonizing mangroves 76% of the time. The size of the bare patch increased with the diameter of the colonizing mangrove. No hypothesis was tested to explain the occurance of this bare patch, although several are proposed. Colonized mangrove sites showed evidence of stand development. Different types of analysis were used to examine stand structure, and spatial relations of mangroves including nearest neighbor, mean neighbor, and theissen polygon configurations.

## Introduction:

Introduced exotic species can have devastating effects on native flora and fauna. Long term impacts such as extinction of native species, changes in the trophic structure of communities, alterations of nutrient cycling, or changes in species composition of communities can result from these biological invasions (D'Antonio 1992). Invasions of different mangrove species have occurred on several Pacific islands, including the Hawaiian Islands, the Society Islands, and the Marshall Islands (Woodroffe, 1987). The consequences of these introductions are poorly understood. Increased sedimentation, and choking of freshwater fishponds are the only reported effects of mangrove colonization in the Hawaiian Islands (Wester 1981). In Moorea, French Polynesia, the area chosen for this study, Cavaloc (1987) documented mangrove colonization on a spatial and temporal scale, as well as describing the flora and fauna found in colonizing areas. Loss of habitat of *Paspalum vaginitum*, an intertidal perennial grass, associated with an increase in mangrove individuals was the most significant noted impact of



colonization.

*Rhizophora stylosa* was introduced to Moorea in 1933 for oyster farming. Fifty nine years of mangrove colonization on the island has resulted in a gradual spread along the coast line, as well as inland for some of the older colonized sites (Cavaloc 1987). Cavaloc (1987) argues that the spread of mangroves will continue around the island because there are many unoccupied favorable habitat sites. He also showed that the rate of population growth of the mangroves has been exponential (Cavaloc 1987). Yet recent human intervention has altered stand density and distribution of the mangroves, significantly impacting natural rates of spread, and population growth.

The objective of this study was to examine stand structure, and geographic spread of the colonizing mangroves. Specifically, I examined: 1) factors limiting the distribution of mangroves around the island. 2) the relationship between colonizing mangroves, and bare patches seen to occur in *Paspalum vaganatum* habitats. and 3), stand structure and spacing of adult trees in sites colonized during different periods.

#### Study site:

Moorea is located in French Polynesia, in the South Pacific. The location of the seedling transplants on the island are indicated in figure 1. The control (and location of the seed source) for both transplants was located in the establishing site (see figure 1.). Bare patch patterns were studied in the establishing site. The location of just-establishing, establishing and established study sites are indicated in Figure 1. These sites, it is believed, are experiencing different stages of colonization (Cavaloc 1987), and were used to compare stand structure and seedling growth in sites colonized at different times. Density estimates of mangroves in *P. vaganatum* habitat were made at the establishing site, and the just-establishing site located on the north side of the island.

#### Methods:

1) Mangrove distribution: Seedling transplants were done in an area not yet colonized by mangroves to see if there were any factors that would limit the distribution of the mangroves around the island - such as nutrient conditions, salinity, unfavorable substrate, or herbivory. The site chosen to test seedling survival was in the airport lagoon area. This area was identified as a potential habitat site by Cavaloc (1987). Transplanted seedlings were taken from the intermediate site. The roots were flushed thoroughly to remove residual soil and mud. The roots were then left over-night in salt water tanks. Plastic bags tied well over the roots to prevent drying out were used to transport the seedlings.

In the airport/lagoon area, three sites, each with a different substrates were chosen. Substrate, and salinity were measured at each site. Substrate was measured qualitatively (sand vs mud vs silt observations). Salinity was measured using a conductivity meter. Thirty to fifty seedlings were then placed at each location, and at the seedling source site for a six week

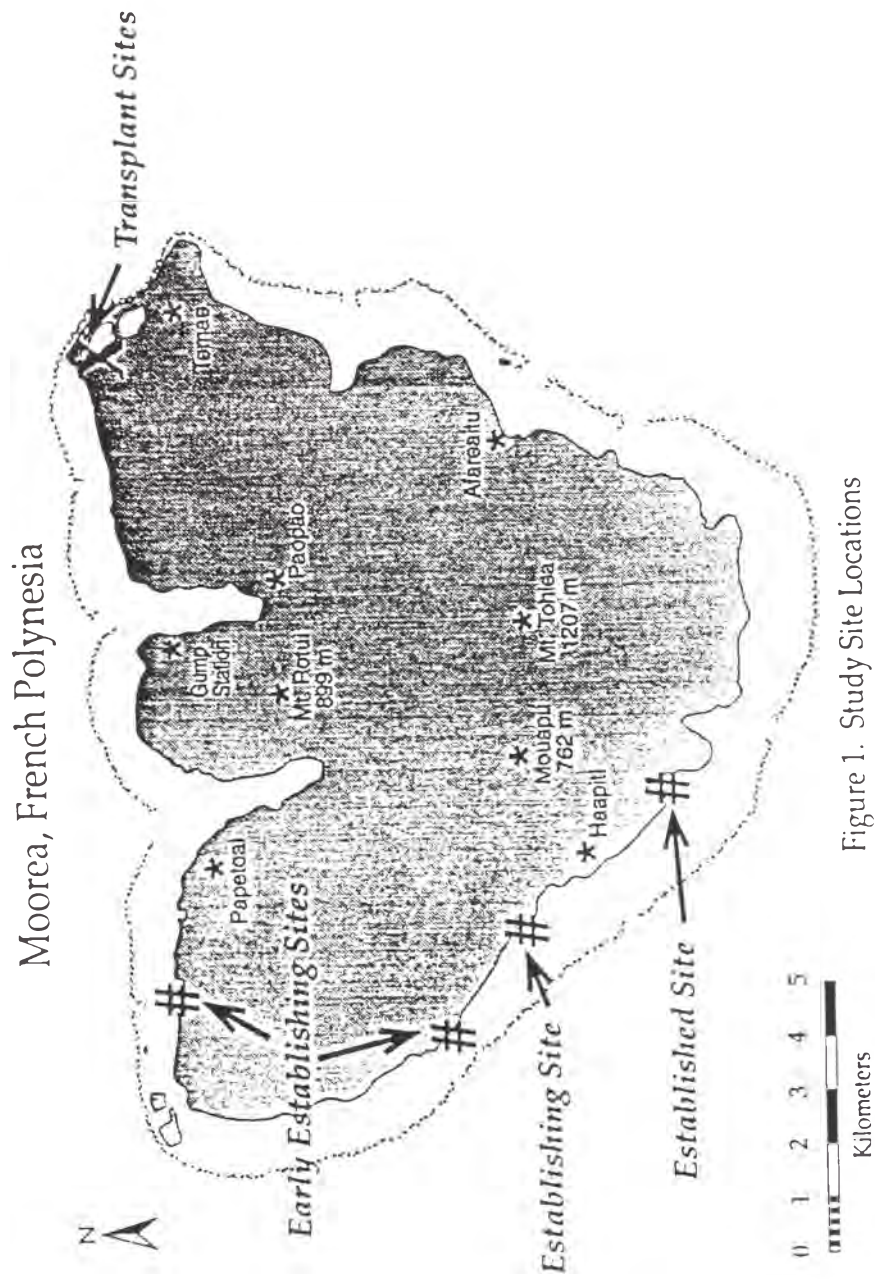


Figure 1. Study Site Locations



period. Five out of every eight seedlings planted were measured in height from the base of the propagule to the tip of the apical meristem, and the number of nodes were counted. Evidence of herbivory at the second site prompted a second transplant at the third site. The same methods were used as in the first transplant, except no height or node data was taken. Twenty to thirty individuals were placed in three different types of transplants for four weeks. 1) A screen mesh enclosure to exclude herbivory 2) An open cage with screen mesh on the top to control for shade and 3) Seedlings planted without an enclosure to control for herbivory. The cages were constructed of pvc pipes at each corner, with wide plastic mesh (3cm) attached by plastic ties along the sides. Screen mesh (1mm x 1mm) was then laid over the frame and attached by plastic ties.

2) Bare patch pattern: The occurrence of bare, grassless patches in relation to establishing mangroves were described by looking at height, diameter and location of each mangrove greater than 1 meter in height, in relation to the size of the patch of grass exclusion beneath the mangroves. The location of each tree was mapped by using a top-con survey rod, tied into a drain pipe by the road. A defined area of grass habitat was obtained by mapping the perimeter of the plot surveyed, again, using the top-con, then obtaining the area of a definite polygon. Density estimates, and size class distributions were calculated for both the establishing site, and the early establishing site.

3) Stand structure: Stand structure was examined by looking at the spatial relations of mangroves to its neighbors in mangrove dominated sites. At the oldest site (est age 40-60 years), eight plots consisting of an area containing 10-20 trees > 10 cm, or 15-25 trees < 5 cm, were randomly chosen for spatial analysis. At each of these plots the distance and angle of each tree from a control point was measured. By relating all of the trees in a plot to a control point, the distance and position of each tree in relation to its neighbors was calculated. This same method was used at two plots in the establishing site. Spatial analysis made possible by this technique includes theissen polygon configurations per tree, nearest neighbor analysis, mean distance to a neighbor, and density estimates per diameter size class. Theissen polygons are defined by the perpendicular bisector of a trees nearest neighbors (Methen, 1984). The mean distance to a neighbor for trees in each height class (figure 6) was used to add pseudo-competitors to trees located on the edge of the stand. This allowed trees that lacked neighbors to have a closed theissen polygon based on the mean spacing (figure 6B). The small size of the mangrove forest (due to human disturbance) found at the established site limited the number of size classes that could be sampled: (0-5, 10-15, 15-20, 20-25 cm) Suppressed trees were defined as those having less than a 10 cm diameter in a stand where trees 10-25 cm were found. These trees were found in low densities throughout plots of > 10 cm trees and were not included in the spatial configurations. Diameter was obtained by measuring the circumference of the largest portion of the trunk on each tree in the plot, not the diameter breast height. Multiple trunks, and trunks that did not taper uniformly made

taking the greatest circumference size more appropriate. Cintron (1984) recommends taking the diameter of each stem at breast height, rather than the largest trunk, so the employed methodology will result in diameter readings higher than dbh measurements.

#### Results:

1) Mangrove distribution: The airport/lagoon area was chosen because it was the largest unoccupied potential habitat (Cavaloc 1987). The three transplant sites in the lagoon represent three distinct portions of the lagoon; the entrance, the middle and the back (Figure 3a). Figure 12 shows conductivity, substrate, number of transplants, number of survival, as well as suspected cause(s) of mortality for both transplants.

Site	#plant	#alive.	cond.	substrate	suspected cause of mort.
1	32	0	24.7 dS	organic mud	poor substrate
2	32	0	23.67 dS	coral mud	herbivory
3	40	0	53.4 dS	coral mud	human disturbance
control	37	35	55.38 dS	silty mud	transport damage

Site #1 = back of lagoon.

Site #2 = middle of lagoon.

Site #3 = entrance of lagoon.

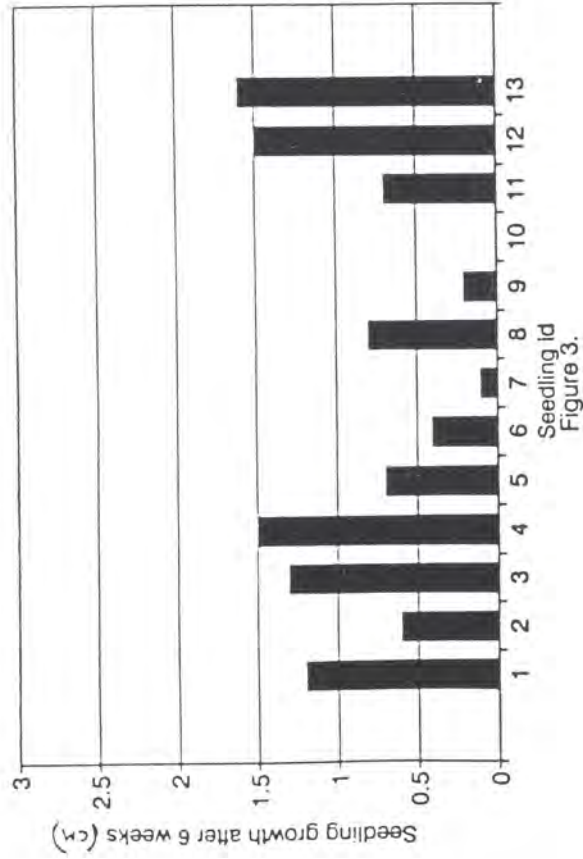
control = establishing site (source of seedlings).

Figure 2. Results of first 6 week transplant study.

Survival at the end of the six week period was 0%, or 0/104 for the first transplant. A poor substrate at the first site-which was a boggy, organic matt >1 meter depth with large-size (>1 cm) coral rocks on the bottom, did not provide the support necessary for seedling establishment (the seedlings were no greater than 20 cm in height). The cause of mortality at the second site is suspected to be herbivory. Seedlings both dead and alive all showed signs of herbivory including partial or complete loss of leaves, an eating away of the stalk, and in some cases complete consumption of the exposed portion of the seedling. There was no evidence of root consumption, or of any subterranean plant parts. This site was particularly lacking in vegetal matter, with no exposed green leafy matter found in the entire mud flat area. Crabs were found at the site regularly, particularly *Carnifax cardisoma*, (Tupa), a land crab found throughout the island. At the third site, there was greater abundance of green leafy matter including *Hibiscus Teleasus*, and intermittent low density patches of *Paspalum vaganitum*. While evidence of herbivory was found at this site, it was not as widespread or as apparent as in site # 2. Human disturbance was believed to have been the primary cause for seedling mortality, which included removal, and clipping of

# Seedling growth after six weeks

Control for transplant experiment



# Area of bare patch vs tree height

(excluding patches < .25 m<sup>2</sup>)

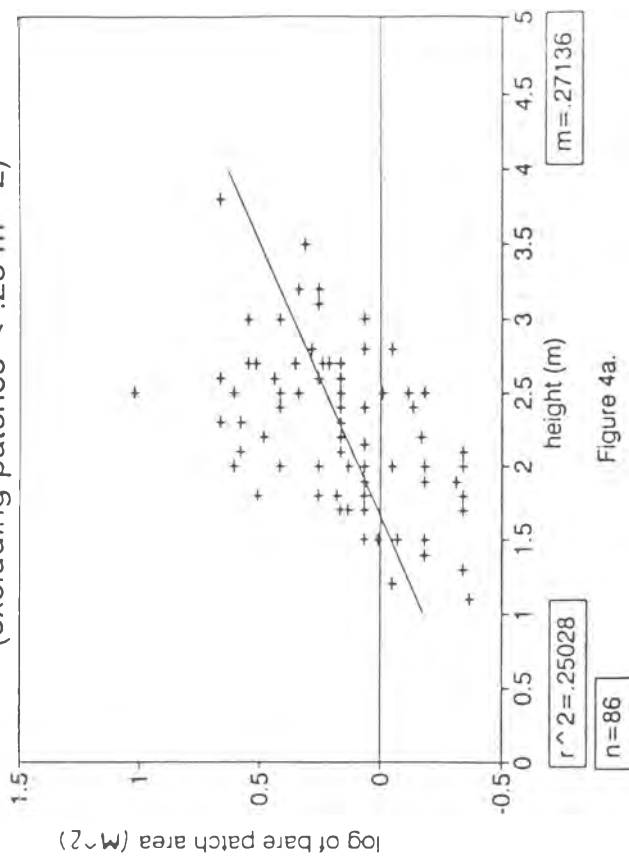


Figure 4a.

# Size of bare patch vs biomass

(excluding patches < .25 m<sup>2</sup>)

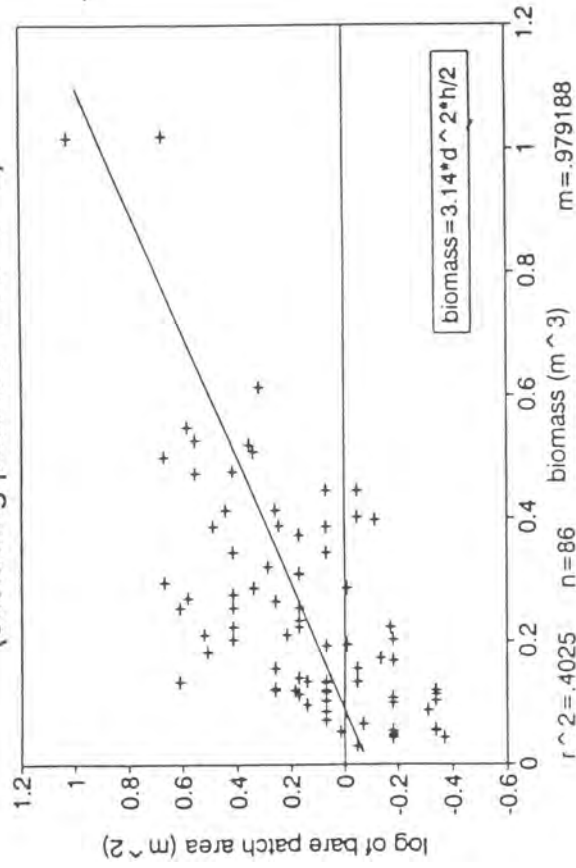


Figure 4c.

# Area of bare patch vs tree diameter

(excluding patches < .25 m<sup>2</sup>)

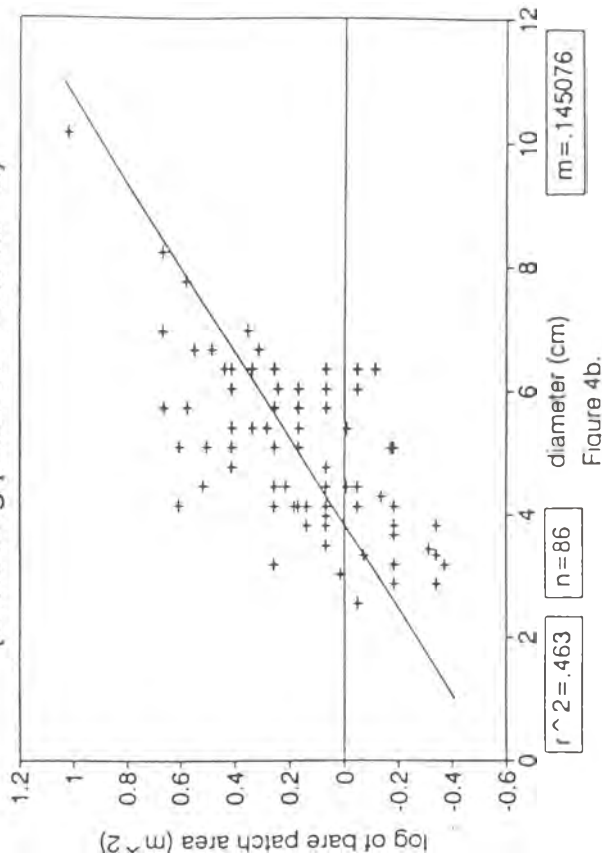


Figure 4b.



the seedlings. Growth measurements taken from the seedlings that survived in the control are shown in figure 3.

The second transplant, run for a four week period at site #2 was done to see if the seedlings could survive in the absence of herbivory. Conductivity was 23.67 dS, and the substrate was a sandy coral mud, unlike the more detrital, silty mud found at the source site for the seedlings. Evidence of herbivory was strong in the open cage. Tupa were seen at the site regularly, and more than 55%, or 14/25 of the seedlings were eaten in the open enclosure. Survival was 97%, or 34/35 in the closed caged.

2) Bare patch pattern: A patch of bare, grassless area  $>.25 \text{ m}^2$  occurred in 76% of the trees sampled. 18% of these 76% showed the formation of a poor, but nonetheless apparent pattern of grassless area. Substrate varied from a sandy mud substrate to grainy sand with no mud, and microtopographic conditions were seen to vary throughout the extent of the site surveyed (personal observation).

Figures 4a, 4b, and 4c show height, diameter, bio-mass of *R. Stylosa*, as they vary with the size of the bare patch area ( $\text{m}^2$ ). Transformed regressions between height vs grass exclusion, and diameter and grass exclusion (Figure 4.) show that the diameter of the primary trunk is a better correlate to grass loss. Both of the r-values from the regression yielded statistically valid correlations. A regression between trunk volume ( $=3.14 \cdot \text{diam}^2 \cdot \text{ht} / 2$ ) and bare patch was done for comparison. Without data on foliar density, or net biomass including leaves and branches, these regressions tell us little about possible causes behind bare patch occurrence.

3) Stand structure: The size class distribution of the trees measured in the established site was a bi-modal one (see figure 7.). The behavior of this missing size class (5-10 cm) was assumed to be linear, as with the first and third size class measured. Figures 5a, b, c, show nearest neighbor distance, mean neighbor distance and theissen polygon area as they vary with tree diameter. Slopes between nearest neighbor, mean neighbor, and thiessen area ( $\text{m}^2$ ) all passed the t-test, and were therefore all statistically different from each other. Figure 5d shows density vs tree diameter ( $1/\text{thiessen area}$  vs diameter). Figure 6a shows the distances to neighbors that formed the theissen polygon for each size class. Figures 6b and 6c show thiessen polygon configurations of two plots mapped in the established area. Between the 5 cm and 20 cm size class, nearest neighbor distances increased less than the mean spacing, or the maximum spacing that defined theissen polygons. The lower distance values in Figure 6. show this. Figure 5b also shows mean spacing vs diameter obtained from the establishing site, which was higher than that of the established site. Figure 8. shows the size class distribution for the establishing and just-established sites. The spacing of the establishing site is almost a gaussian distribution, while the early established is bi-modal. Densities from these two sites, not including seedlings were .09 individuals/ $\text{m}^2$  in a area of 1,331  $\text{m}^2$  with an average diameter of 4.49 cm, and .13 individuals/ $\text{m}^2$  in an area of 500  $\text{m}^2$  with an average diameter of 1.86 cm respectively,

Nearest neighbor vs tree diameter

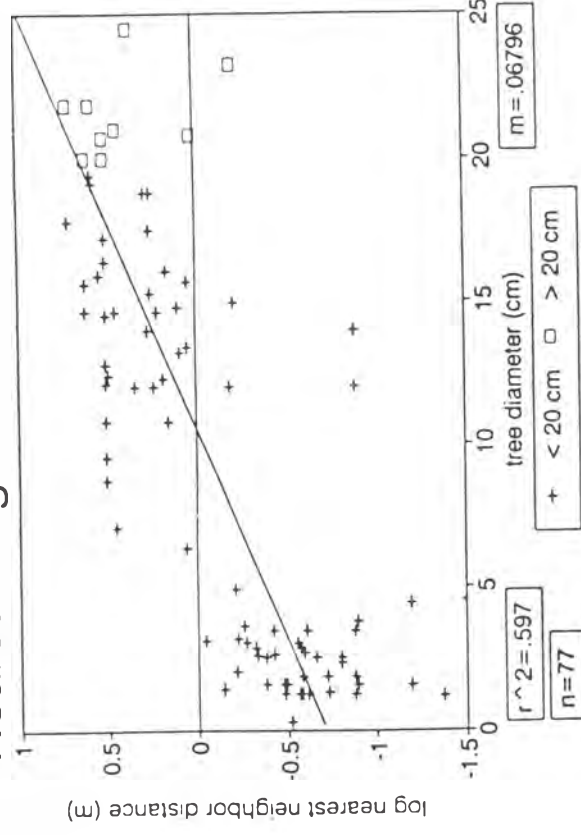


Figure 5a.

Mean spacing of neighbors

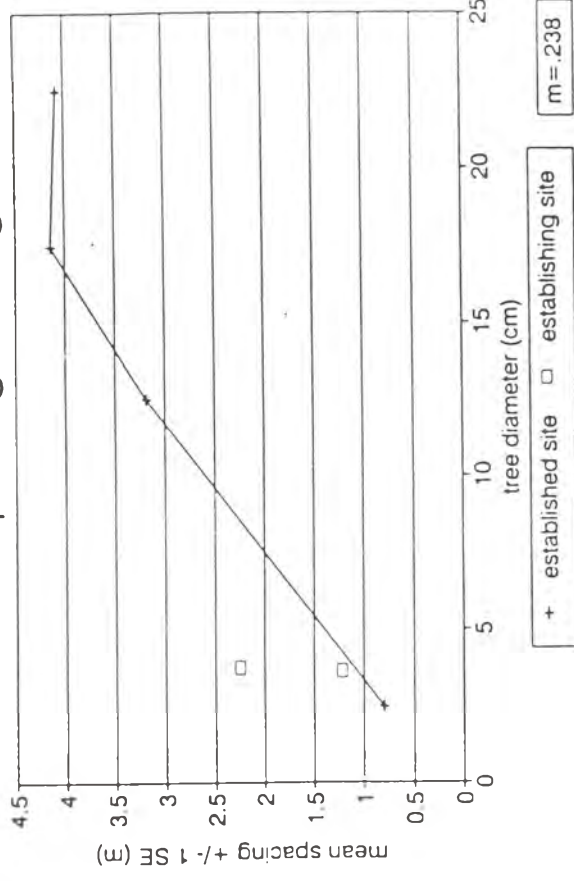


Figure 5b.

Theissen area vs tree diameter

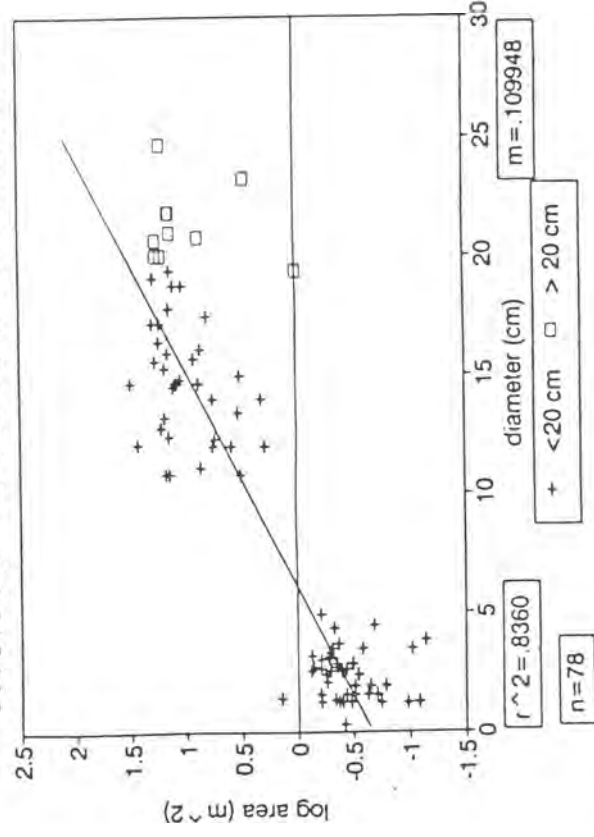


Figure 5c.

Stand density vs tree diameter

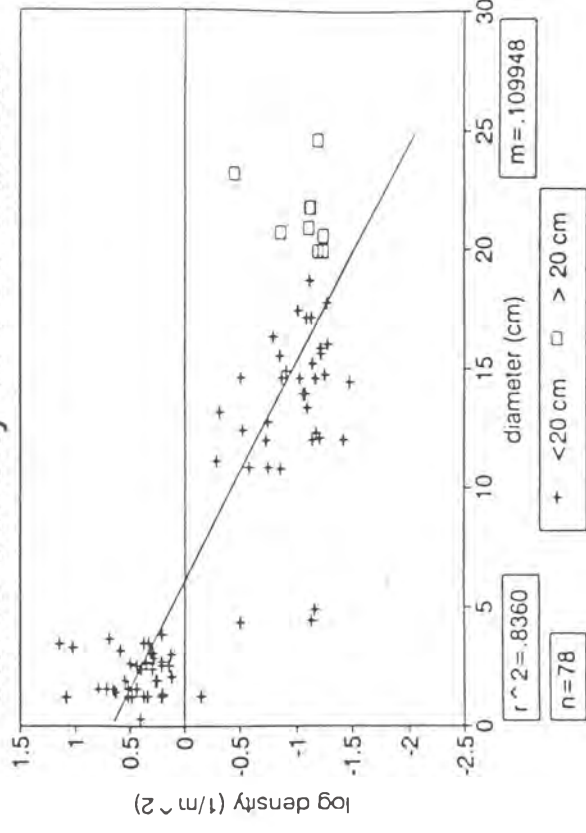


Figure 5d.



# Distance to neighbors (theissen polygon neighbors)

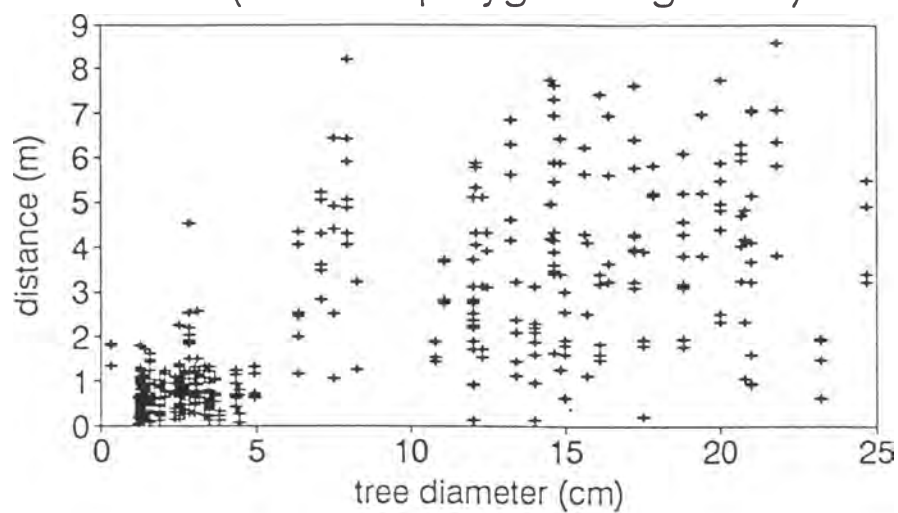


Figure 6.

figure 6a. Spacings (m) of all theissen neighbors per tree.

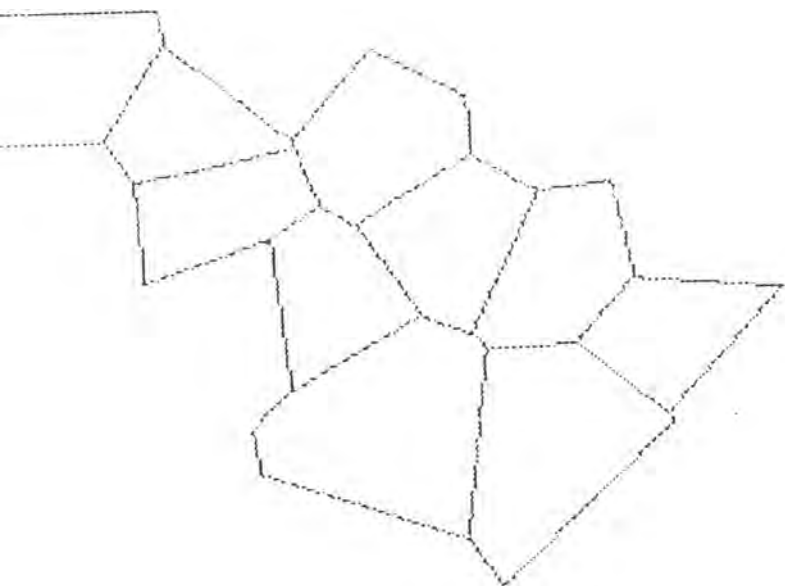


figure 6b. Theissen polygons of  
trees 10-25 cm diameter.



figure 6c. Theissen polygons of  
trees < 5 cm diameter.

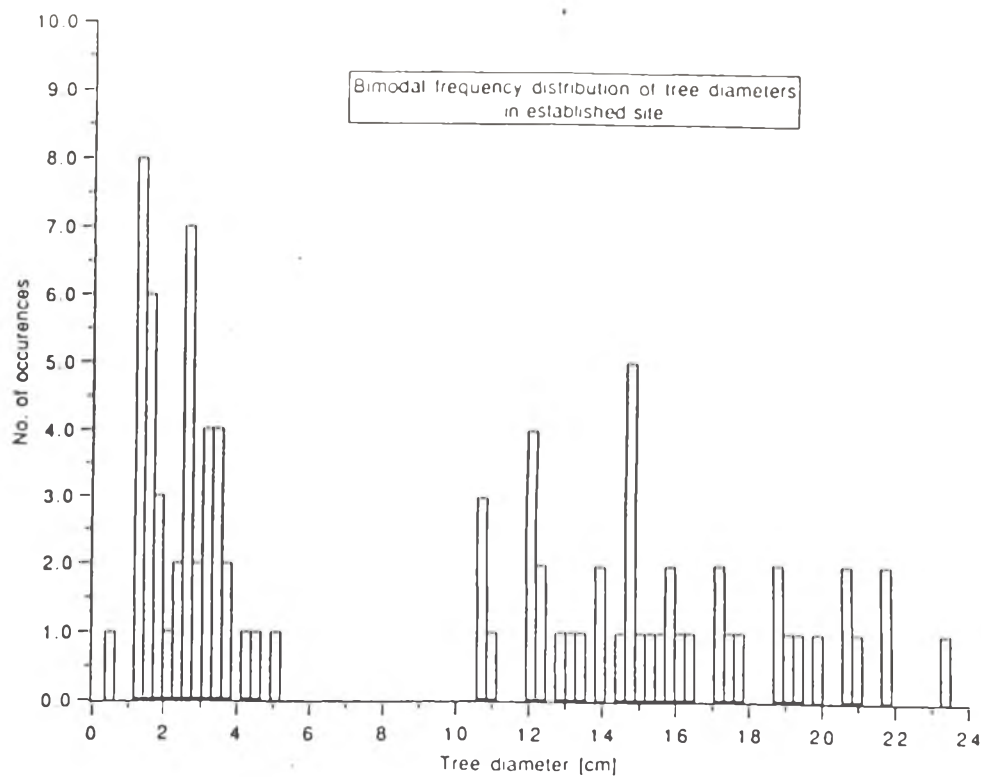


figure 7. Histogram of trees diameters found in established site.

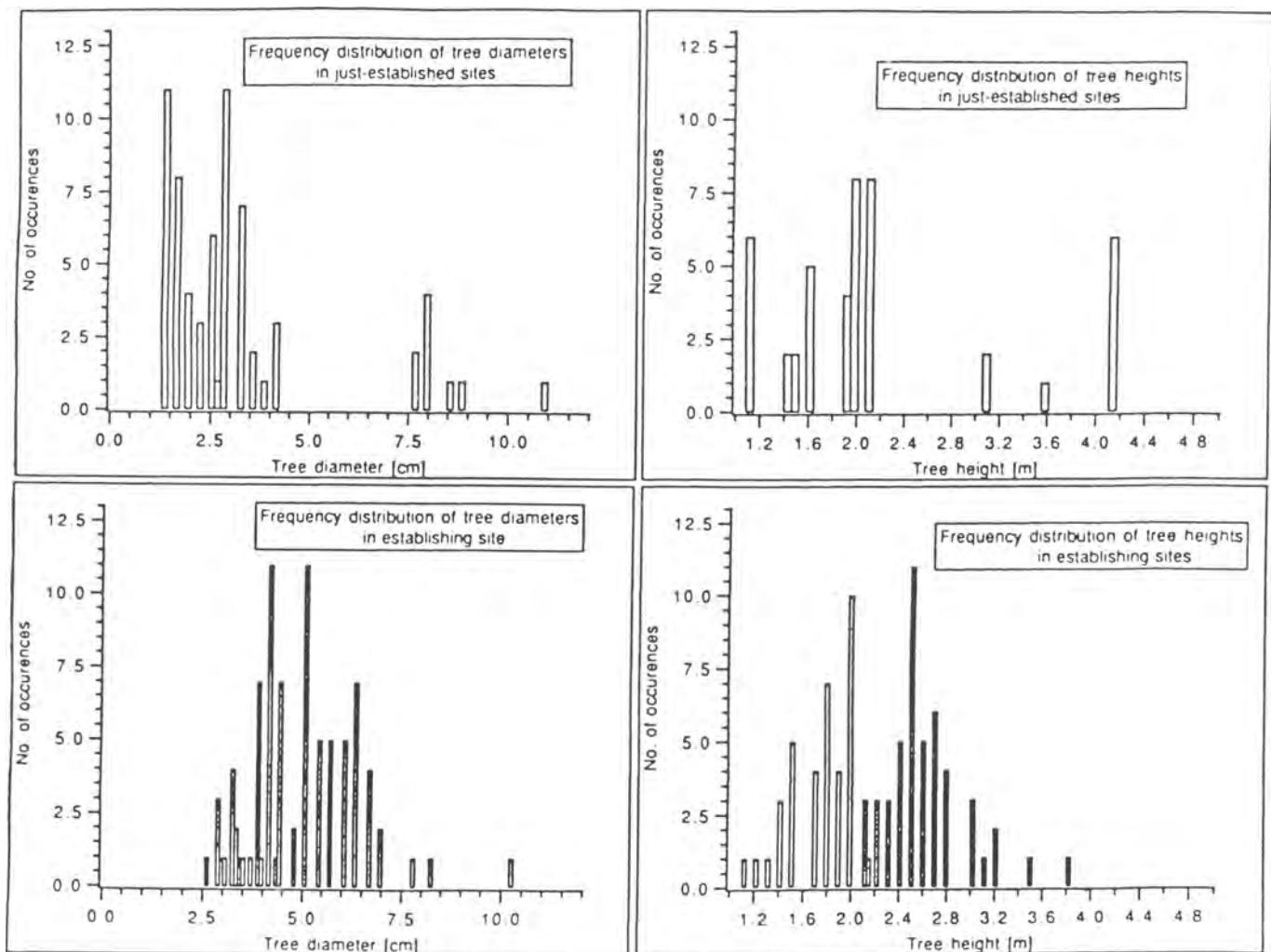


figure 8a,b,c,d. Histograms of tree heights and diameters of trees in establishing and just establishing sites.

Seedlings found inside defined plot boundaries numbered over 400 at the establishing site vs 107 at the just-establishing site.

#### Discussion:

1) Mangrove distribution: The transplant studies done in this paper suggest that seedling consumption by *C. cardisoma*, and possibly other crabs found in the mud-flat area, play a definitive role in limiting the distribution of mangroves around the island. These findings are consistent with herbivory studies done on mangroves in Australia. Smith (1986) was able to show in mangrove forests of north east Australia, that seed predation of *Avicennia marina* by graspid crabs, in combination with shade intolerance, were limiting the distribution of *A. marina* across the intertidal region. Other herbivores known to play a significant role in determining the composition, and in some cases distribution of mangrove forests include molluscs, gastropods, and insects (Robertson, 1991). The impact of herbivory is not always direct. Litter consumption by crabs in mangrove forests can play an important role in nutrient cycling. Availability of nutrients in the soil can in turn affect the species composition of mangrove forests (Robertson 1991).

All of the sites around the island which were successfully colonized by mangroves had *P. vaganatum* in, or around them (Cavaloc 1987), and in many cases *Hibiscus tiliaceus*. *C. cardisoma* was seen at all of these sites (personal observation). This suggests that herbivory of mangroves is not so intense as to prevent establishment and subsequent colonization, when these other food sources are present. Food preference would explain why herbivory is not preventing colonization altogether. A study done in post-fire southern California chaparral by Mills (1983) found preferential feeding of *Ceanothus greggii* (ceanothus) over *Adenostoma fasciculatum* (chamise) by small mammals, which allowed a higher establishment of chamise seedlings over those of ceanothus. Smith (1987) found preference for different species of mangrove propagules over others by graspid crabs in an Australian mangrove forest. The nutrient composition was found to be different for each of the species of mangrove propagules, and accounted for 97% of the variance in the amounts of predation. Thus, food preference for *P. vaganatum* over *R. stylosa* by Tupa, could play a significant role in determining the distribution pattern of *R. Stylosa* on the island of Moorea.

2) Bare patch pattern: A bare, grassless patch was shown to occur 76 % of the time beneath mangroves colonizing *Paspalum* habitat. Two hypothesis are suggested to account for this pattern. 1) Mangroves cannot survive or establish in the grass, therefore are only found in bare, grasseless areas. 2) intraspecies competition results in grass mortality, and subsequent exclusion. The first hypothesis can be discounted by the number of seedlings found growing in the grass. Over four-hundred seedlings were found in the study area growing in the grass without the presence of an grassless patch beneath them vs 88/92 trees over one meter tall found with a bare patch beneath directly beneath them. Additional evidence which disproves this hypotheses is the correlation found between the diameter of the

mangrove tree, and the size of the bare patch (figure 4b). Cavaloc's study further supports this view. (Cavaloc 1987). His data showed that *Rhizophora* has a competitive effect on *P. Vaganitum* on the island of Moorea, but he was only able to show a net loss of *Paspalum* habitat associated with an increase in numbers of mangrove individuals through time. While it is likely that this conspicuous bare patch is the result of grass mortality, and subsequent exclusion, no work has been done to find the cause behind this relationship.

Factors which might cause grass exclusion beneath the mangrove include shading, nutrient competition, allelopathy, mangrove root mats in the substrate, or possibly patterns of *P. vaganitum* herbivory that develop as a result of the presence of the mangroves. As the tree ages, root development could become more extensive. A dense root matt was found at the established site (personal observation). Such an extensive root matt could lead to an increase in nutrient competition between *P. vaganitum*, possibly resulting in grass exclusion. D'Antonio (1991) found that root competition between *Carpobrotus edulis* (an invasive perennial) and *Haplopappus ericoides* (a native Californian shrub) had a pronounced effect on water intake, shoot size and overall morphology of *H. ericoides*.

Favorable herbivory conditions brought about by the presence of the mangrove tree could result in the presence of this bare patch. Halligan, (1974) showed than small mammals living in California sagebrush consumed grassland vegetation in the vicinity of the sagebrush, resulting in the formation of a bare patch.

While shading might play a role in creating unfavorable *Paspalum* conditions nutrient competition, or allelopathy are more likely to be the driving force behind the grass exclusion. This conclusion is based on qualitative feild observations which showed that the amount of shading seen to occur at noon was low for many of the trees, and the fact that the bare patch pattern was always centered around the tree, in spite of low leaf densities which were seen to occur on many of the trees. 3)

Stand structure: Among the three techniques employed; nearest neighbor, mean spacing to a neighbor, and theissen configurations, thiessen polygons provide the best description of spatial relations between neighbors in a stand because they incorporate both the distance and the location of the nearest neighbor, and all neighbors that help form the smallest thiessen area. Another advantage to using the theissen technique is that by having a definite area associated with each tree, density can be obtained, on a per-tree basis ( $1/\text{theissen area}$ ), rather than using the total number of trees greater than a given diameter per unit area, a technique which Cintron (1984) recommends when characterizing mangrove stand structure.

The bi-modal distribution of trees (figure 7) renders the  $r^2$  value of the correlation-test between density and tree diameter invalid. However the negative direction of the slope of the line drawn from these points suggests that natural thinning is occurring in the established stand for size classes between 0 and 20 cm. This relationship is consistent with the one found by



White (1985) for hardwoods in the Harvard Black Rock Forest. White was able to show a pattern of lower densities with an increasing size of survivors in plots, which experienced almost no recruitment, monitored for a fifty three year period. Figure 5d shows that at the largest mangrove size class (20-25 cm), density does not decrease, but remains relatively constant at .1 trees/m<sup>2</sup>. The likely explanation for this behavior is that at >20cm, mangroves have occupied the maximum amount of canopy/root space possible, therefore thinning no longer occurs. A larger sample size of trees in that size class, and larger ones would be required to conclusively determine if spacing was in fact not changing at all, or was changing at a lower rate (a less steep slope). Christiansen (1980) found that thinning in Pine forests reached a minimum (but that density induced mortality was still thought to occur), due to limitations in height and net biomass found in mature pines. In the context of mangrove colonization on the island, the spacing of trees >20 cm suggests that stand development on some parts of the island has climaxed (where photosynthesis ≤ respiration), and that those trees have reached maturity in the fifty nine years since mangroves were introduced.

Since colonization has occurred in different parts of the island at different times, as new propagules arrive and establish themselves, the structure of these stands can be expected to vary considerably. Christiansan (1980) separated stand development into four distinct phases. 1) Rapid recruitment and growth owing to available resources and space, 2) competition coupled with net production (-3/2 thinning slope of density vs biomass), 3) reciprocal growth in relation to thinning and 4) population degeneration. In a colonizing area with an abundant seed source (such as in the established site), thinning can be expected to take place early on, due to high initial propagule density. As a result, this type of stand should have a more uniform height, and tree diameter. Stands with a more limited seed source, or ones with un-favorable propagule transport factors can be expecting to begin thinning at a later period, after the trees have obtained a larger size class. A more uneven aged stand is likely result in this type of situation, with wider variance of growth behavior among individuals (since the size (age) at which their neighbors begin to constrain growth is variable). Histograms of plots measured in the established and just-established site support this argument (Figure 8). The distribution of size classes is varied in the grass portion of the establishing site, and bi-modal in the just-established. The densities are so low at these sites (.09/m<sup>2</sup>, and .13/M<sup>2</sup> for trees with an average diameter < 5 cm), thinning is not likely to occur for sometime. The mean spacing for tree diameters less than 5 cm in the fringe portion of the establishing site, (figure 5b), is higher than the spacing found in the established site. This again would indicate that this stand is less developed, and that thinning is not as intense in the establishing site, because trees of the same size as those in the established site have more space between thier neighbors.



## Conclusion:

Established mangroves have been seen on the islands of Moorea, Tahiti, Bora-Bora, and Manihi. To date, no survey of nearby island chains, such as the Tuamotoes, or the Marquesis Islands has been done. But these island chains, and others are well within the dispersal range of *R. Stylosa* (Woodroffe, 1988). These island chains share similar flora and fauna, and are within the same climatic regime. Thus we can expect the pattern of *Rhizophora* colonization to be similar in all of these places.

In Moorea, herbivory could play a considerable role in limiting the distribution of mangroves around the island. Transplants done suggest that where herbaceous matter is limited, or lacking, seedling establishment is improbable. All of the areas currently colonized have *Paspalum vaginatum* growing in, or near the colonization site (Cavaloc, 1987). This suggests the *P. vaginatum* could be a preferred food choice for Tupa, although at this point, it is largely speculative. Interspecies competition is a likely explanation for the presence of bare grasses patches found beneath the mangroves. The pattern is concentric, and centered directly beneath the tree. The size of the pattern was shown to correlate well to an increase in the diameter of the tree, and was not found beneath the four hundred seedlings counted in the study area. Four hypotheses suggested to explain this relationship are allelopathy, herbivory, nutrient competition, and shading.

Acknowledgments: I would like to thank all the students and faculty in IB158 for help in this project. Carla D'Antonio, for her endless enthusiasm and encouragement. Stuart Cohen, and Larry Vaughn for their infinite patience, and assistance, and last but not least, Frank Murphy, the Gumb Biological Station Manager. Without help from these individuals my project would not have been possible

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**A Comparison of the Effects of Agriculture and  
Development on Two Bays in Moorea, French Polynesia**

**and**

**The Effects of a Water Outflow on a Nearshore Coral  
Community**

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IDS 158  
Fall, 1992



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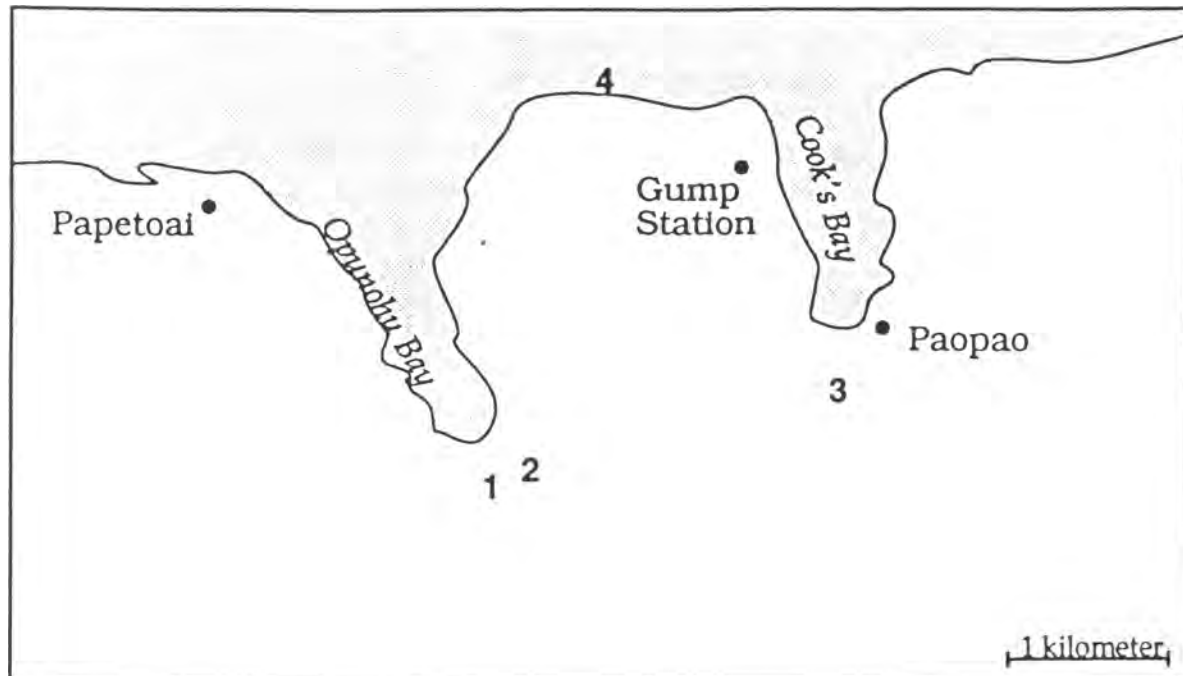
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**Part II: The Effects of a Water Outflow on a Near Shore Coral Community**

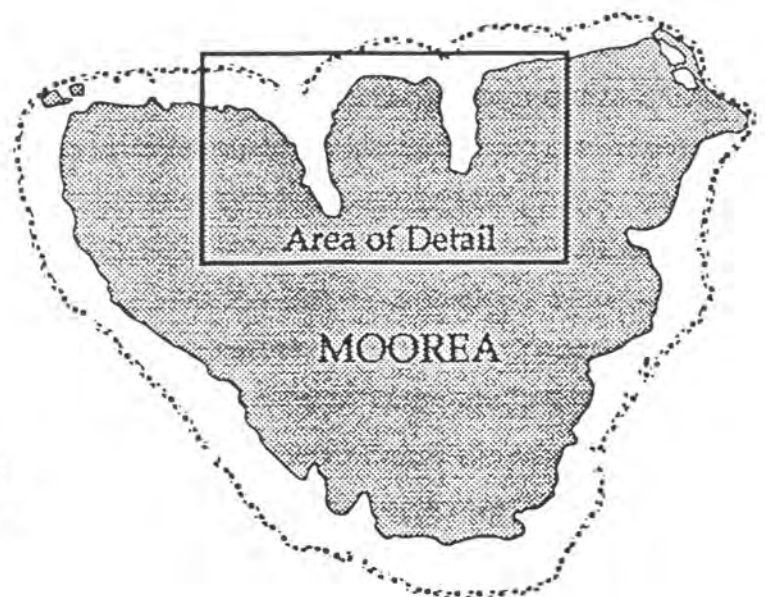
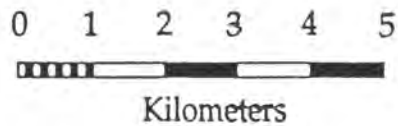
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## Opunohu Bay and Cook's Bay, Moorea, French Polynesia



- 1 Opunohu Bridge 1 site
- 2 Opunohu Bridge 2 site
- 3 Cook's Bay site
- 4 Coral Diversity site



S. London

Figure 1, Study Site Location

**Title: A Comparison of the Effects of Agriculture and Development at Two Bays on Moorea, French Polynesia**

**Abstract:**

Development and agriculture in Cook's Valley, Moorea, French Polynesia is increasing the sediment load in the riparian systems that feed into Cook's Bay. The development, agriculture, and sediment loading in the Cook's Bay drainage basin were compared with the same in the Opunohu Bay basin as they are similar in size, topography and non-agricultural vegetation. Pineapple plantations in Cook's Valley contribute to an increase in the amount of sedimentation and smaller particle size in Cook's Bay in comparison to amount and size of sediment in Opunohu Bay.

**Introduction:**

**Question:** How does development and agriculture affect sediment loading in the major tributaries of Opunohu Bay and Cook's Bay?

**Hypotheses:** We believe Cook's Bay will have more sediment than Opunohu Bay due to greater development and agriculture, specifically pineapple plantations, in Cook's Valley.

Agriculture and development often produce many unwanted and unforeseen byproducts, including toxic chemicals, land degradation, and loss of vegetative matter to bind soils, which increases sediment loading in fluvial, estuarine and marine systems. Throughout the tropics, as development has increased, the health of surrounding coral reefs has suffered, as documented in Thailand, the Caribbean and Hawaii (Rogers 1990, Hubbard, 1986, Brown et al 1986). This degradation reaches critical levels because corals display an extreme sensitivity to fluctuations in water temperature, salinity, nutrient levels, and sediment, all of which are affected by development and agriculture (Dodge and Valsnys 1977). Sedimentation can also cause severe damage to marine ecosystems by reducing the light available for photosynthesis, which affects the entire food chain (Rogers 1990). In order to understand the harm sedimentation can have on a reef environment, it is crucial to quantify how much and what type of sediment is flowing into a system.

### **Study Area:**

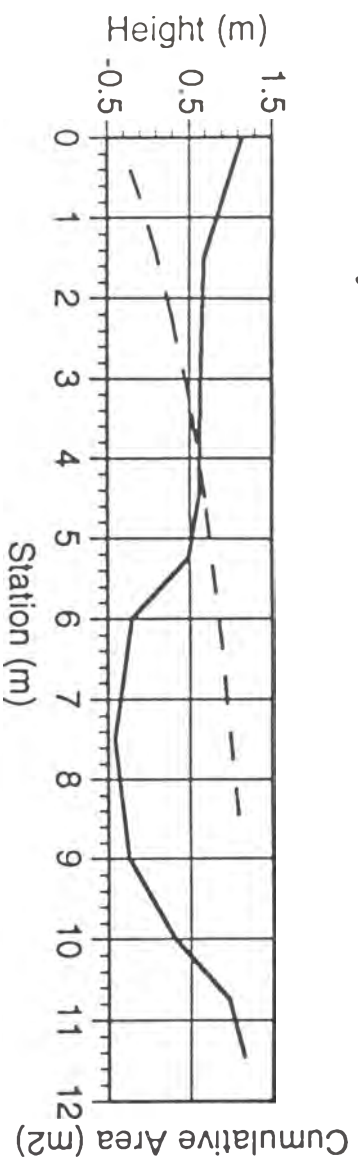
This research took place in the two main drainage basins on the northern half of the island of Moorea, in French Polynesia (*Fig.1*) . These two sites are compatible for comparison because they are physically similar in both geography and non-agricultural vegetation. Opunohu Bay can act as a control for Cook's Bay because the amount of development is less in Opunohu Bay and the type of agriculture, specifically pineapple plantations in Cook's Bay, is significantly different (Galzin 1990). Therefore, the two drainage systems offer an ideal situation in which to study the effects of development and sedimentation.

In the Opunohu Bay system, two tributary streams were sampled because the confluence of the two streams is within the tidal influence and therefore an unsuitable measuring station. The gauge sites were located at the first and second bridges on the Belvedere road (*sites 1 and 2, Fig.1*). For a total Opunohu reading, the data from both sites was added together. In the Cook's Bay system a site on the main stream just above the tidal influence and below the last tributary was selected. This gauge site was located behind the public works building and opposite to the main soccer field (*site 3, Fig.1*).

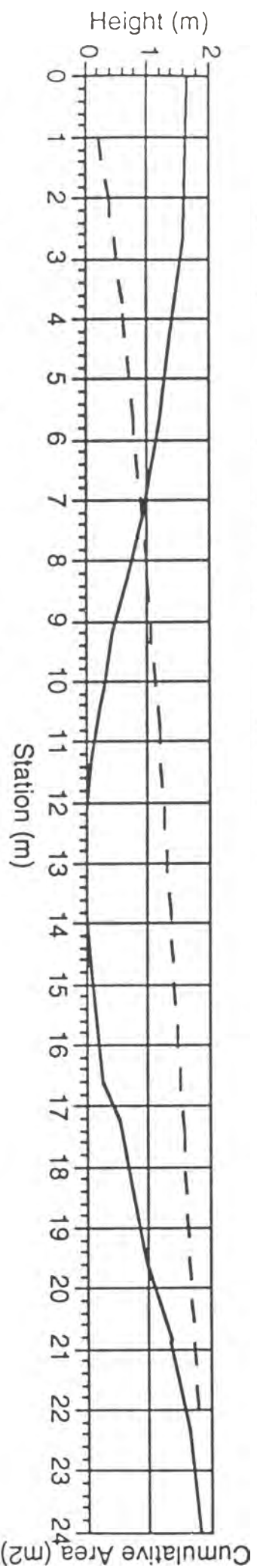
### **Methods and Materials:**

Standard USGS hydrology procedures were followed in the stream analysis (Leopold 1976). Using a Top Con model GTB-35 surveying instrument, stream cross sections at each gauge site were surveyed, including the height and location of each gauge (*Fig.2A*).. The data was collected between October 13, 1992 and November 27, 1992, the latter time of which falls at the beginning of the rainy season on Moorea. Baseline readings were taken at various times of day to measure daily hydrological fluctuations, while storm event readings were taken throughout each storm, as well as after the storm. The velocities, stream height data and water samples for the three sites were collected during clear weather to establish base-line conditions for the streams. After obtaining the baseline data, the majority of the readings were taken when the weather indicated possible rainfall.

### Cook's Bay Cross Sectional Area with Cumulative Area



### Opunohu Bridge 1 Cross Sectional Area with Cumulative Area



### Opunohu Bridge 2 Cross Sectional Area with Cumulative Area

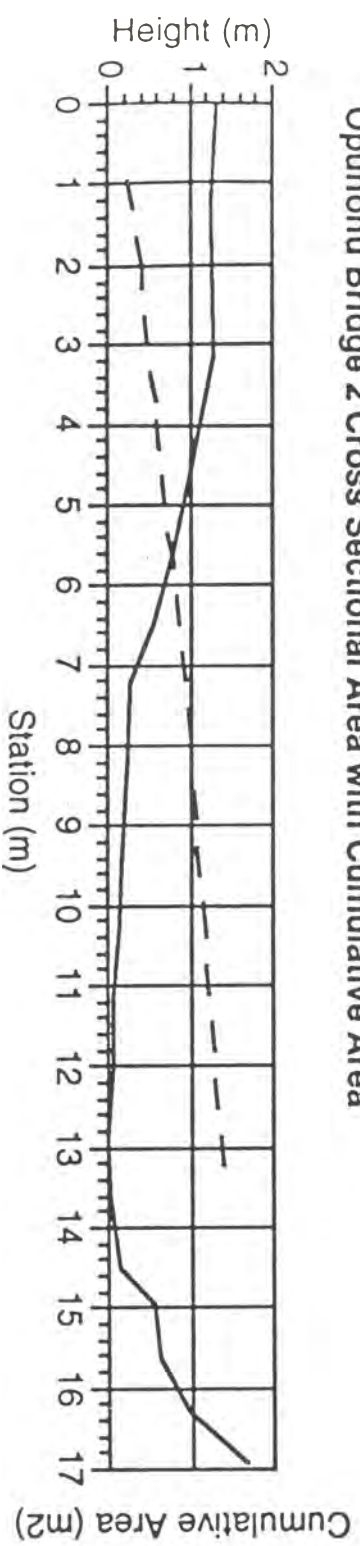


Figure 2A



The velocity was measured by two different methods. The first method entailed using an OTT C-2 current meter with a #2 propeller placed at three spots across the stream representing left bank, right bank, and center. These velocities were used to calculate an average stream velocity by taking into account the relative volume of each section (Leopold et al 1964). The second method used "the orange peel test," which entailed tossing an orange peel into the current, ideally the center of the flow, and measuring its travel time along a pre-measured distance. The velocity in m/sec was then multiplied by 0.8 to represent average cross-sectional velocity (Leopold 1976). For each sample, three ten-meter interval readings were taken which were later averaged for a more accurate velocity reading. Both methods were used to ensure accurate velocity measurements.

Surface water samples were collected at each site for suspended sediment analysis. A wide-mouthed plastic bottle was placed into the stream at its center of flow at 10 cm deep and the collected sample transferred into a plastic 1500 ml bottle. The amount of sediment was measured by filtering the water samples through pre-weighed Wattman #1 filter papers and calculating the remaining sediment with an electronic scale. The net and gross weights were both taken after the papers were baked at 38° C for one hour. Because of measurement errors most likely caused by humidity in Moorea, all sediment samples were re-weighed using equipment in the Terry Chapin laboratory at U.C. Berkeley.

To examine sediment loading into the two bays, calculations were made to establish the base flow and daily (non-storm) total sediment input into each bay, followed by sediment loading from storm events. Daily baseline inputs were derived from estimations of base flow discharge rates ( $\text{m}^3/\text{sec}$ ) and total suspended sediment concentration ( $\text{mg}/\text{l}$ ) extrapolated for a 24-hour period. This calculation assumes no diurnal fluctuations in these two parameters during non-storm conditions for the period of this study. Storm inputs were calculated from repeated measurements of discharge rates and total suspended sediment concentrations during the storm event and extrapolated for the period of time representative of the storm duration.



The calculation of discharge rates and total sediment input involved a four step process. First, cumulative area curves were calculated for each cross section from the field survey data. Second, discharge rates ( $\text{m}^3/\text{sec}$ ) were calculated by taking the cross-sectional area at a given water height and multiplying it by the measured velocity. Third, total discharge ( $\text{m}^3$ ) over a given period of time was calculated by multiplying discharge rate by time. Finally, total sediment load (mg) over a given period of time was calculated by multiplying the total discharge by the total suspended sediment concentration (mg/l). These calculations were conducted for the storm events and the baseline readings to provide a total sediment load figure for a given period of time.

The difference in particle size distribution was assessed qualitatively by the passage of suspended sediment through Wattman #1 filter paper, which has a filter size of 11 microns( $\mu$ ). If the filtrate was clear to the eye then particle sizes were determined to be greater than 11 $\mu$ . If the filtrate had suspended sediment noticeable to the eye, then it was determined that a fraction of the suspended sediment was less than 11 $\mu$  in size. The percent falling into this size class was not determined quantitatively.

The volume of each drainage basin was calculated by using topographic maps and computer analysis.

Finally, Secchi disc readings were taken at the two main bridges of each bay to show variation in water clarity. The readings were taken from the middle of each bridge and measured to the nearest cm.

## Results:

### *Water Discharge Rates*

Water discharge rates can be summarized as follows:

Water Discharge Rates	Opunohu Bay	Cook's Bay
Average Baseline Flow	0.211 m <sup>3</sup> /sec	0.987 m <sup>3</sup> /sec
Daily Baseline Flow Average	18230.4 m <sup>3</sup>	85276.8 m <sup>3</sup>
Range of Flow:		
high	5.81 m <sup>3</sup> /sec	4.41 m <sup>3</sup> /sec
low	0.23 m <sup>3</sup> /sec	0.72 m <sup>3</sup> /sec
Total Storm Discharge	106229.64 m <sup>3</sup>	120134.04 m <sup>3</sup>
(storm duration: 14 hrs and 10 min)		
Storm Discharge	182107.95 m <sup>3</sup>	205944.07 m <sup>3</sup>
(24 hour approximation)		

*Figure 3A*

The baseline flows during non-storm events vary greatly in each bay since Cook's Bay is significantly larger than Opunohu Bay. However, storm discharge rates are similar. Figure 4A shows the marked increase in water discharge during storm events.

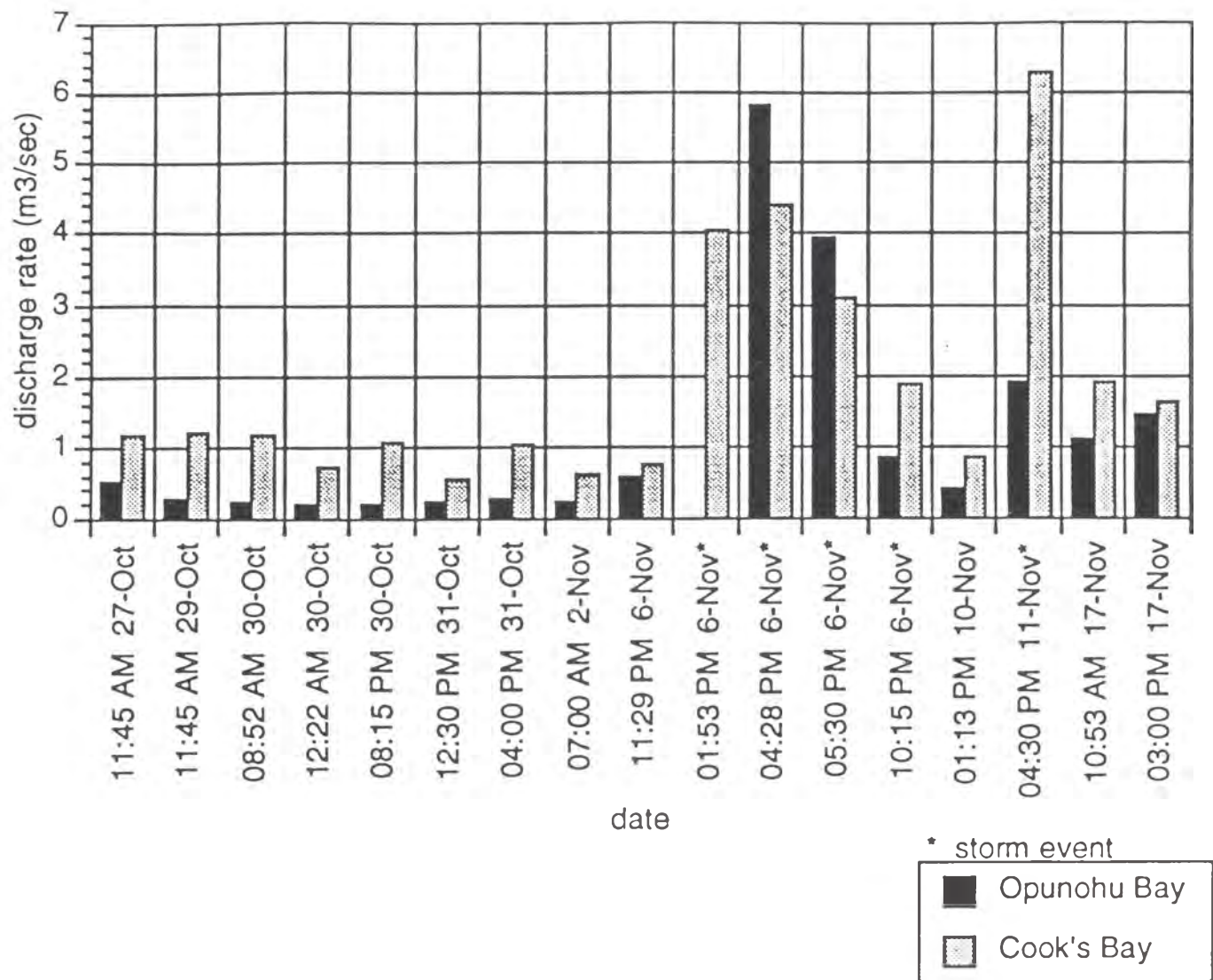


Figure 4A: Water Discharge Rates from Opunohu Bay and Cook's Bay,  
October 27, 1992 to November 17, 1992

### *Sediment Loading Rates*

Sediment loading rates can be summarized as follows:

Sediment Loading Rates	Opunohu Bay	Cook's Bay
Average Baseline Load	.081 mg/l	.067 mg/l
Total Average Daily Load	1.48 kg/day	5.71 kg/day
Range of Load:		
high	.456 mg/l	.674 mg/l
low	non-detectable	non-detectable
Total Storm Load	35.73 kg	35.28 kg
(storm duration: 14 hrs and 10 min)		
Storm Load	61.25 kg	60.48 kg
(24 hour approximation)		

*Figure 5A*

The baseline sediment loads are similar between the two bays, as are the storm load outputs. The greatest variation falls at the average daily baseline load. Figure 6A shows the dramatic rise in total suspended load during a storm event, as well as the similarities at baseline readings.

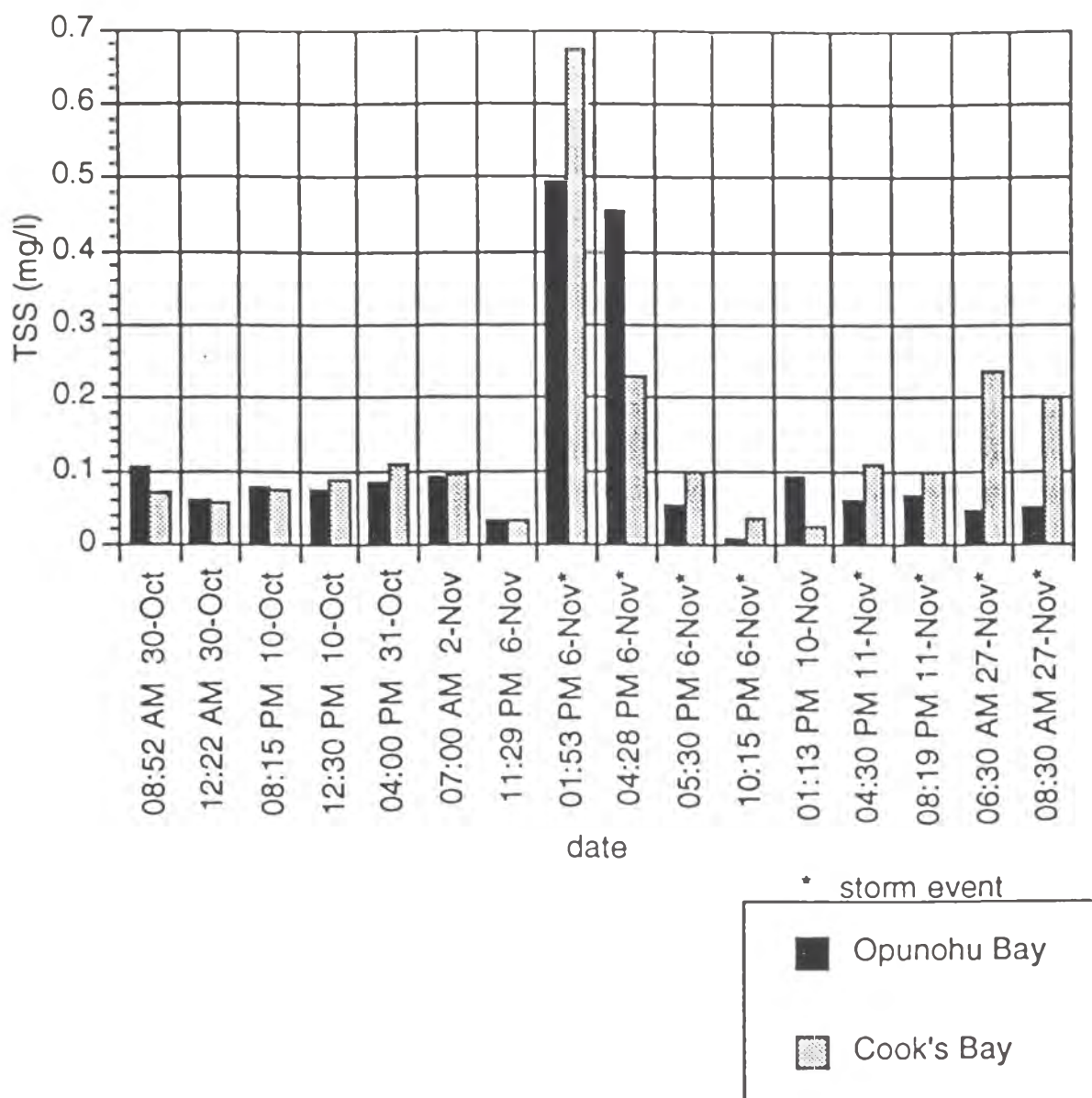


Figure 6A: Total Suspended Sediment Concentration (mg/l) in Cook's Bay and Opunohu Bay Primary Streams.

### Particle Size Distribution

During storm events, particle size of suspended sediment between the two bays varied, but during baseline readings, they were the same (negligible). Cook's Valley storm event sediment consistently produced a cloudy filtrate, while sediment from Opunohu storm events did not flow through the filter paper and the filtrate was consistently clear to the eye. Therefore, some of the sediment from Cook's Bay must be smaller than the filter paper size of 11  $\mu$ . A particle is considered to be clay by the



USDA if it is  $<0.002$  mm, which is the range within which sediment from Cook's Bay falls (Cox 1964).

The coloration of the sediment between the two bays also varied. Sediment from Cook's water samples was an orange-red color, like the fields in the pineapple plantations, while sediment from Opunohu Bay was a rich brown color with noticeably larger particulate matter.

#### *Secchi Disc Readings*

Secchi disc readings indicated that Cook's Bay was not as clear as Opunohu Bay (*Fig.7A*) . In only two instances during storm events were the readings exactly the same, and Cook's Bay never fell below Opunohu Bay.

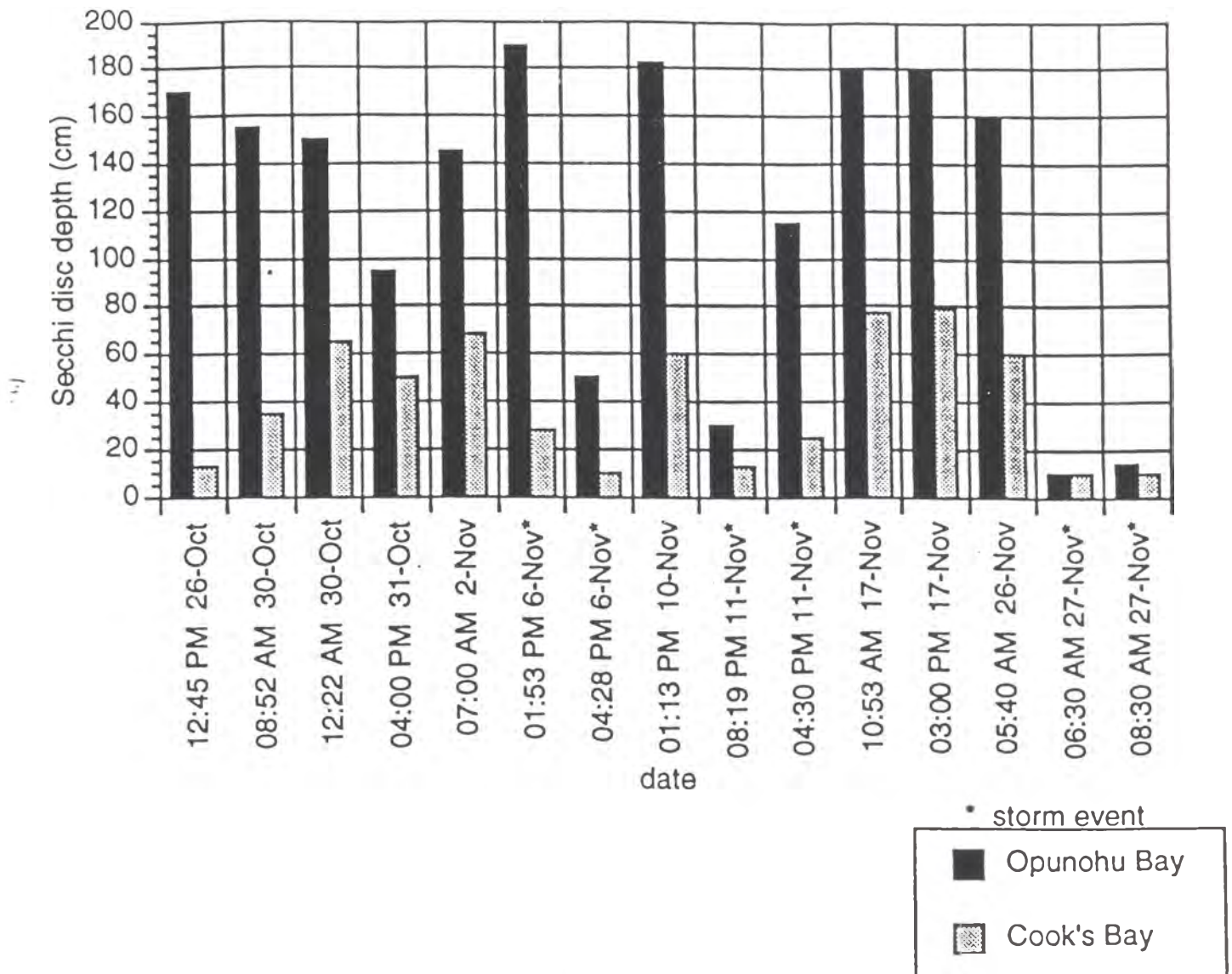


Figure 7A: Secchi Disc readings at Cook's Bay and Opunohu Bay

A regression for corresponding secchi readings between the two bays shows the range for Cook's Bay is only from 10-60 cm, while Opunohu Bay varies from 10 cm to 190+ cm (clear to the bottom) (Fig.8A). The linear equation between the points indicates a strong relationship between each bay and the fluctuations in clarity. As Cook's Bay increases in sedimentation, so does Opunohu Bay. Yet, the range in Cook's Bay is significantly smaller than the range for Opunohu Bay. Clarity at the Cook's Bay bridge is significantly less than at the Opunohu Bay bridge (Wilcoxin Signed Rank Test one tailed  $T=0$ ,  $n=16$ ,  $0.0005$ ).

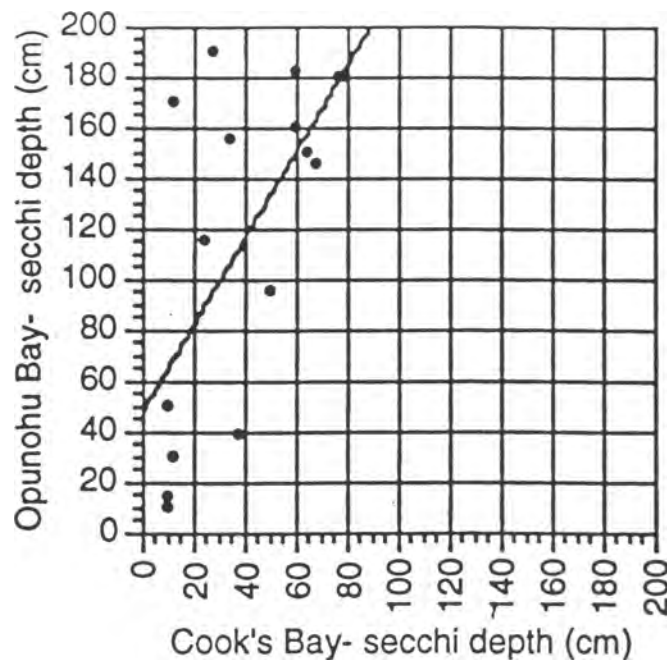


Figure 8A: Regression Chart for Secchi Disc readings at Opunohu Bay and Cook's Bay.

#### *Drainage Basins*

The drainage basins, though similar in scale, have enough variation in size and geomorphology to effect the hydrology of the bays. The drainage basin of Cook's Valley is  $7.59\text{km}^2$ , which is half that of Opunohu Valley at  $15.98\text{ km}^2$  (Ferris 1992). Cook's Valley is much narrower with steeper slopes while Opunohu Valley is broader with gentler slope.

#### *Agriculture and Development*

Development is dramatically higher around Cook's Bay (Fig.9A). The two bays are both used for agricultural purposes but differ greatly in type of crop being grown (Fig. 10A). The differences between the two bays are greatest in the livestock and pineapple categories. Two significant aspects of pineapple agriculture which were observed are: frequent use of ditches for drainage and complete lack of ground cover in the fields.

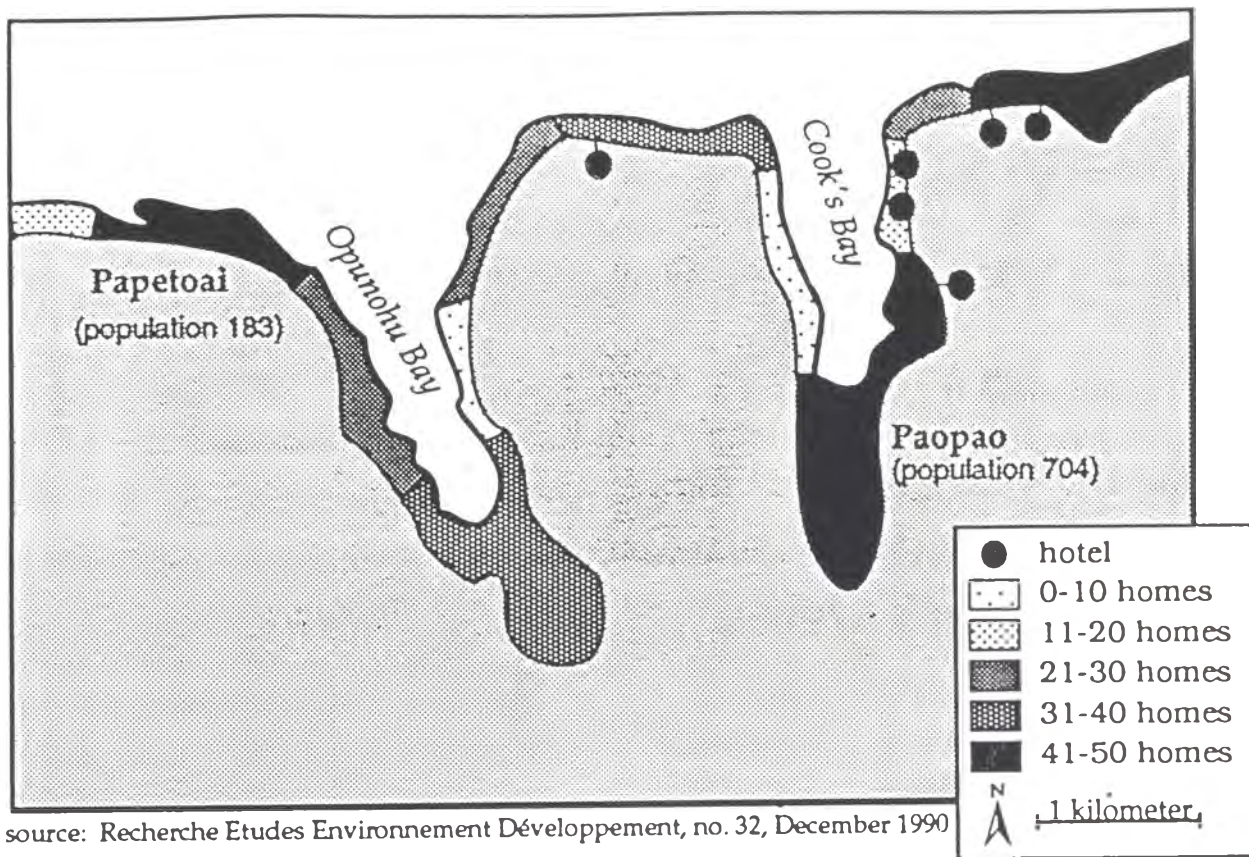


Figure 9A: Residences Around Cook's Bay and Opunohu Bay



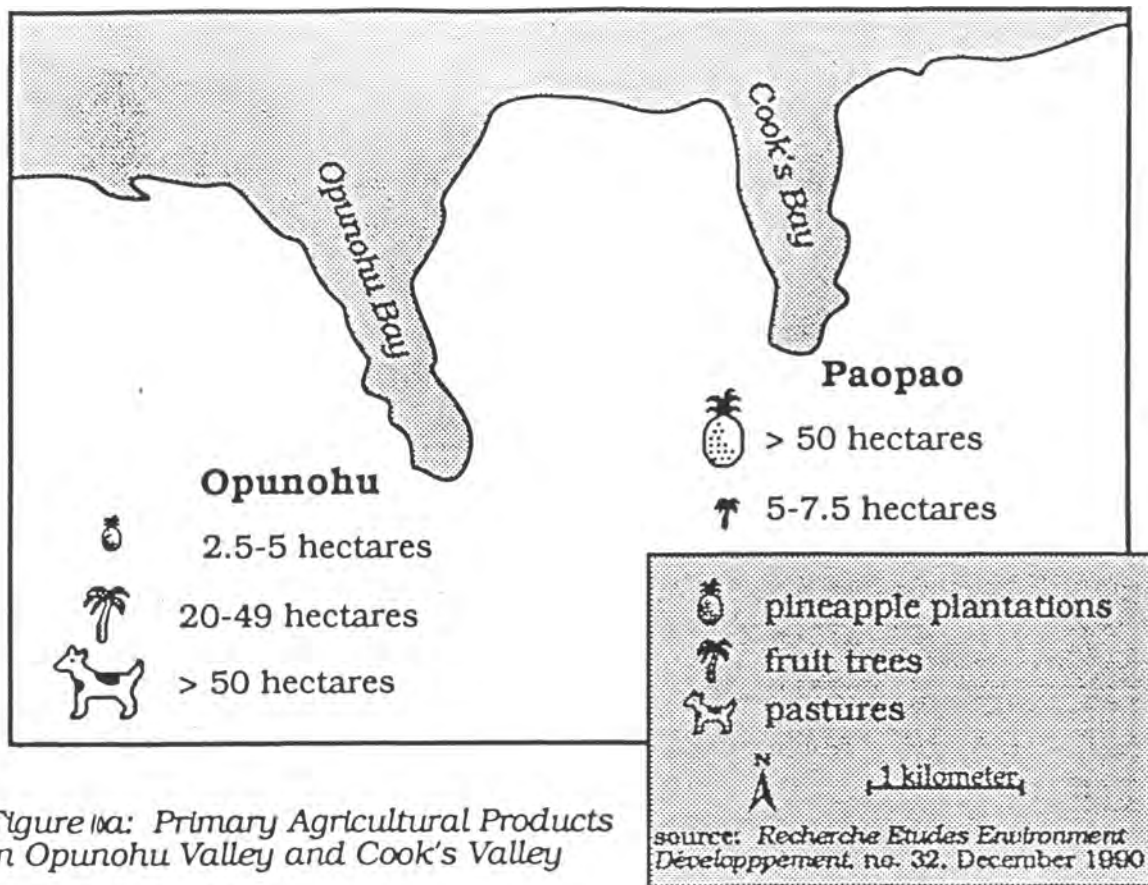


Figure 10a: Primary Agricultural Products in Opunohu Valley and Cook's Valley

#### The November 6 Storm Event

The November 6 storm event was the largest storm during the study. Readings were taken over a ten hour and fourteen minute period, which includes the storm surge in each bay and the return to baseline conditions (Fig. 11A). Despite differences in the discharge rates, the actual amount of sediment that flowed into each bay from the monitored streams during the storm event was almost equal: Opunohu= 35.73 kg, Cook's= 35.28 kg (Fig. 3A).

Comparing the baseline discharge rates to the storm discharge rates shows that the increase in Cook's Bay was only 2.4x while Opunohu Bay increased 10x (Fig. 3A). The baseline sediment loading rates compared to the storm sediment loading rates show that the increase in Cook's Bay was only 10.6x while Opunohu increased 41.4x (Fig. 5A).

The data collected is not precise enough to determine if there were any differences in time or duration of the storm outflow surge (Fig. 12A). More frequent readings within the storm event as well as synchronized



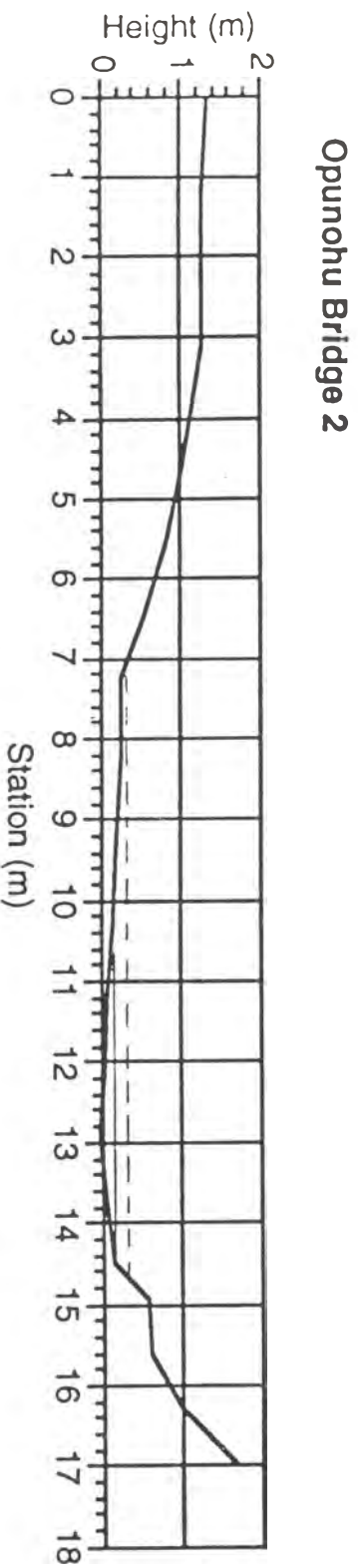
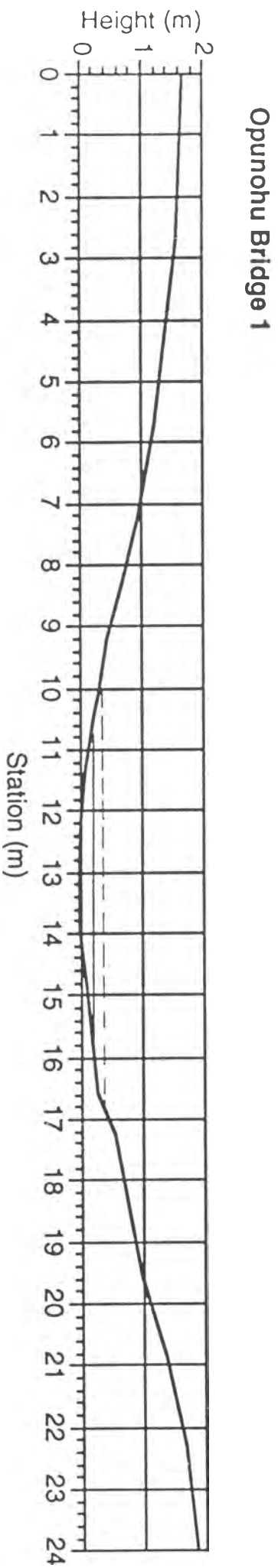
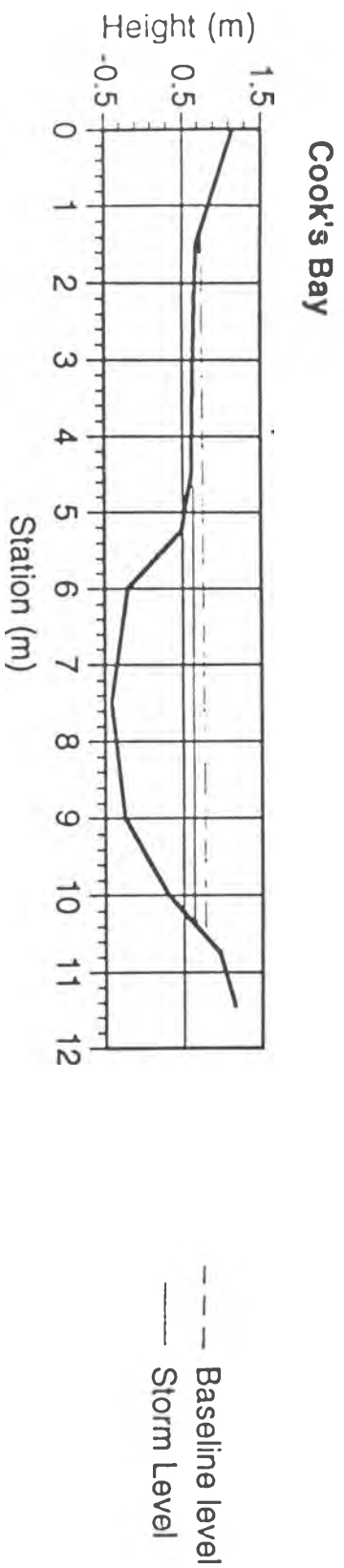


Figure 11A: Cross Sectional Areas of sites with average baseline and storm levels.

readings between the bays are necessary to make an analysis of the surge.

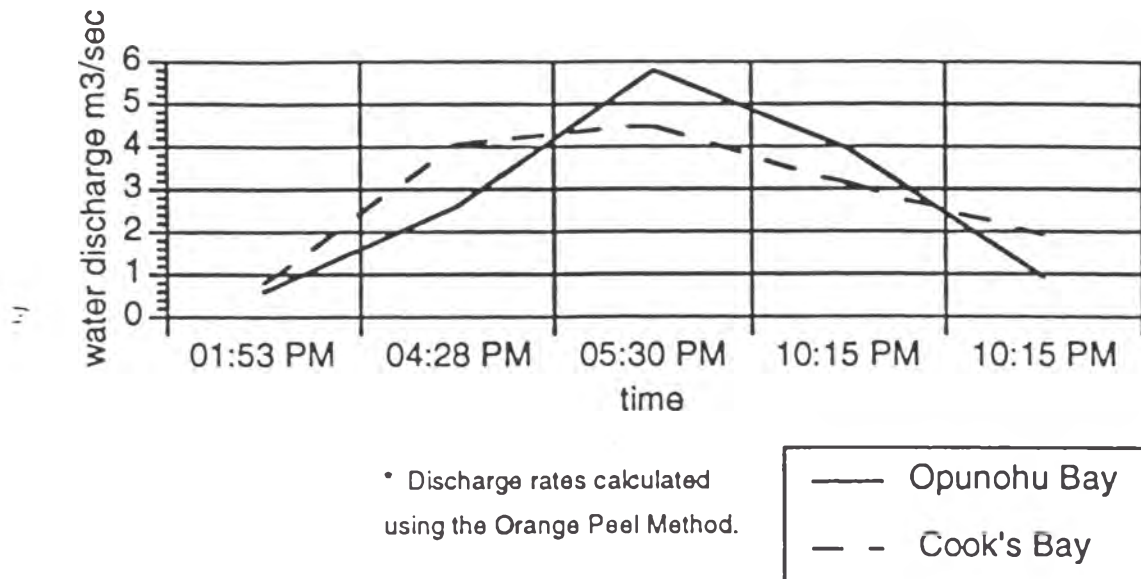


Figure 12A: Stream Discharge Rate over time for Nov. 6, 1992.\*

## Discussion:

### *Water Discharge Rates*

The fact that the water discharge rate ( $\text{m}^3/\text{sec}$ ) in Cook's Bay is much greater than Opunohu Bay's discharge rate at baseline, but equals out during storm events can be explained in five non-exclusive ways.

First, the differing geomorphology of the drainage basins leads to a greater geologic retention time in Opunohu Valley and a shorter geologic retention time in Cook's Valley. This is because Cook's Valley drains more rapidly because the slopes are steeper and the drainage basin is half the size of Opunohu Valley. Second, the greater amount of development in Cook's drainage basin creates more impermeable surfaces, which lead to greater overland run-off and consequently a shorter retention time during both storm and non-storm measurements. This increased overland run-off leads to further loss of topsoil which also reduces retention time. Third, the greater percent of pineapple agriculture in Cook's Valley suggests a much more frequent use of trenches for drainage, which in turn implies a more rapid drainage. The

trenches in the land, carved out by the pineapple plantation owners, may increase the rate the water flows through the valley since they provide numerous channels for collecting and removing the rainfall that otherwise would move as overland or subsurface flow to the stream.

Fourth, the lack of ground cover associated with pineapple fields in Cook's Valley would somewhat increase the rate of overland flow. In Opunohu Valley, greater plant cover decreases runoff because plants absorb the water or catch water on their leaves that later evaporates. Finally, the equalization during the storm event could be explained if the majority of the storm water was traveling overland and therefore not related to geologic retention.

Rain intensity and differences in total rainfall may also be an important factor affecting water discharge rates. Rain data from the Service Economie Rurale in Opunohu Valley did not record intensity, however, it did record actual amount of rain per storm. The weather station lies half way between the two bays at the Service Economie Rurale (Agricultural School), so the amount of rainfall measured can, with fair accuracy, be applied to both bays. Nonetheless, rainfall is sporadic on Moorea as it can rain in one bay without any precipitation in the other. This is an area which could be further documented with a need for better precipitation records.

### *Sediment Loading*

The fact that both streams have similar total sediment output (mg) during a storm event, yet very different sediment output during baseline readings can also be interpreted in several non-exclusive ways. First, the large particulate detritus observed in Opunohu sediment, but not in Cook's sediment, may have been lifted from the bed load to the suspended load only during storm events. These large particles increase the weight of the sediment load, but quickly fall out of the water column once a storm has subsided. Second, during baseline measurements, the greater retention time due to geomorphology, lack of development or agriculture in Opunohu Valley (see water discharge discussion) could also reduce sediment load. Finally, the higher baseline sediment loading

in Cook's bay could be explained by the higher baseline velocity in Cook's Bay.

#### *Particle Size Variations*

A possible explanation for the color difference in the sediment is that there is exposed and erodable topsoil in Cook's Valley due to pineapple plantations. Opunohu Valley has minimal exposed topsoil and more organic material, which means less potential for erosion. (Poole, pers comm. 1992). Also, clay particles are more likely to be found in areas where there is exposed topsoil, like Cook's Valley (Cox 1964).

#### *Secchi Disc Readings*

After every major storm event, both bays form a visible sediment plume. Yet, from our visual observation and from talking to the local people, the sediment plume almost always remains in Cook's Bay for a longer period of time and is larger and more obvious. The secchi disc readings also support this observation.

Since Opunohu Valley suspended sediment does not visibly contain the finer ( $<11\mu$ ) sediment, deposition of suspended sediments more likely to occur sooner and thus closer to the mouth of the stream. Because of the fine grain fraction present in the Cook's Bay suspended sediment, deposition takes longer and the plume therefore remains for a greater time period and extends further into the bay as currents transport it. Therefore, the aerial extent of potential impact is likely greater in Cook's Bay and, likewise, the nature of the impact may differ due to the different grain sizes.

#### **Conclusion:**

Cook's Bay and Opunohu Bay are an especially interesting comparison because the development and agricultural practices of the two bays differ greatly, yet they are in close proximity to each other. The physical characteristics of the bays have many similarities, including abundance of rainfall, orientation to the storms, prevailing winds, and non-agricultural vegetation. Opunohu Bay provides a natural control site for Cook's Bay to show that development and agriculture, in

particular pineapple plantations, do affect the sedimentation rates and characteristics in the two bays.

The hypothesis, which predicted greater sedimentation in Cook's Bay due to agriculture and development in the valley was basically supported in that overall sediment deposition is higher in Cook's Bay. There were three aspects of the results which were surprising. First, the significance of agricultural type, especially pineapple, was important in determining suspended sediment rates. Second, particle size affected both and plume characteristics. Finally, the differences in baseline readings and the similarities in storm event readings was especially surprising.

These results can and should be analyzed to show the effects of sedimentation on an entire bay ecosystem. Our study provides only the groundwork for understanding the sedimentation patterns in Cook's Bay and Opunohu Bay, Moorea. Further study is necessary to understand the complex hydrology in each bay where tidal currents, wind currents, and geomorphology affect water flow and sediment distribution. Further research could include: more accurate rainfall data, sediment cores of the bays, the bathymetries of the bays, water column samples from the bay and more storm event replicates.

The significance of this issue should not be overlooked or confined to Moorea, French Polynesia as development is proceeding unchecked in many areas where coral reefs now or once thrived.



# **Title: The Effects of a Water Outflow on a Near Shore Coral Community**

## **Abstract:**

Development has a great effect on the near shore coral communities in the vicinity of water outflows. Heavy sedimentation is associated with few coral species and low coral abundance (Rogers 1990). The Wilder dock outflow area in Moorea, French Polynesia shows a lower coral abundance of three growth forms as compared to an adjacent area unaffected by the outflow. The sedimented zone is characterized by more dead coral heads, more algae, and live coral heads that are small in size and mostly massive-type species. The area just beyond the plume, though affected, shows a much greater similarity to the control site.

## **Introduction:**

**Question:** How does an individual stream mouth and the associated sediment load affect coral abundance and diversity in the immediate outflow vicinity in comparison to an area with no outflow?

**Hypotheses:** There will be greater coral mortality, less coral abundance and lower species diversity in an area affected by a land outflow in comparison to an area where no outflow is present.

The Wilder dock and neighboring outflow (*Fig. 2B*) offered the opportunity to study a simple microcosm related to the study sites of the primary project. By comparing an affected site to an unaffected site, the localized affects of sedimentation on coral communities can be examined. These results reinforce the importance of understanding and quantifying the affects of development on aquatic systems. Furthermore, a large body knowledge in this area is required to help shape local development policy and regulation.

## **Methods and Materials:**

The secondary project site was located at the Wilder dock about 1 km west of the Gump Biological Station (*Fig. 1*). This site was chosen

because the pier, acting as a barrier, creates a clear distinction between affected and unaffected coral communities. The site was divided into two equal 60 x 100m areas, one on either side of the dock. Transects were established running parallel to the dock and spaced every 10 m. Along these transects all live and dead corals were counted within 1m in either direction of the transect tape. The corals were categorized by growth form (massive, branching, encrusting, fungiid), size (large, medium, small) and living vs. dead. The size categories were divided as follows: <20cm=small, 20-60cm=medium, > 60cm=large. The area of the sediment outflow plume was also measured.

The data was collected over a period of four days and the transects were swam by one person to reduce observer variation. All data was collected on an underwater slate and then transcribed into a notebook.

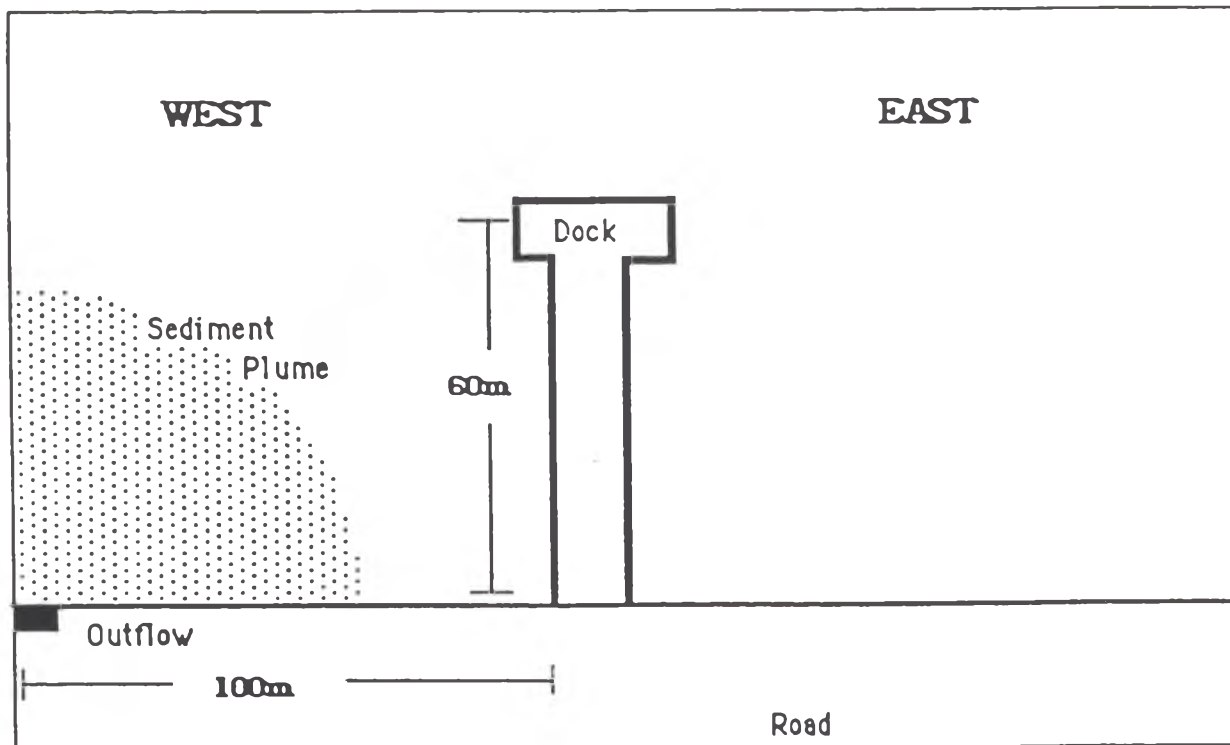


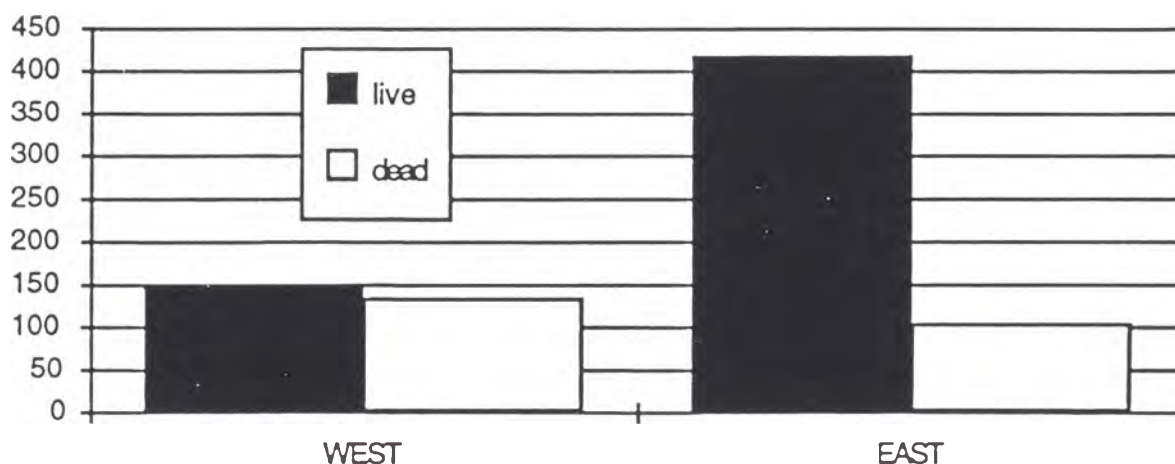
Figure 2B Wilder Dock and Sediment Outflow

## Results:

The total number of coral heads found on the outflow side of the dock (west) was considerably less than the unaffected side (east). When the heads were sub-divided into live and dead categories, the two sides contained similar numbers of dead heads while showing greater variation in live heads (*Fig. 3B*).

Furthermore, the east side showed a much greater difference between the number of live and dead heads whereas the west (outflow) side had almost equal numbers of live and dead heads (*Fig. 3B*).

Using the chi-squared test, the null hypothesis was tested: The proportion of live and dead coral heads is the same on both sides of the dock ( $\chi^2=66.83$ ,  $df=1$ ,  $p<0.001$ ). This shows that a statistical variation exists.



*Figure 3B Coral Heads at Wilder Dock*

Breaking the data down into size categories reveals that the two sides contained both similarities and differences (*Fig. 4B*). On both sides, small heads were the most abundant live size observed, followed by medium size heads, while large live heads were least common. A slightly different trend was found in the occurrence of dead heads as both sides had the greatest number of medium heads, followed by large size heads, while small dead heads were the least common.

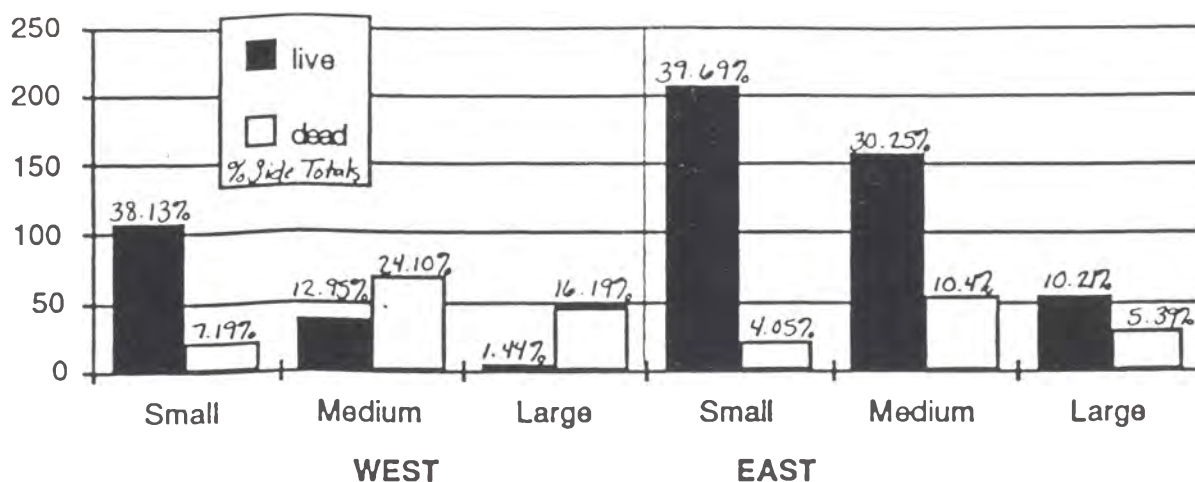


Figure 4B Coral Mortality Comparison by Size

The differences between the two sides can be best expressed as percentages of size totals (Fig. 4B). The east side had only 19.8% dead heads of all size classes combined, while the west (outflow) side had a total of 47.5%. These percentages also show that most of the live heads on both sides are small.

The data, when divided by growth forms, again shows variability between the two sides of the dock. The massives, branching and encrusting were represented on both sides, but there was an absence of Funglids on the west side. By percentage, the two sides are distinctly different; the east side (control area) contains a majority of branching species (60.1%) while the west side (affected area) contains a majority of massive species (58.5%). The large difference in percentage of encrusting corals is also worth noting (Fig. 5B).

Using the chi-squared test, the null hypothesis was tested: both sides will have the same distribution of growth forms ( $\chi^2=143.4$ ,  $df=3$ ,  $p<0.001$ ). This again shows that there is significant variation.

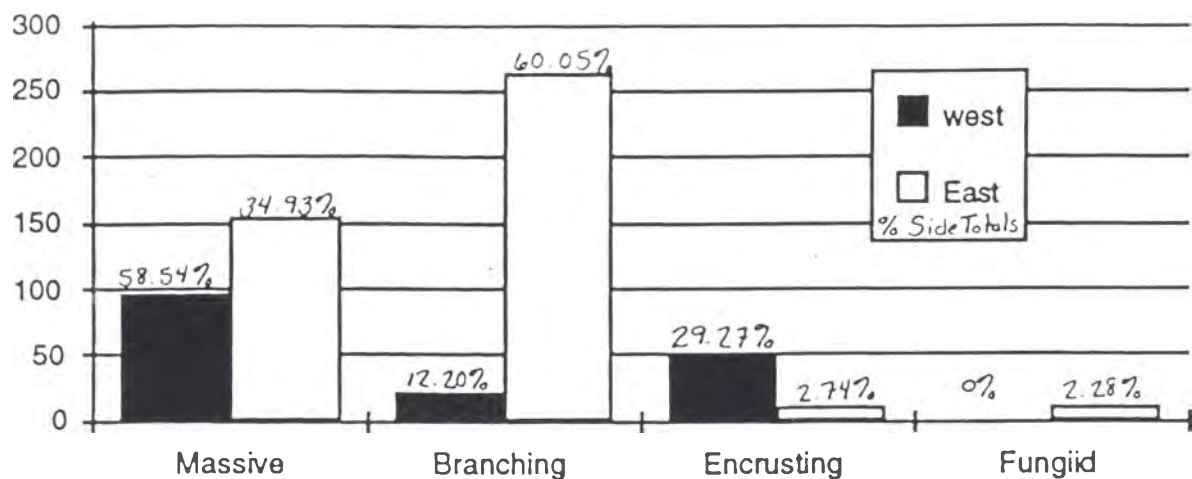


Figure 5B Coral Growth Form Comparison

Finally, the numbers of live coral heads in the area outside the sediment deposition zone on the west (outflow) side was compared with the number of live coral heads in the corresponding area on the opposite side of the dock. The area on the west (outflow) side contained one half as many live heads as the opposite area on the east side.

However, when calculated as heads/m<sup>2</sup> in the non-deposition area of the west side vs. heads/m<sup>2</sup> in the entire east side, the two numbers were fairly similar: non-deposition west = .05heads/m<sup>2</sup> while total east side = .07heads/m<sup>2</sup> (Fig. 6B)..

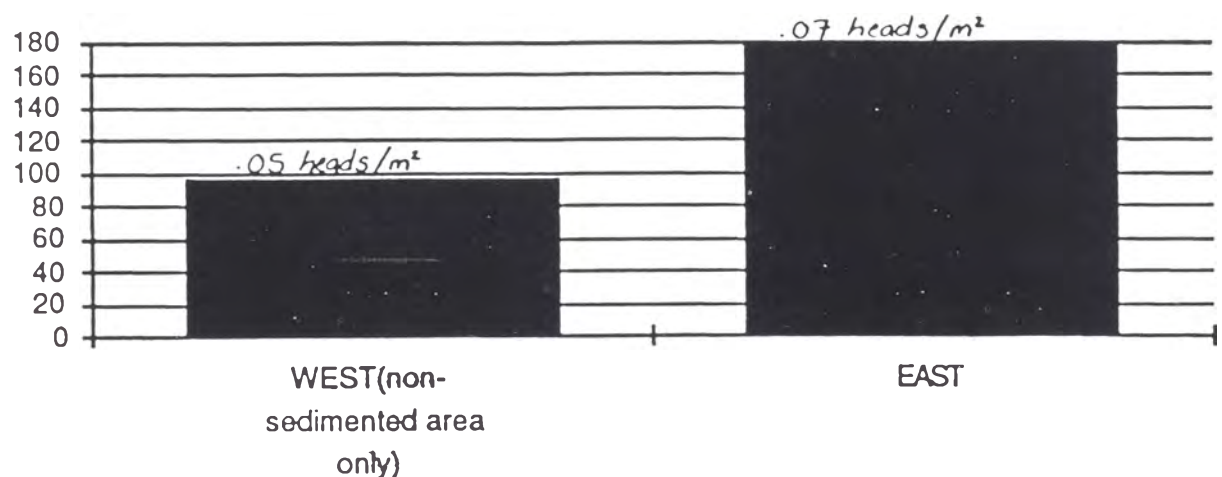


Figure 6B Coral Heads in the Non-depositional Area of the West Side vs. Similar Area on the East Side



## Discussion:

The greater number of dead large heads vs. live large heads on the west (outflow) side of the dock indicates that the conditions for corals must have been better in the past. The fact that there were many more small live heads vs. medium or large live heads on the west (outflow) side can support two theories: 1.) The system is in a state of recovery from the past disturbance, or 2.) Small coral heads have a lower mortality than larger heads in the present conditions. Either possibility requires more research, both historical and field oriented.

The data also indicates that growth forms respond differently to the effects of a water outflow. The striking difference in massive abundance vs. branching abundance between the two sides corresponds with the literature, which suggests that the massives are able to withstand greater stress than other growth forms (Bouchan 1982). On the other hand, the absence of branching species on the west (outflow) side is contrary to the literature, which suggests that abundance of branching species will increase in sedimented areas (Rogers 1990). This contradiction is an area that deserves further study.

The complete absence of Fungliids on the west (outflow) side suggests that these Fungliids are less able to deal with the outflow sediment than the other growth forms. As the Funglid is typically found on the sandy bottom and must deal with continual sediment movement, it is possible that the fungliids might be more sensitive to the fluvial sediment which has a smaller particle size and greater percentage of clays as compared to reef sediment. Another hypothesis is that the Fungliids were carried away by some variation in current due to the outflow. This is also an area that will require further study.

Despite the great differences found between the two sites, it appears the effects of the water outflow and its sediment load are isolated to a fairly immediate area. This conclusion is supported by the data which shows a similar number of heads/m<sup>2</sup> in the non-sediment deposition zone of the west side compared to the heads/m<sup>2</sup> on the total east side.

Although the data indicates there are definite differences between the sites and that the outflow has apparently affected the system, this has not proven that the outflow sediment is the cause. Other testable

hypotheses are: 1.) the fresh water is altering the salinity and stressing the corals 2.) the outflow is causing eutrophication in the immediate area. 3.) the outflow is substantially changing the water temperature and altering the system.

The land abutting the outflow studied has one large home site as well as a large area cleared of trees and used as a playing field. A local resident suggested that the field has been there for no more than ten years and that it was only recently donated for public use. The removal of the trees and the bared top-soil during the construction of the field may have increased the run-off and the sediment load. This could be a possible explanation for the earlier conclusion which states that the site has been healthier in the recent past, and also support the option that the system is in a state of recovery as the playing field, once re-planted with grasses, would produce less sediment than during construction. This hypothesis, based on oral history, requires further research into the land use history of the area.

### **Conclusion:**

The hypothesis was supported as there was less coral abundance on the west (outflow) side of the dock as well as lower species diversity, as indicated by the growth forms comparison. Furthermore, both size and growth forms showed significant variation. On the other hand, evidence of recovery, though inconclusive, was not expected. Similarly, the zone of sedimentation had less affect on the surrounding corals than expected as evidenced by the similarities in number of heads/m<sup>2</sup>

Throughout the tropics, changes in land use are affecting the near shore communities. To prevent further damage and to look ahead into the future, there is a great need to understand these impacts as well as possible recovery strategies. Furthermore, as many of the countries which have coral reefs strongly depend on the local tourism industry which is based on water recreation, a healthy coral reef is essential to the maintenance of a healthy economy.

There is an urgent need for careful planning and implementation of protective measures during construction projects, such as silt screens,

settling ponds, and berms, to reduce damage to the marine systems (DuBois & Towle 1985, White 1987, Salvat 1987). Furthermore, the scientific community must combine their efforts and produce long term, interdisciplinary data on land use changes and the effects on corals and coral communities (Rogers 1990).

### Acknowledgments:

We would like to extend our overwhelming gratitude to the teaching staff who assisted us above and beyond any and all expectations. David Stoddard, Carla D'Antonio, Gere Lipps, and Roy Caldwell each provided much needed advice and insight into our research. We would also like to thank Stuart Siegel and Larry Vaughn for their patience and tireless guidance throughout the entire research period as their assistance was invaluable.

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Finally, maruru roa to each and every fellow Gump Station researcher.

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# Patterns of the Understory Community of Inocarpus fagiferus on Moorea

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Integrative Biology 158  
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# Patterns of the Understory community of Inocarpus fagiferus on Moorea

Louis Santiago  
Dec. 3, 1992

## Abstract

Inocarpus fagiferus produces a region of suppression beneath its canopy in Moorea. Comparisons between Inocarpus and Metrosideros calina communities show significant differences in %canopy, understory density, understory diversity and %ground cover of understory species. Regressions show significant correlations between %canopy and Simpson's Diversity Index as well as between %canopy and %ground cover. Sample plots of cleared leaf litter show no evidence of leaf litter as a suppression mechanism. Investigations of a treefall gap understory community created by a fallen I. fagiferus tree suggests shading as a mechanism of understory suppression.

## Introduction

Inocarpus fagiferus (Leguminosae), also known as the Tahitian Chestnut or 'Mape', is a fair-sized tree growing up to 20 meters tall and bearing edible seeds. Its grooved trunk forms large abutments as it matures which may play a role in erosion control. The natural history of Inocarpus in Polynesia is unknown. Guppy (1906) found the seeds to float, but they apparently decay soon after contact with sea water making dispersal by ocean currents seem unlikely. However, Ridley (1930) considers the species to be a native of the Pacific, having reported local dispersal by rats, crabs and bats. It now occupies most of the regions on Moorea around rivers and streams.

Observations have shown that the understory of Inocarpus is often depauperate. Shading is a well known mechanism of suppression of understory plants (Hartshorn 1980). Canopy cover in Inocarpus

forests ranges from 65-95% and thus may be causing light limitation for the understory vegetation.

Allelopathy is also a possible mechanism of suppression of understory plants. Muller (1966) has discussed terpenes from aromatic shrubs and how they contribute to stands of single species dominance. Finally, leaf litter, aside from possible chemical effects, could be another mechanism of suppression. Observations suggest that a layer of leaf and branch litter as deep as 15cm could prevent germination of understory species.

In this study, I document the canopy cover, diversity, density and cover of understory species in Inocarpus forests and compare those measurements to the understory of sites dominated by the native tree Metrosideros collina (Myrtaceae). I then present preliminary information on mechanisms responsible for some of the observed patterns.

### Site Descriptions

This study took place on the island of Moorea in French Polynesia (18°S, 149°E). The specific study sites were on the north-facing slope of Mt. Tohivea, along the Opunohu River. The climate is tropical with approximately 3500mm of rainfall annually. The flora is representative of the South Pacific which includes a mixture of native species, exotic species brought by Polynesians and exotic species brought by Europeans.

Sampling of the understory was conducted in three Inocarpus communities, two Metrosideros communities and one Inocarpus treefall gap community. All Inocarpus sites were on the East Fork of the



Opunohu River between the Belvedere lookout and the Marae Tetiroa. (See Table 1 for complete site specifications, and figure 4, Moorea base map, for relative locations). Both Metrosideros sites were located just south of the Belvedere lookout. The Inocarpus light gap site was located on the West fork of the Opunohu River on the trans-island trail.

## Materials and Methods

In order to detect possible understory patterns, three large stands of Inocarpus and two large stands of Metrosideros were chosen. At each site the altitude, slope aspect, and slope angle was recorded. Values for altitude were determined using an electronic altimeter/barometer. Values for slope aspect and slope direction were determined using a Brunton Compass.

Within each site, 5 X 5 meter plots were chosen through a stratified random design and sampled for %canopy cover and the number and %ground cover of each understory species present (between 10cm and 4m tall). Relative percentages of ground covered by tree litter (leaf and branch litter), bare soil, exposed rock and exposed root were also recorded. All values for %ground cover and composition were estimated subjectively. Values for %canopy were determined using a spherical densiometer. In addition, a 5 X 5 meter plot in an Inocarpus treefall gap was sampled using the same procedures as described for the Inocarpus and Metrosideros sites. This site was located in a large Inocarpus stand and was chosen because of the difference in understory composition. The plot within the treefall gap site was chosen randomly.

Densities of individuals per meter-squared and stems or clumps per meter-squared were calculated for each plot. This was done because of the presence of Dicranopteris linearis, or the matting fern which often covered over 80% of Metrosideros plots as one individual. I therefore calculated densities representing Dicranopteris in genets and ramets. However, Dicranopteris was counted in genets for all other calculations. Simpson's diversity index (1-D) and Simpson's reciprocal index (a value for the number of equally occurring species required to produce the same diversity index, or 1/D) were calculated. Values for 1-D, 1/D, %ground cover, density of individuals per meter-squared and density of stems or clumps per meter-squared were analyzed for each plot using the Mann-Whitney U test. Values for % canopy cover were analyzed for each plot using an unpaired, one-tailed t-test.

Simple regressions with an upper confidence level of 95% and a lower confidence level of 90% were used to examine the effect of %canopy on both Simpson's diversity index (1-D) and %ground cover.

A cluster analysis was performed on Systat 5.3 using Euclidean distances to determine the similarity of all plots, including the treefall gap, based on %canopy, 1-D, 1/D and %ground cover.

To test for suppression by tree litter, 4-1meter-squared plots on level ground in L. tagiferus site #2 were cleared of tree litter. As a control 4-1meter-squared plots were cleared of litter and again covered. Both sets of plots were monitored for germination for nineteen days.

## Results

The species richnesses based on all sites were 14 for Inocarpus communities, 15 for the Metrosideros communities and 7 for the Inocarpus treefall gap (table 2: species list).

For statistical analysis, each plot was treated as a replicate. Per cent canopy cover varied significantly according to canopy tree species ( $p=.0001$ ;  $t=25.06$ , table 4). Both Simpson's Diversity Index ( $p=.0017$ ;  $U=151$ ) and Reciprocal Index ( $p=.0017$ ;  $U=151$ ) were significantly different according to canopy tree species (table 5). Per cent ground cover by understory plants also differed significantly according to canopy tree species ( $p=.0002$ ;  $U=6$ , table 5). Density of individuals per meter-squared ( $p=.0073$ ;  $U=22.51$ ) and density of stems or clumps per meter-squared ( $p=.0002$ ;  $U=01$ ) differed significantly based on canopy tree species (table 5). According to the density of individuals, or genets, the mean density of Inocarpus understory is 5.16 individuals per meter-squared while the mean density of Metrosideros understory is 1.81 individuals per meter-squared (table 3). However, according to the density of stems and clumps, or ramets, the mean density of Metrosideros understory is 26.41 stems and clumps per meter-squared compared to 5.16 stems and clumps per meter-squared (table 3).

The density of individuals per meter-squared in the light gap was 10.92 as compared with the average of all Inocarpus plots which was 5.18. The light gap micro-community was also 82.1% Centosteca lappacea which was only encountered four times in all 15 Inocarpus plots.

There was a significant correlation between %ground cover of understory vegetation and %canopy (slope = -.99; R-squared = .57;

$p=.0001$ , figure 1). There was also a significant correlation between Simpson's Diversity Index (1-D) and Canopy (slope =  $-.0044$ ;  $R^2=.37$ ,  $p=.0018$ , figure 2).

The Cluster Analysis showed that Inocarpus plots were more closely related to each other than to Metrosideros plots (figure 3). The Inocarpus treefall gap plot was clustered with all of the Metrosideros plots except one. This one outlier was a plot dominated by Metrosideros. It had an unusually high value of 157% ground cover by understory vegetation which isolated it.

All of the cleared tree litter plots and their controls had a value of 0 for sprouts per plot after 19 days (table 6). Tree litter plot #1 was washed out by rain.

### Discussion/Conclusion

The understory community of Inocarpus is less dense, less diverse and less abundant than that of Metrosideros. This suggests that there is a limiting factor in the understory community of Inocarpus. The correlations that have been shown between canopy cover and diversity, and canopy cover and ground cover suggest that either canopy cover or something that displays a similar pattern is inhibiting growth.

Observations of treefall gaps further support this hypothesis. The treefall gap which was sampled had an obviously different composition of understory species and a much greater density of understory plants. The abundant presence of Centosteca lappacea suggests that one of the factors that changes when a tree falls is inhibiting this grass from growing in the sub-canopy space. Therefore, the specific interactions between Centosteca and Inocarpus probably involves the limiting factor

in the understory community. In a separate light gap that I observed, there were 108 seedlings in a 5 meter-squared plot. I was unable to identify these seedling because the gap was only 7 days old, and the seedlings about 3 days old. However, I suspect these seedlings were Centosteca. This also supports the idea that one of the factors that changes when a tree falls is the suppression mechanism.

Since light changes most dramatically when a tree falls it appears to be shading or a related variable such as soil temperature that is inhibiting growth. However, since both treefalls I observed were uprooted there were changes in topsoil that took place. It has been demonstrated on Barro Colorado Island in Panama that treefalls caused by uprooting are more likely to be colonized (Putz 1983). Since Inocarpus has buttressing roots which appear to affect soil erosion, it may also be influencing the understory community. This supports the hypothesis that the suppression mechanism is something that changes when a tree falls.

Because the mean %cover by tree litter was higher in Inocarpus communities (table 3), it was hypothesized to be a mechanism of suppression. Although there was no sprouting in any of the cleared leaf litter plots, nineteen days was not enough time to draw any conclusions. Yet, is reasonable to visualize a layer of leaf litter preventing germination. This could be determined with more treatments, replicates and time.

Although diversity values are significantly different, the species richness values of the two communities are almost identical. The variation in diversity thus stems from the relative unevenness of the Inocarpus community. It is possible that the Yellow Ginger, which had a



relatively high abundance in many Inocarpus plots, and probably caused some of the unevenness may be especially tolerant to the limiting factor in the understory community. Investigations of the specific interactions between the Yellow Ginger and Inocarpus fagiferus may expose the limiting factor in this understory community.

I conclude that the understory of Inocarpus fagiferus forests has low species diversity and cover relative to that seen in more open native forests of Metrosideros collina. There is qualitative evidence for canopy shading as a suppression mechanism.

### **Acknowledgments**

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## Figure Legends

- Table 1: Site specifications of all study sites.
- Table 2: Species list indicating presence in Inocarpus, Metrosideros and Inocarpus treefall gap communities.
- Table 3: Statistical data for variables. 1-D represents Simpson's Diversity Index. 1/D represents Simpson's reciprocal index. Density is given in both individuals per meter-squared and stems and clumps per meter-squared. %canopy is the per cent of the sky that is shaded. All other percentages are of area covered.
- Table 4: T-test results showing significant difference in %canopy between Inocarpus and Metrosideros forests.
- Table 5: Mann-Whitney U test results showing significant differences between two forest types for %ground cover, two density measurements, Simpson's diversity index and Simpson's reciprocal index.
- Table 6: Results of tree litter plots. Tree litter was removed from tree litter plots 1-4. Tree litter was removed and replaced for control plots. Tree litter #1 was destroyed.
- Figure 1: Relationship between %ground cover and %canopy in 24 plots sampled within Inocarpus and Metrosideros sites. %ground cover is a measure of area covered by understory plants, %canopy is a measure of overstory shading. The graph shows a significant correlation.
- Figure 2: Relationship between 1-D and %canopy cover in 24 plots sampled within Inocarpus and Metrosideros sites. 1-D is Simpson's diversity index and %canopy is a measure of overstory shading. The graph shows a significant correlation.
- Figure 4: Cluster analysis showing similarity of groups based on %canopy cover, %ground cover, Simpson's diversity index (1-D) and Simpson's reciprocal index (1/D). Inocarpus plots are numbered 1-15, Metrosideros plots are numbered 16-

24, and the Inocarpus treefall gap is numbered 25. The figure shows all Inocarpus plots grouped together. the treefall gap is grouped with the Metrosideros plots. One Metrosideros plot was clustered alone.

Table 1: Site Specifications

	<u>ALTITUDE</u>	<u>SLOPE ASPECT</u>	<u>SLOPE ANGLE</u>
INOCARPUS #1	134m	260°	26°
INOCARPUS #2	230m	290°	20°
INOCARPUS #3	160m	325°	5°
INOCARPUS LIGHT GAP	240m	240°	0°
METROSIDEROS #1	245m	220°	18°
METROSIDEROS #2	220m	300°	22°



Table 2: Species List

	<u>Ino</u>	<u>Ino gap</u>	<u>Met</u>
Angiopteris evecta	X	X	
Asplenium nidus	X		
Canthemum barbatum	X		X
Centosteca lappacea	X	X	
Colocasia esculenta	X		
Davallia solida	X	X	X
Dicranopteris linearis			X
fern #1	X	X	X
fern #2	X		
grass #1			X
Hibiscus tiliaceus	X		X
Inocarpus fagiferus	X	X	
Lantana camara			X
Lycophyte #1			X
Melastoma			X
Metrosideros collina			X
Mimosa pudica			X
Pandanus odoratissimus			X
Phillipine violet			X
Psidium guajava			X
Unknown seedling #1	X	X	
Vine #1	X		
Vine #2	X	X	
Wikstroemia			X
Yellow ginger	X		

Table 3: Means, standard deviations from mean and standard errors

	<u>mean</u>	<u>std. dev.</u>	<u>std. err.</u>
<u>1-D</u>			
Inocarpus	.455	.171	.044
Metrosideros	.704	.125	.042
<u>1/D</u>			
Inocarpus	2.0	.575	.148
Metrosideros	3.76	1.05	.350
<u>Density ind/m</u>			
Inocarpus	5.16	.347	.90
Metrosideros	1.81	.48	.16
<u>Density st-cl/m</u>			
Inocarpus	5.16	.347	.90
Metrosideros	26.41	5.18	1.73
<u>% Canopy</u>			
Inocarpus	85.31	4.45	1.15
Metrosideros	31.59	6.04	2.01
<u>%Ground cover</u>			
Inocarpus	50	25.07	6.47
Metrosideros	103.6	23.23	7.74
<u>%Bare soil</u>			
Inocarpus	6.47	7.71	1.99
Metrosideros	1.67	5	1.67
<u>%Tree litter</u>			
Inocarpus	75.67	13.35	3.45
Metrosideros	32.22	12.77	4.26
<u>%exposed root</u>			
Inocarpus	6	5.07	1.31
Metrosideros	0	0	0
<u>%exposed rock</u>			
Inocarpus	11.73	9.68	2.50
Metrosideros	1.11	3.33	1.11

Table 4: t-test results

	<u>df</u>	<u>t VALUE</u>	<u>p VALUE</u>
% CANOPY	22	25.06	.0001

Table 5: Mann-Whitney U test results

	<u>U</u>	<u>p VALUE</u>
% GROUND COVER	6	.0002
DENSITY (STEMS OR CLUMPS/M )	0	.0002
DENSITY (INDIVIDUALS/M )	22.5	.0073
SIMPSON'S DIVERSITY INDEX (1-D)	15	.0017
SIMPSON'S RECIPROCAL INDEX (1/D)	15	.0017

Table 6: results of soil plot manipulations

	<u>Number of sprouts</u>
tree litter #1	N/A
tree litter #2	0
tree litter #3	0
tree litter #4	0
tree litter-control #1	0
tree litter-control #2	0
tree litter-control #3	0
tree litter-control #4	0

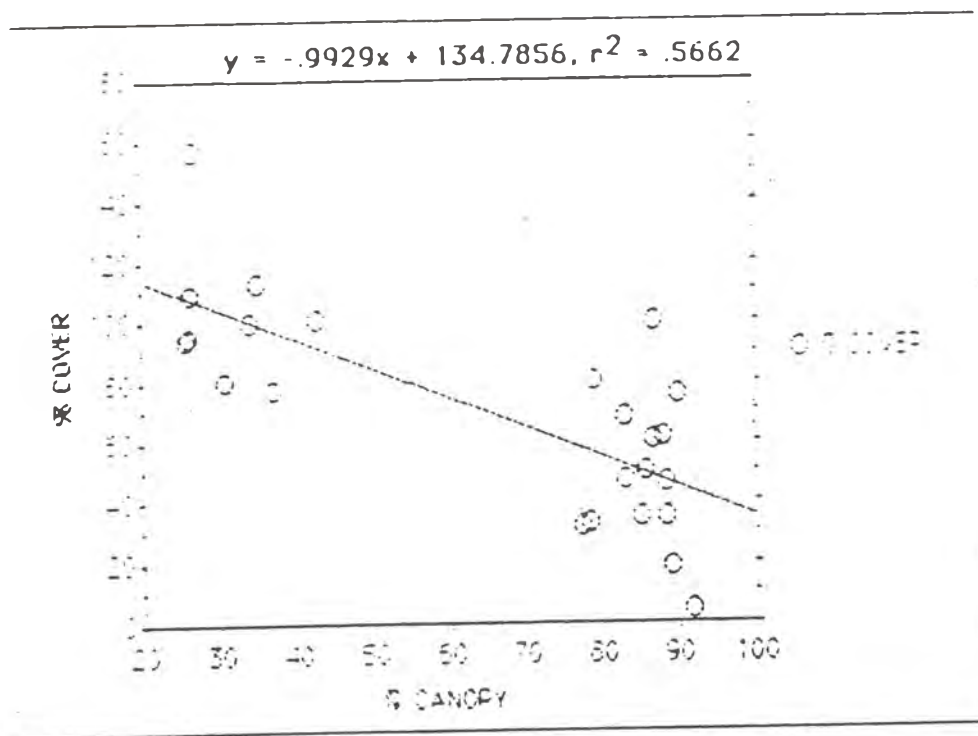
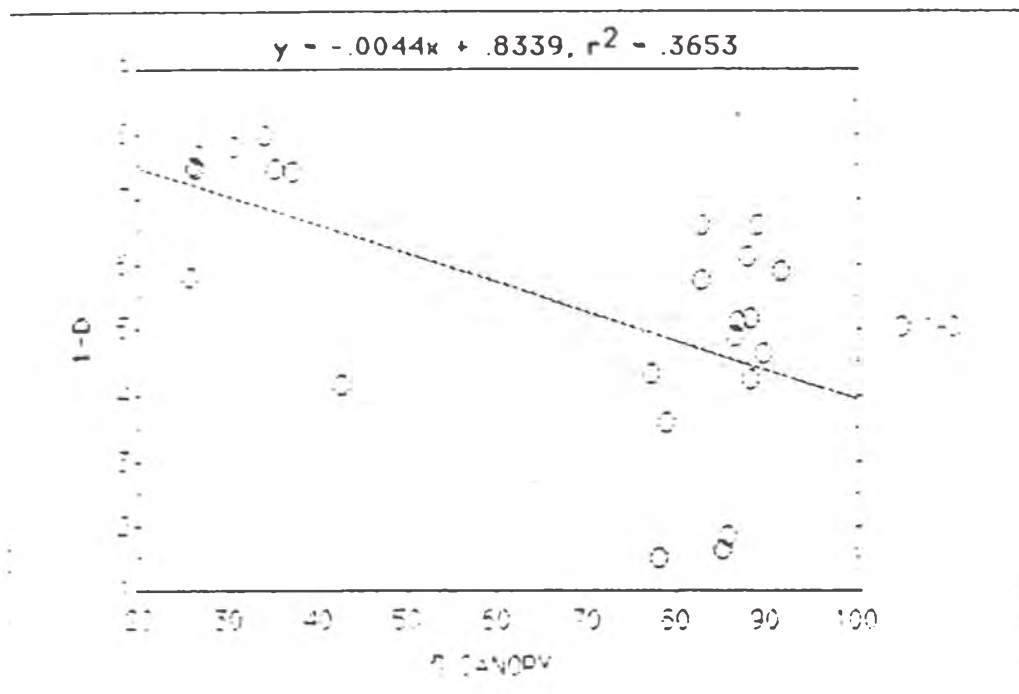




Figure 1



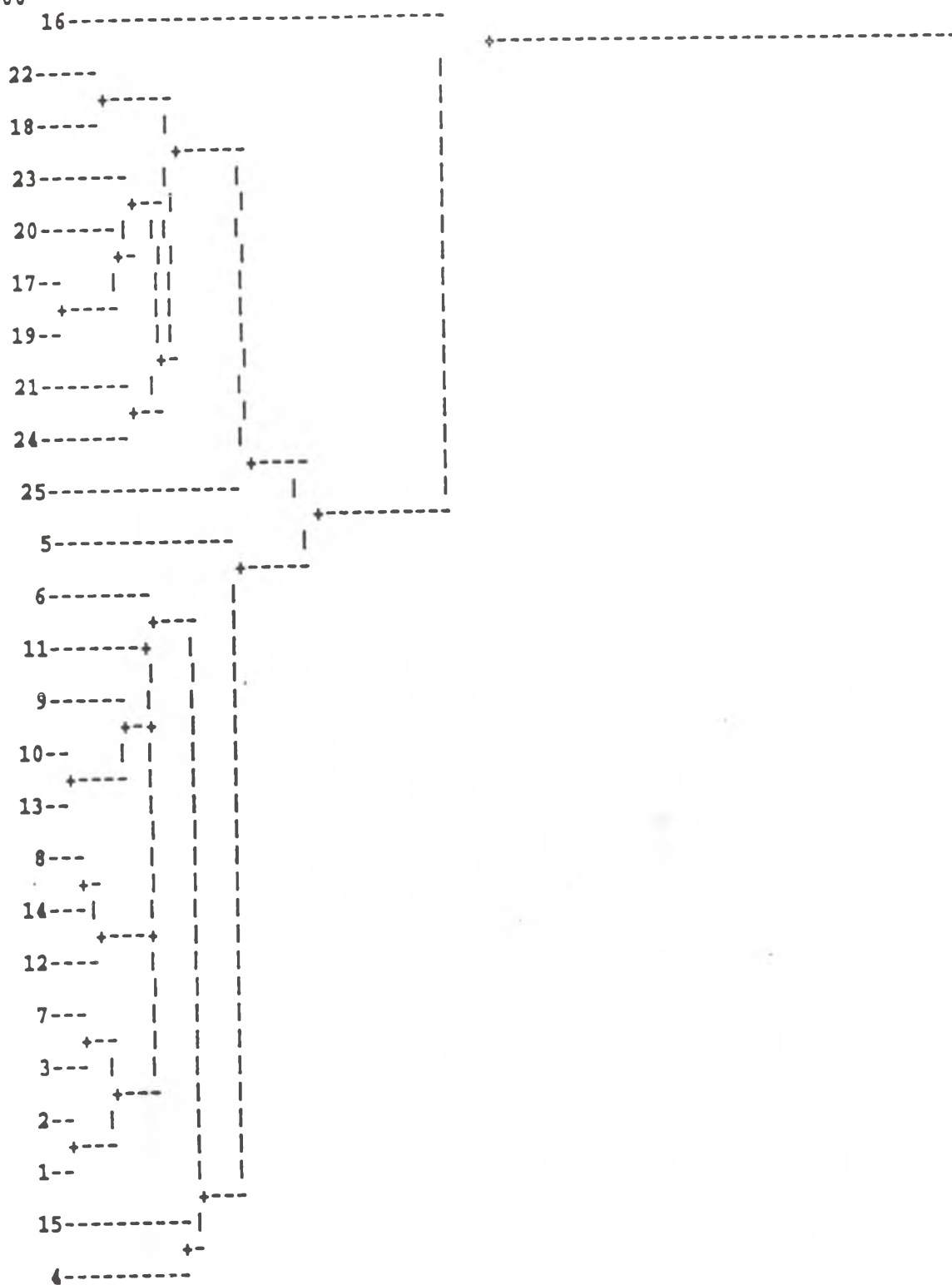
DISTANCE METRIC IS EUCLIDEAN DISTANCE  
 SINGLE LINKAGE METHOD (NEAREST NEIGHBOR)

REE DIAGRAM

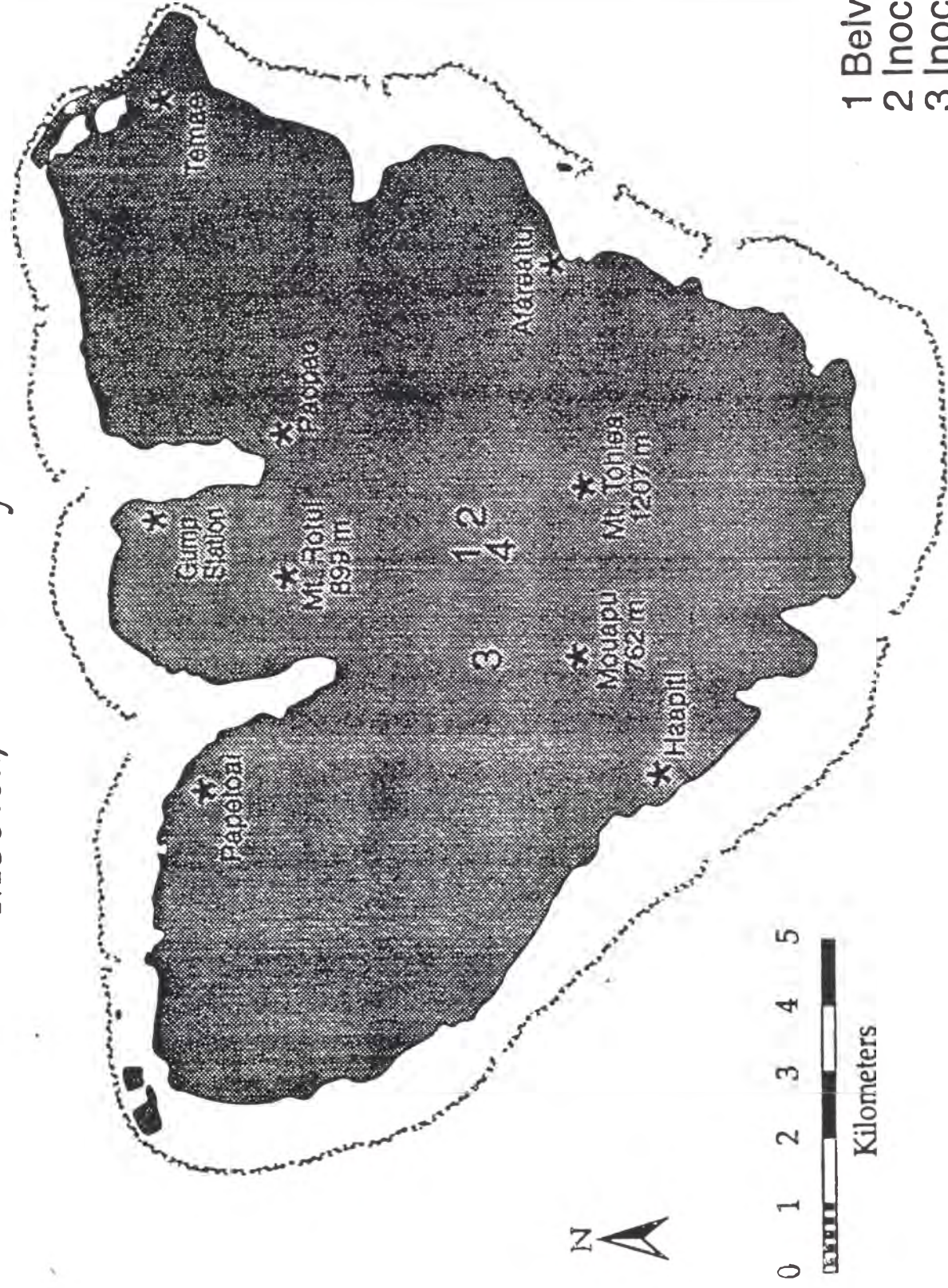
DISTANCES

0.000

50.000



# Moorea, French Polynesia



- 1 Belvedere lookout
- 2 Inocarpus sites
- 3 Inocarpus treefall
- 4 Metrosideros sites

Figure 5: study site location

**Effects of Disturbance on Stream Algal Communities  
of Moorea, French Polynesia**

Sam Shiley<sup>1</sup>  
Integrative Biology 158  
Fall 1992

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# Effects of Disturbance on Stream Algal Communities of Moorea, French Polynesia

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## Abstract

Effects of three types of anthropogenic disturbance on the stream algal communities of Moorea, French Polynesia were evaluated. The disturbed stream sections included two sites subject to canopy removal, one site blocked by a dam and two sites adjacent to a pineapple plantation. Respectively, these disturbances have caused added sunlight, altered current and sedimentation, and increased sedimentation and influx of toxins. The following questions were addressed: Are the algal communities occurring in disturbed stream sections, in terms of taxonomic composition and abundance, different from those of unmodified sections? If so, how might the disturbances account for these differences? The study entailed the quantification of the abundance of each algal type within zones of disturbance and comparison with unmodified upstream and downstream control sites. Part 1 of the experiment involved the sampling of the natural algal community while part 2 involved the measurement of algal colonization on marked and inserted rocks.

Three species of macroscopic algae were found: *Schizothrix mexicana*, *Mougeotia genoflexa* and *Hildenbrandia rivularis*. In addition, there were three dominant genera of diatoms: *Navicula*, *Gomphonema* and *Synedra*; all are pennate in structure (Fritsch, 1935). Comparison with upstream and downstream control sites revealed that *S. mexicana*, *M. genoflexa* and *Synedra* were more abundant within the zones of disturbance at the sites of canopy removal. This corresponds with the observation that these algal types, because of their high photosynthetic rates, grow more successfully with higher light levels (Tiffany, 1951; Smith, 1951). Within the reservoir at the site of the dam, *M. genoflexa* was abundant while *H. rivularis* was not present. Conversely, within the falls at the outflow of the reservoir, *H. rivularis* was abundant and *M. genoflexa* was not present. This corresponds with the observation that *H. rivularis* occurs most frequently in turbulent, rapid waters while *M. genoflexa*, though not found in stagnant waters, is intolerant of excessively rapid currents (Smith, 1933; Prescott, 1954). Diatoms in general were less abundant within the falls, most likely due to the constant scouring forces present. Data was much less conclusive at the pineapple plantation sites, where no significant variation within the algal community was found. In conclusion, the effects of habitat alteration appeared clearly manifested only in the algal communities of the canopy removal sites and the dam/reservoir site.

## Background

To interpret variations in abundance of each algal type and ascertain correlations with disturbance effects, a more thorough background on the alga is necessary. *S. mexicana*, a filamentous blue-green, requires rocky, stable substrate and high light. This species usually occurs directly below the water surface, even growing above water at times. It is tolerant of a wide range of currents, as long as the water isn't stagnant or overly rapid and turbulent (Tiffany, 1951). *M. genoflexa*, a filamentous green, has similar habitat requirements, although it usually occurs in slower waters and is often found on non-rocky substrata such as mud and logs (Tiffany, 1951). Like *S. mexicana*, *M. genoflexa* has high photosynthetic demands and must grow on near-surface substrata (Prescott, 1954). *H. Rivularis*, an encrusting red, occurs in turbulent, rapid waters, attached to rocks. It is a slow-growing algae with low photosynthetic levels, so it is rarely limited by light and has been observed at depths of 15m (Smith, 1933).

The principal genera of diatoms occurring in the freshwater of Moorea, *Navicula* and *Gomphonema*, have broad habitat requirements. Both grow on submerged rocks, sticks and logs and have low light demands. In addition, these genera are often epilithic, growing on mud and silt (Tiffany, 1937). *Synedra*, however, requires high light exposure and usually occurs in open areas, near to the water surface. Because of its large size, *Synedra* is susceptible to scouring and requires stable rock for substrate (Smith, 1951).

## Introduction

The streams and rivers of Moorea are affected by many forms of human-induced disturbance. Coffee plantations, shrimp farms, grazing pastures, homes and many other types of development line the streams at lowland elevations (0-25m). Pineapple plantations and other, smaller scale agricultural operations occur in the higher elevations (25-100m). These developments have modified physical structure of the catchment, riparian vegetation and often stream geomorphology itself. In turn, within disturbed sections of stream, inputs of allochthonous material and other forms of organic and inorganic matter have been altered. In the present study, the effects of such disturbances on stream algal communities are examined.

Three types of stream disturbance were studied: The removal of canopy (two sites), the presence of a dam (one site) and the presence of a pineapple plantation adjacent to the stream (two sites). These disturbances have subjected the stream community to different types of habitat change. The removal of canopy has caused added sunlight to reach the stream. The dam has caused alterations of current, the formation of a reservoir/falls system and the accumulation of sediment within the reservoir. Finally, the pineapple plantation has caused increased sedimentation due to a lack of erosion control as well as the input of toxic chemicals from herbicides and pesticides during periods of runoff.

Based on the habitat requirements of the algal types, one is able to hypothesize as to algal community responses to disturbance. Within the stream reaches subjected to canopy removal, levels of *S. mexicana*, *M. genoflexa*, and *Synedra*

were expected to be higher than those of upstream or downstream sections, while little variation among *H. rivularis*, *Navicula* and *Gomphonema* was expected.

At the dam/reservoir site, little or no algal success was expected within the reservoir due to the high degree of sedimentation. As the bathymetry of the reservoir (figure 8) reveals, sediment levels reached almost 1m in certain places. Because of this, almost all viable substrata were entirely buried. Even the few rocks that did protrude from the sediment layer were covered by thin patches of unhardened sediment, formed by the constant circulation and settling of sediment occurring in the reservoir. Only *Navicula* and *Gomphonema* were expected to occur in this zone, clinging to any protruding rocks, owing to their ability to colonize sedimented rocks (Tiffany, 1937). In the falls, low diatom abundance was anticipated, due to the constant scouring forces; it was expected that only *H. rivularis*, of the macroscopic alga, would occur in this zone, owing to its ability endure rapid, turbulent flow.

At the pineapple plantation sites, one important consideration was necessary: The effects of sedimentation and influx of toxins could presumably have as large an impact in the downstream section as they do within the disturbed zone. In general, though, it was hypothesized that there would be little variation among the diatoms between disturbed sections and unmodified sections. For one, the degree of sedimentation was far less significant than that of the reservoir; sediment occurred in thin patches on the rocks, and, as mentioned, diatoms are able to colonize sedimented rocks. More importantly, *Navicula* and *Gomphonema*, and to a lesser extent, *Synedra*, are highly resistant to the presence of pollution in the form of toxins and heavy metals (Barley, 1982). Furthermore, because the influx of chemicals occurs during periods of rain and runoff, the algal community is most likely exposed for only brief intervals. For this reason, little variation among the macroscopic alga was also anticipated. If anything, a slight fall in *H. rivularis* and *S. mexicana* was expected in the sections within and below the disturbance, due to the sediment patches covering viable substrata.

This study of stream algal communities is important on both a local and international level, as it is an attempt to characterize quantitatively the effect of human disturbance on an aspect of the stream community. Furthermore, the health of the algal community is of particular importance since so many animals of the stream community depend on algae for survival. Many of the streamside developments on Moorea are managed with little concern for the health of the stream. The algal community is only one part of this stream system, but its study of is a step towards assessing the effects of the rapidly growing Moorean community on the streams. Information such as this study will hopefully be used in the future, in order to maintain the streams properly and ensure health for the stream communities.

### Study Sites

Moorea (136 km<sup>2</sup>) is the third largest island of the Society Island group of French Polynesia (figure 1). It is located 18 kilometers (km) west of Tahiti at approximately 17° S, 149° W (Williams 1933, Gabrie & Salvat 1985). The island is triangular in shape and has a perimeter of approximately 60 km.



Geomorphologically, the island consists of high volcanic peaks reaching 1207 meters (m) and a coral reef lagoon surrounding the entire base of the island. The five sites studied in this experiment are found along two streams, the Opunohu and the Mahaerua, which lie in the Opunohu Valley and the Toto Valley, respectively (Figure 2 & 3). The Opunohu Valley faces northwest, and its streams empty into the Opunohu Bay. Toto Valley faces southeast, and its streams enter the lagoon directly.

The design of this study was comparison of algal communities within disturbed stream sections with those of unmodified areas occurring directly above and below the sites of disturbance. Thus, within each of the five sites, there were three subsites.

**Site 1: Natural removal of canopy.** This site is located 200 m south of the Pao Pao-Belvedere Road Bridge on a second-order reach of the Opunohu Stream. In this area, the closed canopy consists of Tahitian chestnut (*Leguminosae*, *Inocarpus fagiferus*) and hibiscus (*Malvaceae*, *Hibiscus tiliaceus*), and the watershed is shallow-sloped. The stream has an established riffle-pool structure at this point, and the width ranges from 1-5 m. While this study is concerned mainly with effects of human-induced disturbance, site 1 involves a natural disturbance where one of the Tahitian chestnut trees has fallen diagonally upstream and taken most of the canopy with it. As a result, a section of the stream 20 m in length receives more solar exposure than the sections above and below it.

**Site 2: Removal of canopy for shrimp farm.** This site occurs 600 m north of the Pao Pao-Belvedere Road Bridge on a third order reach of the Opunohu Stream. In this section, again with closed canopy, hibiscus is dominant, and the watershed is shallow-sloped. The stream is slightly wider at this point, ranging from 2 to 10 m. Adjacent to the site lies a shrimp farm on the west bank. There is approximately a 10 m strip between the stream and the shrimp pools, but the streamside vegetation is removed on the farm side at occasional spots along the stream. The first portion of exposed stream adjacent to the farm was studied.

**Site 3: Dam and reservoir.** This site occurs on a third order reach of the Opunohu approximately 200 m upstream from site 2. The canopy, watershed and stream structure are the same. The stream is blocked by a dam, 5 m in width and 1 m in height. This dam has created a pool 36 m in length, up to 1 m in depth and up to 8.5 m in width (figure 8). This site is different from the others in that there are two areas of modification: the reservoir and the falls. Both disturbances are studied, so site 2 actually has four subsites.

**Sites 4 & 5: Pineapple plantation, riffle and run.** Sites 4 & 5 are located on a third order reach of the Mahaerua River approximately 1 km from the outflow into the lagoon. Adjacent to these sites is a pineapple plantation growing on the steep watershed slope. The field is approximately 80 m in length and width, and the base of the field lies 15 m from the stream. Here, a strip of streamside Tahitian Chestnut trees has been left, and the canopy is closed. Site 4 entailed a comparison of riffle sections, while site 5 entailed a comparison of run sections.



## Methods

### Physical characteristics of the study sites

Physical parameters of the stream were measured to quantify the extent of the disturbances, to control for certain stream characteristics and to provide site descriptions. Nine parameters were evaluated:

Stream profile: To survey the slopes of the sites, a Kern optical level (GK1-A), Kern tripod and stadia rod were used. The stream thalweg was used for rod placement to attain the stream bottom slope. For site 1, a point was taken for every 3 m of stream length. At the other four sites, a point was taken for every 5 m of stream length.

Bathymetry of reservoir: To quantify the amount of accumulated sediment in the reservoir of site 3, a bathymetric survey was conducted. One transect tape was extended over the length of the reservoir while another was used for the width. At every 3 m in length and every 1 m in width, a meter stick was used to determine the total depth of the reservoir as well as the distance from the water surface to the top the sediment layer. Using these measurements, sediment thickness was determined.

Current: To quantify current, an Ott current meter (model C2) with propeller #2 and an Ott counter (Z 30) were used. Eight measurements were taken at each of the 16 subsites. These included two measurements at each of the three introduced rocks as well as two measurements at the main channel of each site.

Canopy: To quantify the degree of cover, a spherical densiometer was used. Four measurements, one in each direction, were taken at each of the 16 subsites. The spherical densiometer is used by holding a convex mirror at chest level and counting the number of squares reflecting canopy cover (out of 96 total).

Dissolved oxygen: To quantify dissolved oxygen at site 3 (dam/reservoir), the Winkler method was employed. Water samples were collected in 300 ml glass-stoppered bottles following standard methods of water analysis (APHA 1988: 411-417).

Sedimentation: A sedimentation analysis was executed at sites 4 & 5 (pineapple plantation), which entailed the quantification of percent sediment cover on available substrate. The technique used was the same as that used to quantify macroscopic algal cover (described below in Part 1 and Part 2 methods). Because sediment at sites 4 & 5 was present on the rocks only in thin patches, percent cover, rather than absolute quantity, was measured.

Depth: To obtain values for mean stream depth at each site, a meter stick was used. Measurements were taken at each of the three inserted rocks as well as one measurement in the stream thalweg. These measurements were taken at times of low water level (following at least two days of low precipitation).

Water temperature: An FSC 14 983-16 air/water thermometer was used to measure water temperature. Readings were taken at each subsite between 12:00PM-3:00 PM on three different occasions.

Elevation: To obtain the altitude at each of the sites, a Lietz Barometer/Altimeter, model AIR-HB-1L was used.

## Part 1: Sampling of the natural algal community

The first part of this study entailed the selection of the sites and subsites. After finding the areas of disturbance for study, top and bottom boundaries for the disturbed sections were defined. For the canopy removal sites, the boundaries occurred where the canopy became closed once again. Boundaries for the dam/reservoir disturbance were the top of the reservoir and the bottom of the falls. Finally, the pineapple plantation sites were defined simply by the upstream and downstream borders of the field.

Once these boundaries were established, sections for study were designated. As a first step, the rocks for study of algal colonization were inserted (see below). These rocks were placed at the centers of the disturbed stream reaches, so as to span the width of the stream. For the upstream and downstream subsites, rocks were inserted at 20-25 m above the top boundary and 20-25 m below the bottom boundary. The rocks were placed in such a way as to control for habitat characteristics not affected by the disturbance. For the sampling of the natural algal community, plotting tape was used to designate 1 m sections of stream directly 0.5 m below each set of introduced rocks so as not to interfere with the algal colonization but to attain comparable data.

To sample the algal community at my sites, rocks occurring naturally in the stream were numbered from, for example, 1 to 50 (depending on the number of rocks present; only rocks over approximately 100 cm<sup>2</sup> in surface area were counted). Using the random number generator on a calculator, ten numbers were obtained; these ten rocks would be sampled. Next, the rocks were removed one by one and sampling began. Plastic wrap was placed around the rocks and any areas of macroscopic algae were circled. Removing the plastic, the total area of macroscopic algae cover was measured from the circled areas. Next, the rocks were brushed with a toothbrush and the samples were collected in storage bottles. In the laboratory, the brushings were examined for presence and abundance of diatom species, using a compound microscope at 1000X magnification. Five fields of view were observed and catalogued for each of five of the removed rocks. Therefore, the diatom data for the study is based on 25 fields of view per subsite. Finally, to determine area of available rock surface, the rocks were wrapped in foil, stripping away any overlapping sections, and the resulting piece was measured; portions of rock buried in sediment, unavailable for algal growth, were subtracted from the total value.

## Part 2: Sampling of introduced rocks

48 rocks were obtained from the streambed adjacent to the Wilder soccer field near Pao Pao (figure 1). After scrubbing the rocks with a wire brush, they were dipped individually in hydrochloric acid to eliminate any organic matter or algal propagules present. Next, the rocks were marked with 1, 2 or 3 with orange fluorescent paint. 3 rocks were placed within each of the 16 subsites. This procedure was executed from 10/23/92 to 10/27/92.

Four weeks after placement (11/20/92-11/22/92) the rocks were removed from the stream for observation. Here, the same procedure as that of the natural algal community sampling was used, the only difference being that the rock sample size was three, and diatom presence was based on fifteen fields of view per subsite.

Analyses of variance were used to compare abundances of each algal type occurring within the sites (table 2). Differences in abundance were thus determined to be significant or insignificant. Equations for the analysis of variance are explained in *An Introduction to Statistical Methods and Data Analysis* (Ott, 1988) (an alpha value of .05 was used; df<sub>1</sub> and df<sub>2</sub> values were calculated from sample size of the sample being tested).

## Results

The results of the site characteristic measurements are summarized in table 1. As revealed by the canopy measurements, sites 1 and 2 were indeed exposed to increased sunlight. Canopy was over twice as open within the disturbed reach of site 1 and over three times as open in the disturbed section of site 2. The presence of disturbance was also confirmed by measurements at site 3. The bathymetry of the reservoir (figure 8) revealed an accumulated sediment layer reaching 1 m in thickness in certain areas. Furthermore, current in the reservoir was not detectable while the velocity in the falls was approximately 4 times as great as the upstream and downstream currents. Dissolved oxygen readings showed the reservoir to be lowest and the falls to be highest in DO level. However, all the DO levels, including that of the reservoir, were high relative to average freshwater lotic system levels (APHA 1988: 411-417).

At sites 4 & 5, sedimentation was the only parameter measured as a potential disturbance effect. The measurement revealed no sediment in riffle sections and only a small degree in the run sections (3.1% sediment cover on available rock surface in the upstream section, 7.8% in the disturbed zone and 14.1% in the downstream reach).

The results of Part 1 and Part 2 sampling are summarized in appendices 3 and 4 and presented graphically in figures 9-13. At site 1 (figure 9), no *S. mexicana* was present (this species was present only at site 2). *M. genoflexa* was present only within the disturbed zone but covered only .51% of available rock surface. *H. rivularis* was present in all three reaches of site 1, although slightly more abundant within the disturbed zone (5.9% vs. 4.7% and 4.1%). *Navicula*, *Gomphonema* and *Synedra* were all approximately twice as abundant within the disturbed zone. No macroscopic alga were present on the introduced rocks (figure 9), and of the diatom groups, only *Navicula* and *Gomphonema* were present; their abundances were slightly below half their natural rock abundances. Analysis of variance (AOV) tests (table 2) showed that *Synedra* on the natural rocks and *Gomphonema* on the introduced rocks had the only statistically significant disturbed zone abundances.

At site 2 (figure 10), six algal groups had statistically (AOV) different abundances within the disturbed zone. *S. mexicana* was present only within the disturbed section, and it covered 10% of natural rock surface. *M. genoflexa*



was present within all three subsites, and there was little variation in the abundances (27% at, 21% above and 28% below). On the introduced rocks, however, *M. genoflexa* covered 33% of available rock surface within the disturbed zone, while none had colonized the upstream or downstream rocks. Within the entire study, this was the only set of introduced rocks that showed macroscopic algal colonization. *H. rivularis* was approximately twice as abundant within the disturbed section, but the difference was not AOV-significant.

Compared with the population numbers shown in unmodified sections, *Navicula* was slightly more abundant within the disturbed section, while *Gomphonema* was less than half as abundant. *Synedra* showed AOV-significant abundances on both the natural rocks and the introduced rocks. Within the disturbed zone, 11 *Synedra* per 5 fields of view were found, versus 0 above and 2.8 below. The "other" category of diatoms, which included 6 assorted species of separate genera, showed AOV-significant abundance within the open canopy reach, where they were six times as abundant as the upstream and downstream populations.

At site 3 (figure 11), *M. genoflexa* was not present in the falls (AOV-significant), but it did occur in the reservoir, where it was slightly less abundant than it was in the upstream and downstream communities. *H. rivularis* was not present in the reservoir, also AOV-significant, but it did occur in the falls, where it was over twice as abundant as it was above and below. Diatoms were noticeably less abundant in the falls while approximately equal between the other three subsites. On the introduced rocks, no diatoms were found in the falls section, while the reservoir abundance was approximately equal to that of the upstream and downstream sites. Of the diatoms, only the abundances of *Gomphonema* on the natural rocks and *Navicula* on the introduced rocks (both in the falls) were statistically significant.

At site 4 (figure 12), *H. rivularis* was the only macroscopic algae present, and it was most abundant upstream and least abundant downstream (14% at, 25% above, and 5.8% below). Diatom abundance was approximately equal between the upstream and downstream sites and lower within the disturbed zone. *Synedra* was less abundant (AOV-significant) in the disturbed zone. On the introduced rocks, only *Navicula* and *Gomphonema* were present, and their abundances were approximately equal among the subsites.

At site 5 (figure 13), *H. rivularis* was again the only macroscopic algae present, and it was approximately twice as abundant in the downstream section. *Navicula* was less than half as abundant within the downstream reach, and the other species were approximately equal between the subsites. On the introduced rocks, the downstream site had noticeably lower diatom abundance, but only *Navicula* was AOV-significant.

# Moorea, French Polynesia

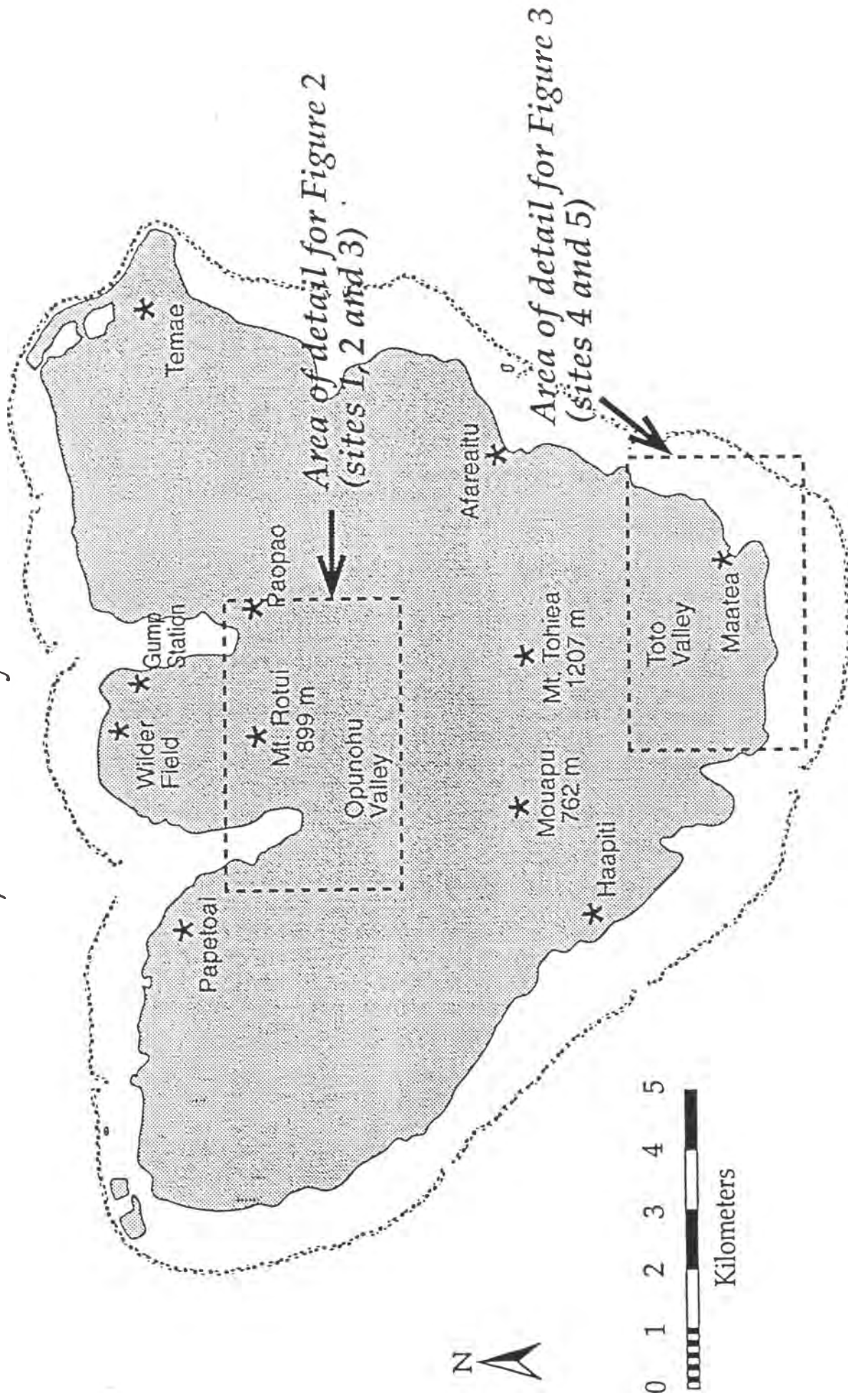
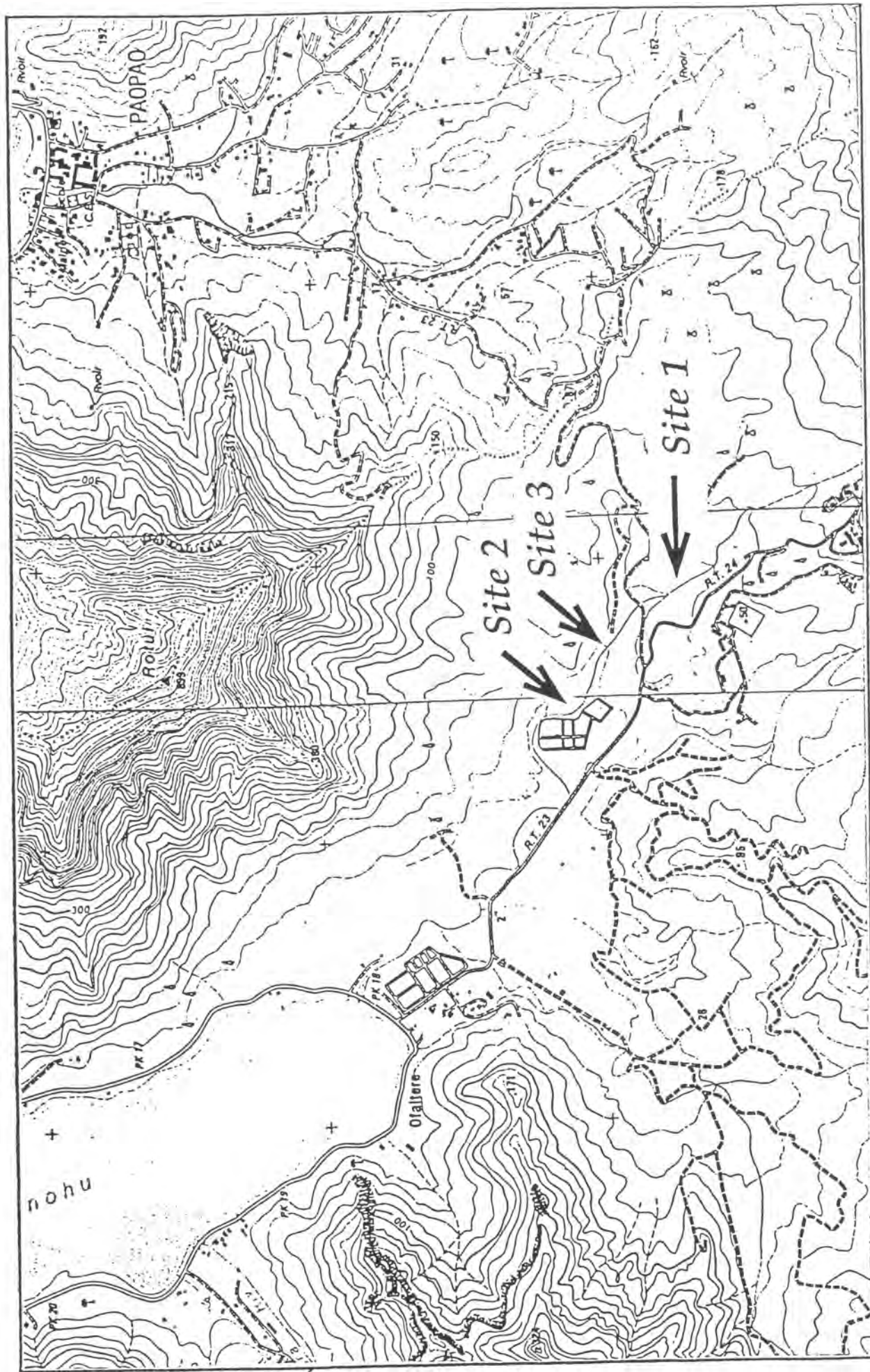


Figure 1. Study Site Locations

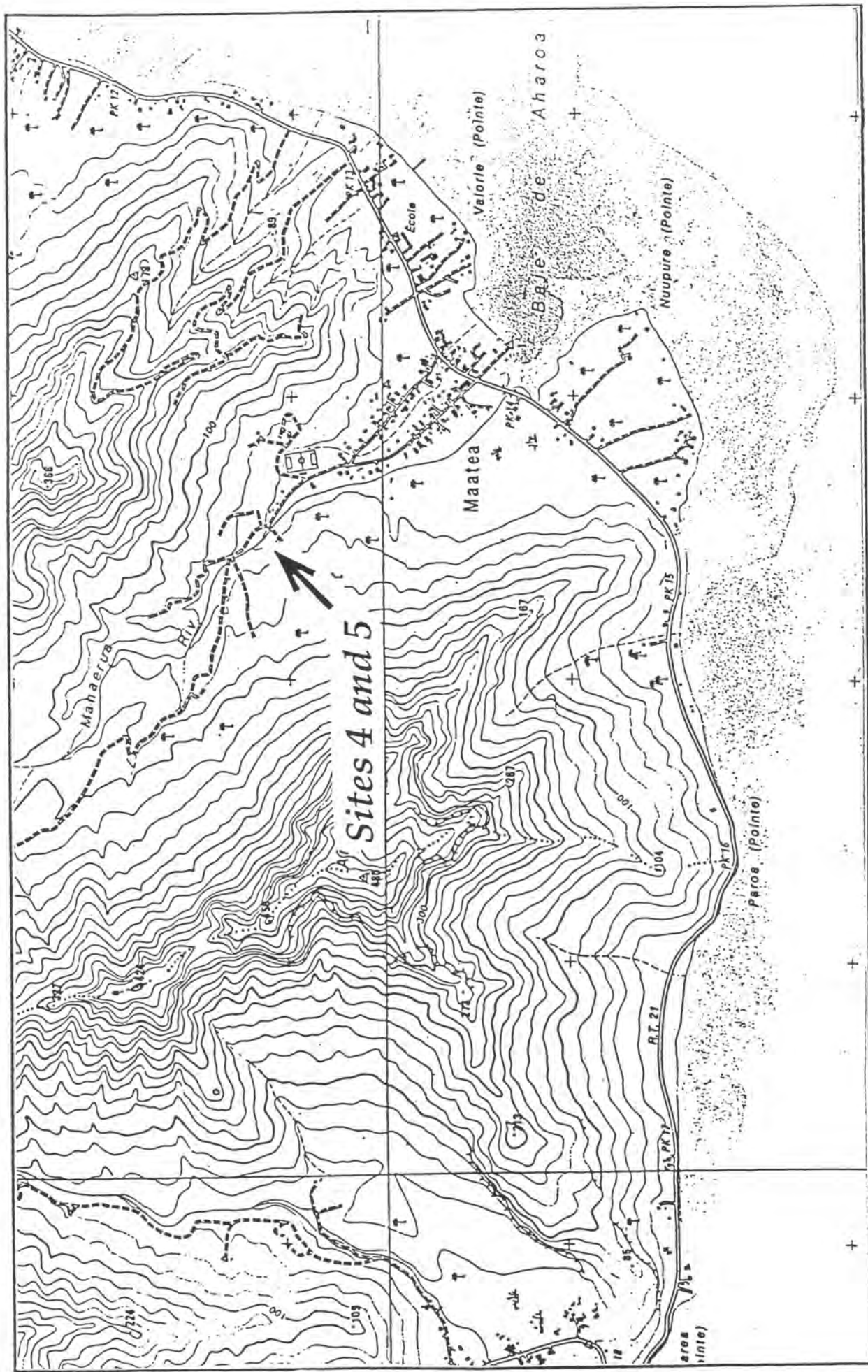




Source: Ministère de l'Urbanisme des Transports Terrestres et de l'Administration Générale 1989

Figure 2. Opunohu Stream Study Sites



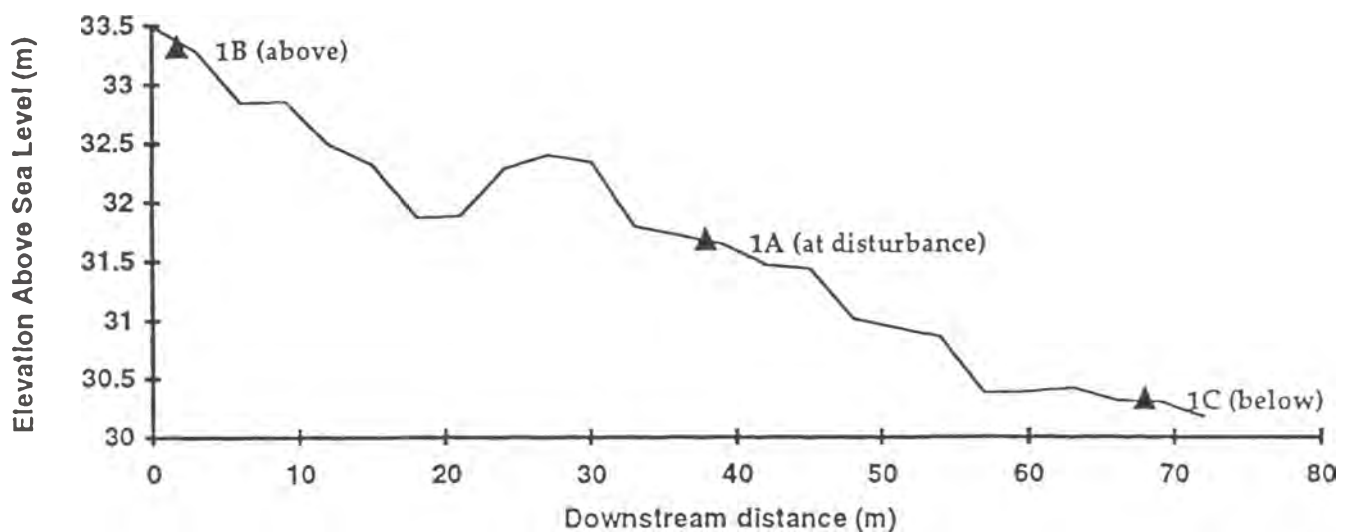


Source: Ministère de l'Urbanisme des Transports Terrestres et de l'Administration Generale 1989

Figure 3. Mahaerua River Study Sites

## Figures 4-7: Stream Bottom Profiles of the Study Sites

Figure 4: Site 1 (Natural canopy removal) Stream Bottom Profile



\* Stream bottom profiles show thalweg elevation. Sampling conducted at marked locations.

Figure 5: Site 2 (Removal of canopy for farm)  
Stream Bottom Profile

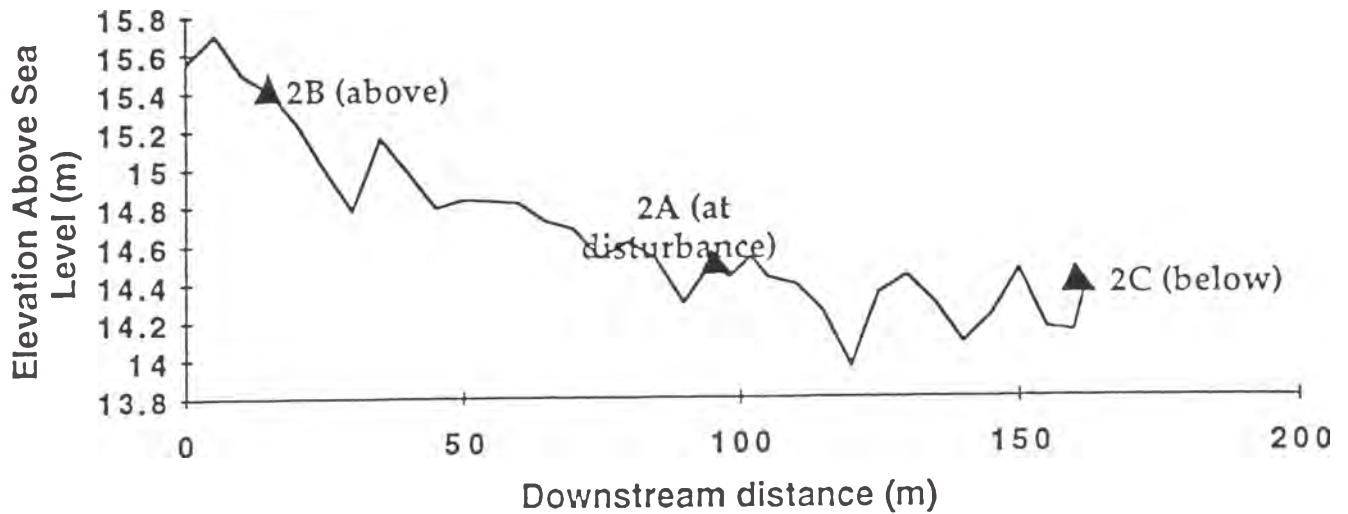


Figure 6: Site 3 (Dam/reservoir) Stream  
Bottom Profile

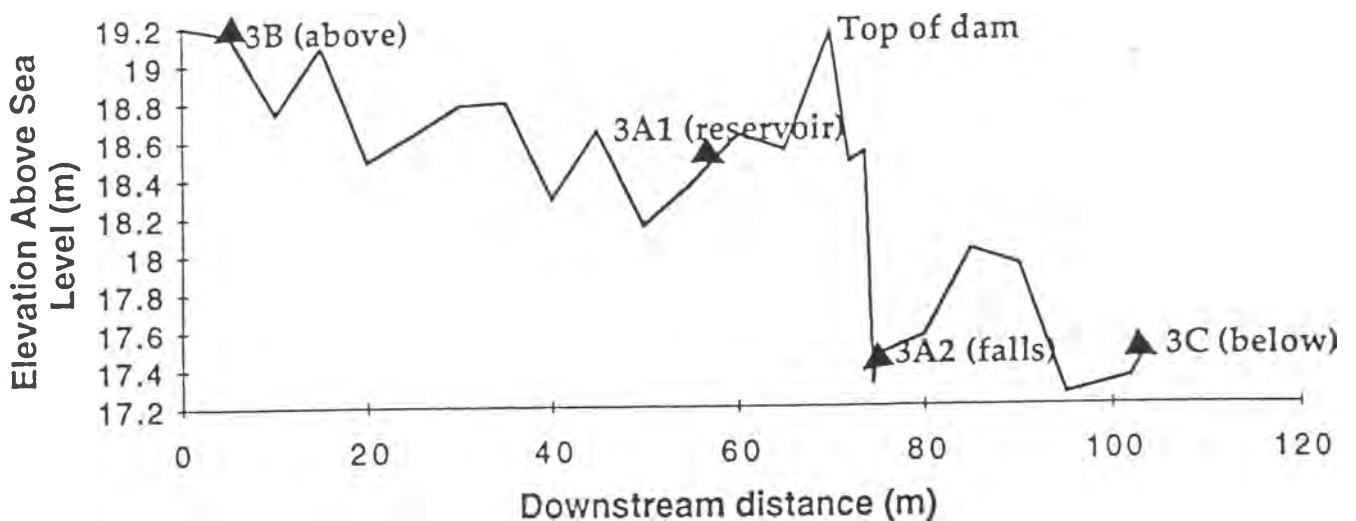


Figure 7: Sites 4 & 5 (Pineapple plantation-riffle/run) Stream Bottom Profile

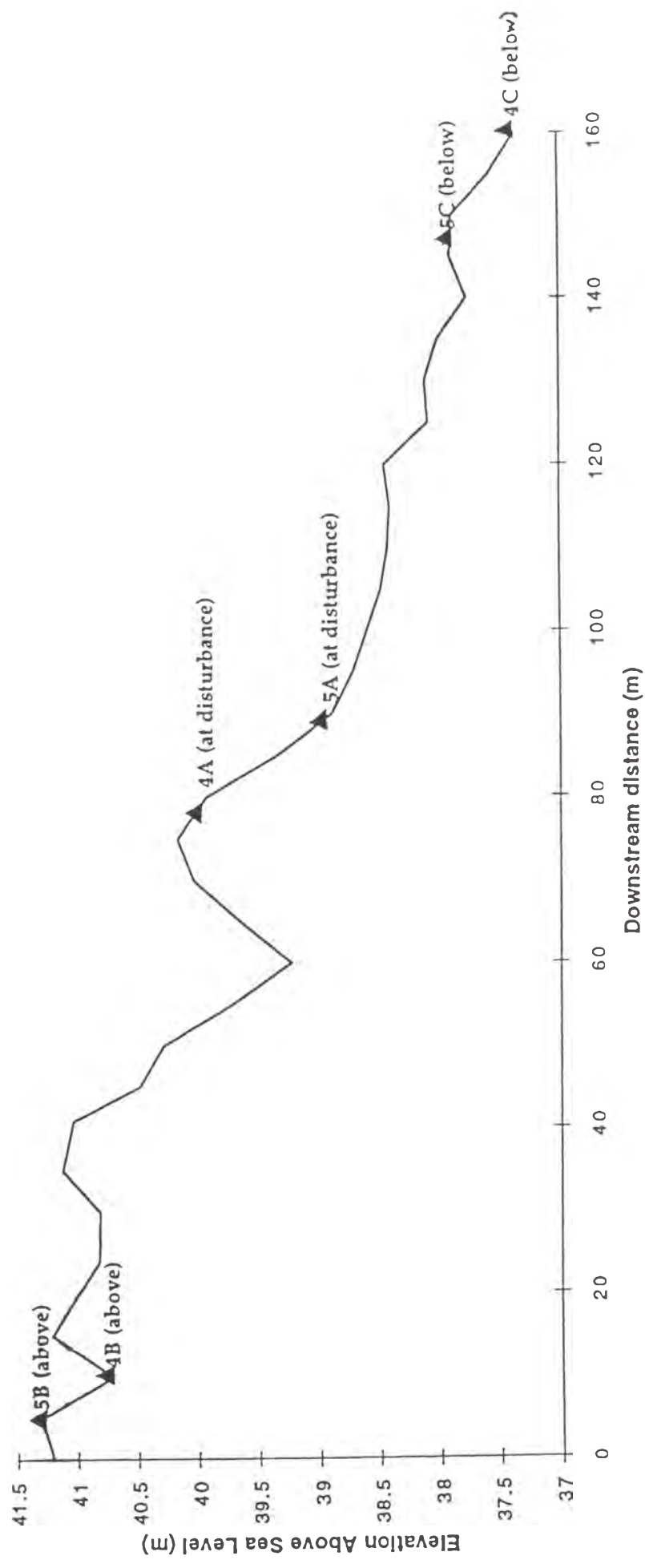
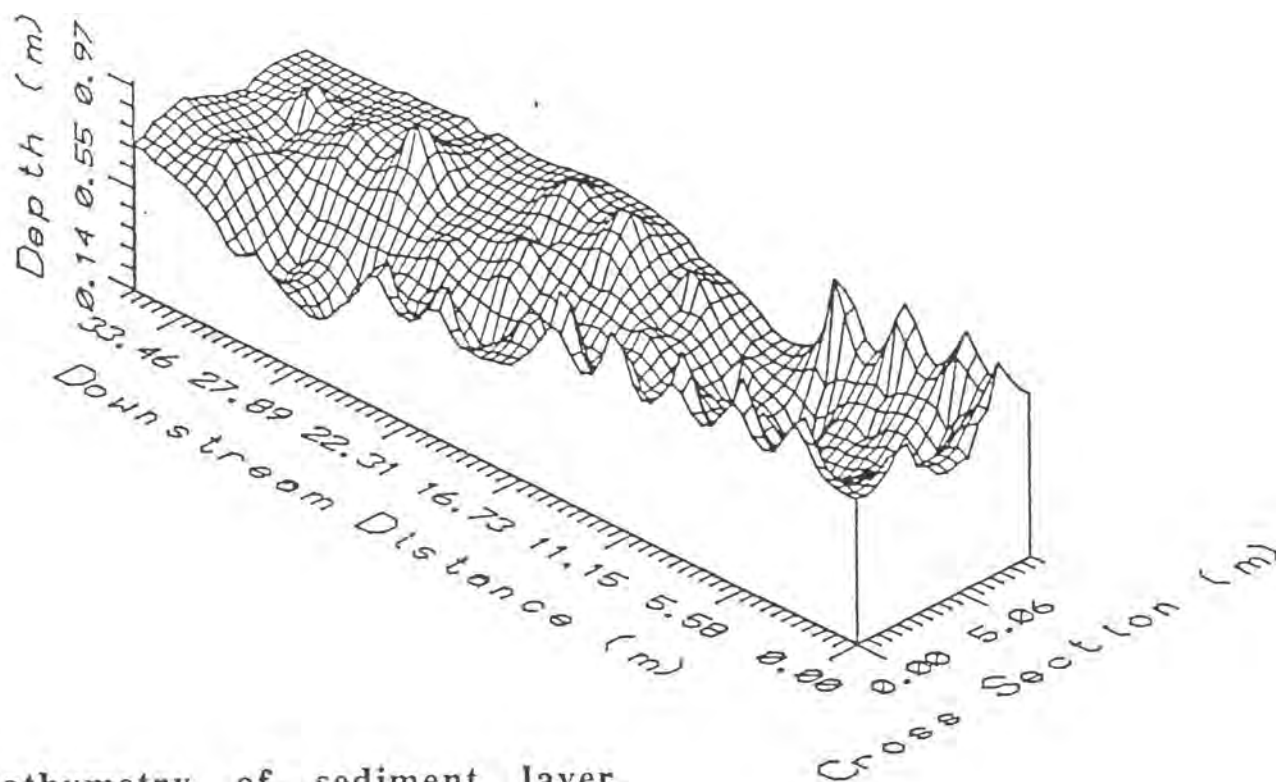


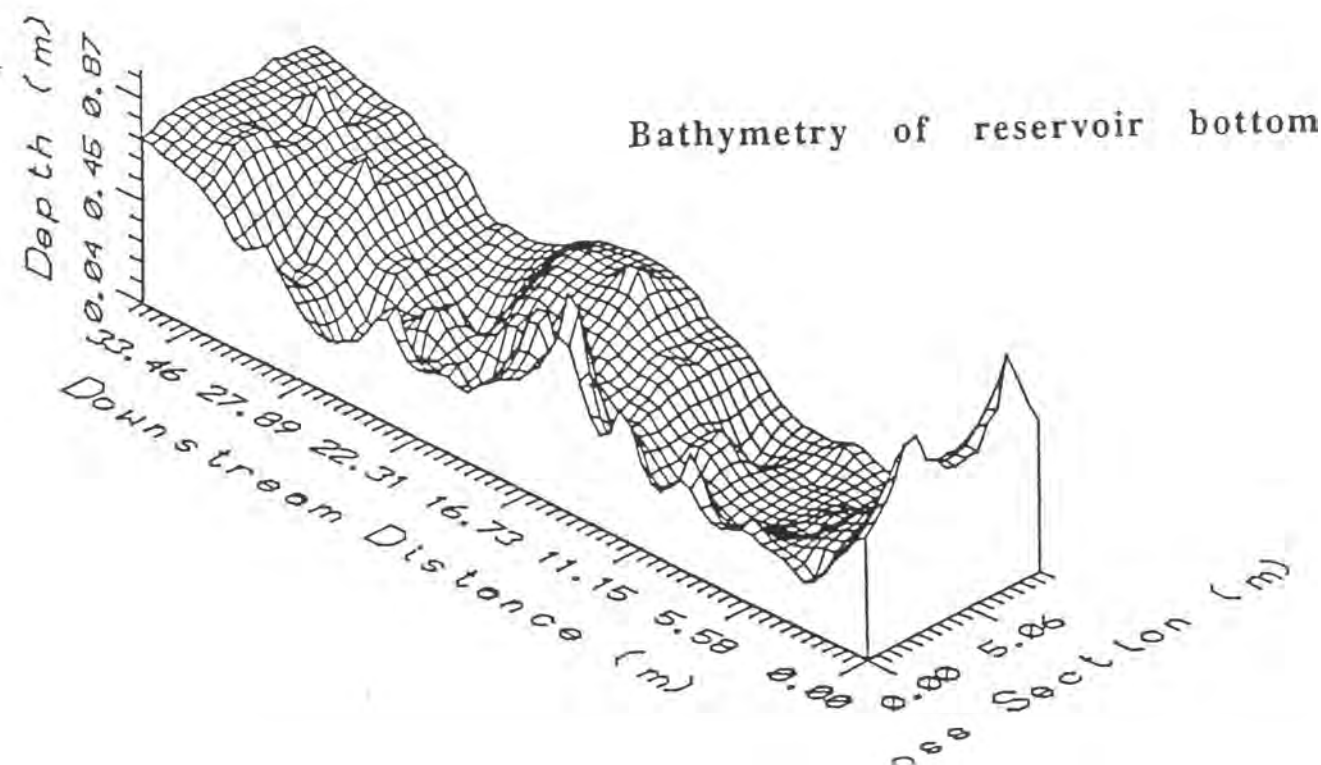
Figure 7



Figure 8: Bathymetry of Reservoir at Site 2



Bathymetry of sediment layer



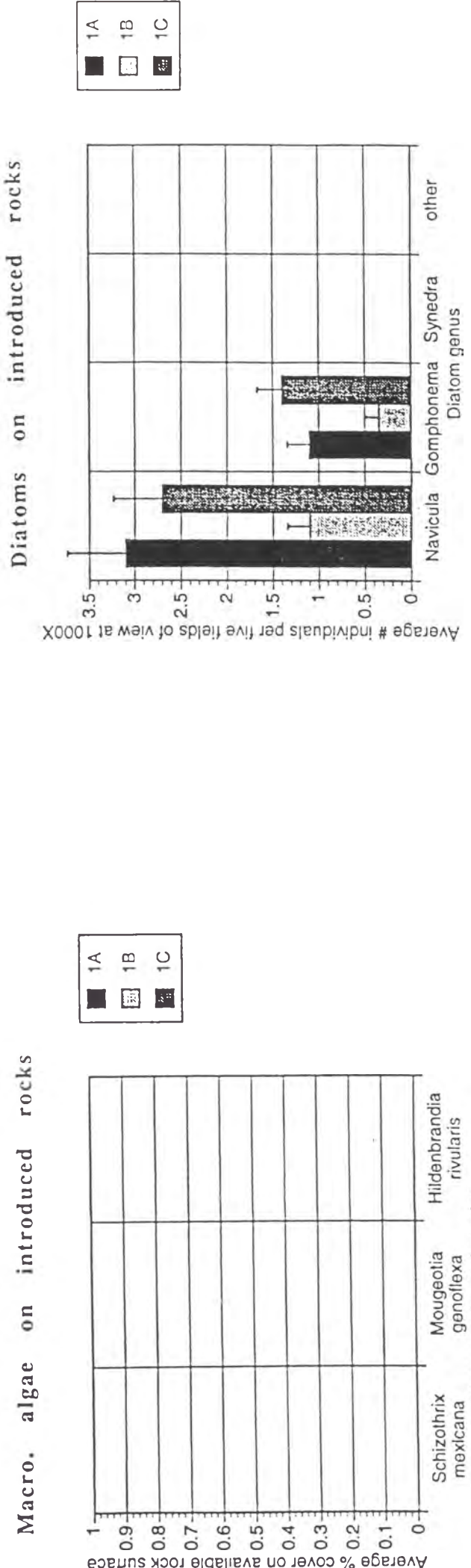
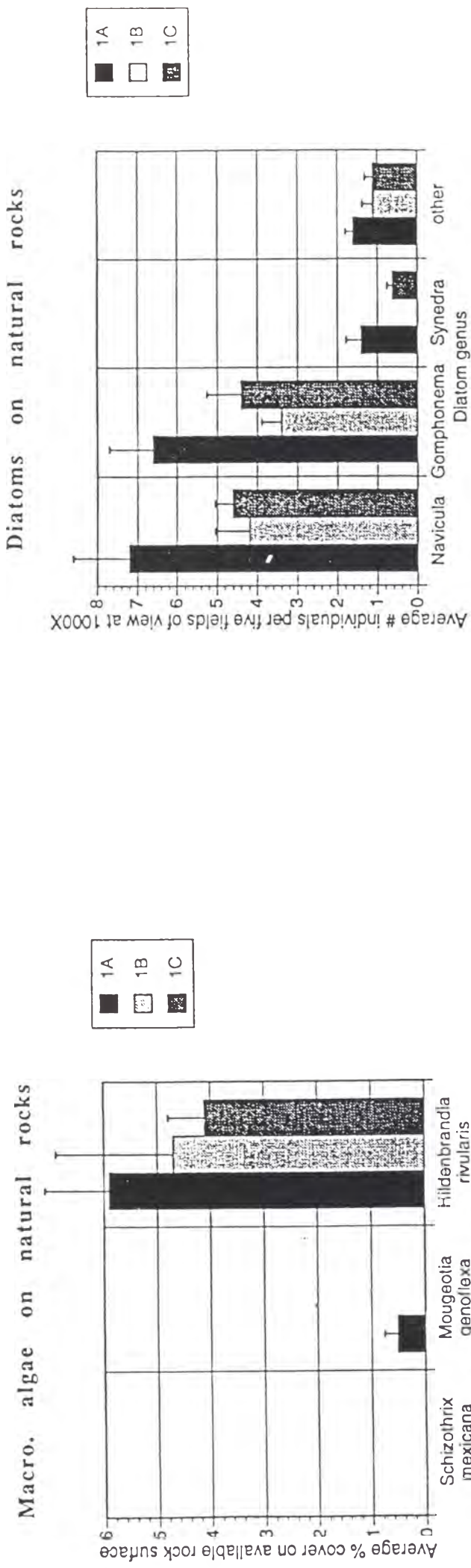
Bathymetry of reservoir bottom

Table 1: Physical characteristics of the study sites														
Site characteristic	Site 1: Natural canopy removal			Site 2: Canopy removal for farm			Site 3: Dam/reservoir			Site 4: Pineapple plantation/rifle			Site 5: Pineapple plantation/run	
	1A	1B	1C	2A	2B	2C	3A1	3A2	3B	3C	4A	4B	4C	5A
	(at)	(above)	(below)	(at)	(above)	(below)	(res.)	(falls)	(above)	(below)	(at)	(above)	(below)	(at)
Elevation (m)	31.6	33.5	30.3	14.5	15.6	14.3	18.5	18.5	19.2	17.5	39.6	41.1	37.1	38.5
Mean Water Temperature (C)	23.8	23.7	23.7	24.3	23.9	23.8	23.8	23.9	23.9	23.7	22.5	22.8	22.8	22.4
Mean Stream Depth (m)	0.1	0.08	0.1	0.26	0.18	0.2	0.35	0.33	0.28	0.29	0.15	0.16	0.18	0.34
Mean Current (m/s)	0.51	0.49	0.51	0.26	0.26	0.25	ND	1.06	0.29	0.22	0.44	0.58	0.55	0.27
Canopy (% open canopy)	29.2	14.3	14.1	50.5	15.1	15.6	18.2	22.4	19.1	17.2	17.4	13.3	17.9	18.5
Dissolved Oxygen (mg/L)							8.2	9.8	8.5	9.2				
Sedimentation (% available substrate covered with sediment)											0	0	0	3.1
														7.8
														14.1

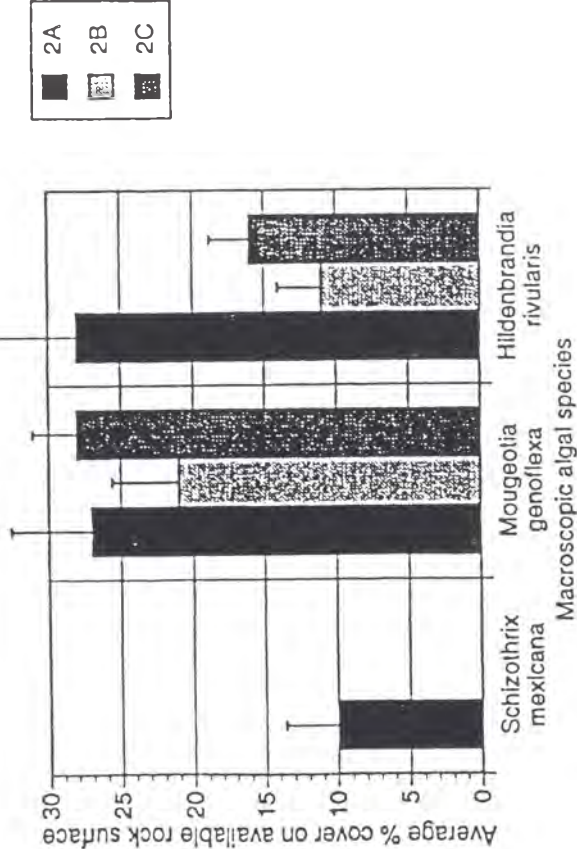
Measurement procedures are summarized in methods section. Dissolved oxygen was measured only at site 3, and percent sediment cover was measured only at sites 4 and 5.



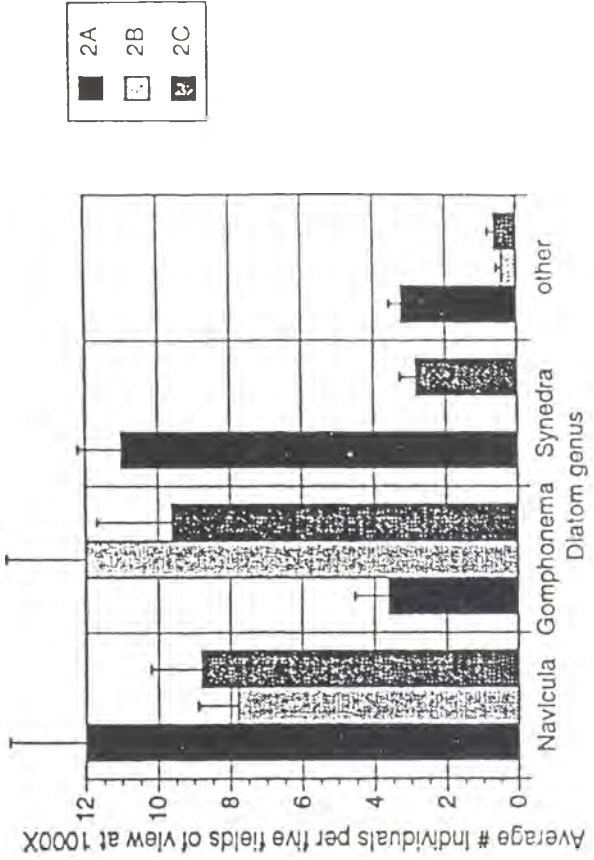
Figure 9: Algal Abundance at Site 1 (Natural canopy removal)



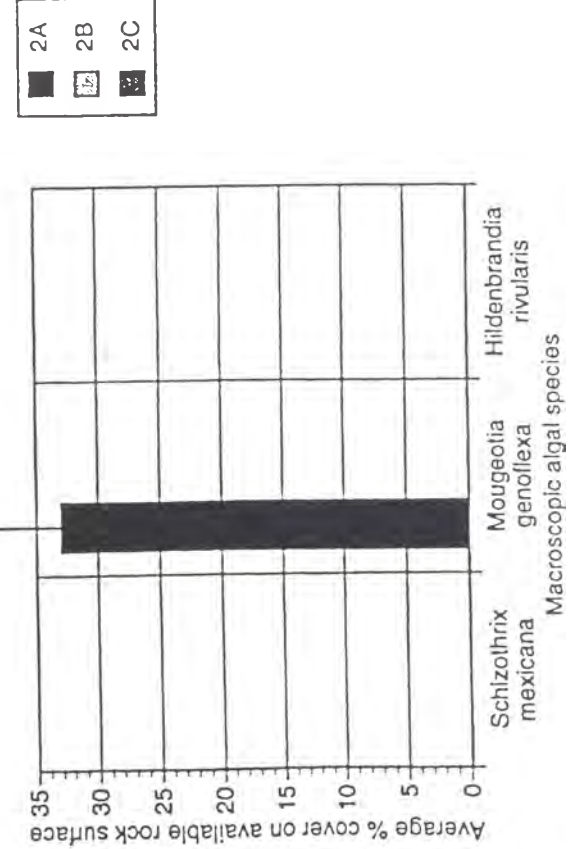
Macro. algae on natural rocks



Diatoms on natural rocks



Macro. algae on introduced rocks



Diatoms on introduced rocks

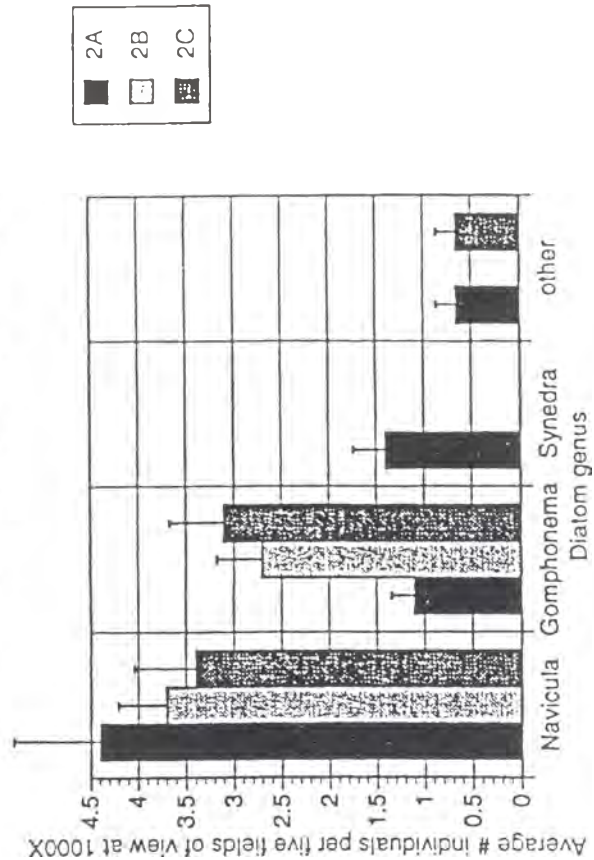


Figure 10

Extended lines=1 standard error (SE)

Figure 11: Algal Abundance at Site 3 (Dam/Reservoir)

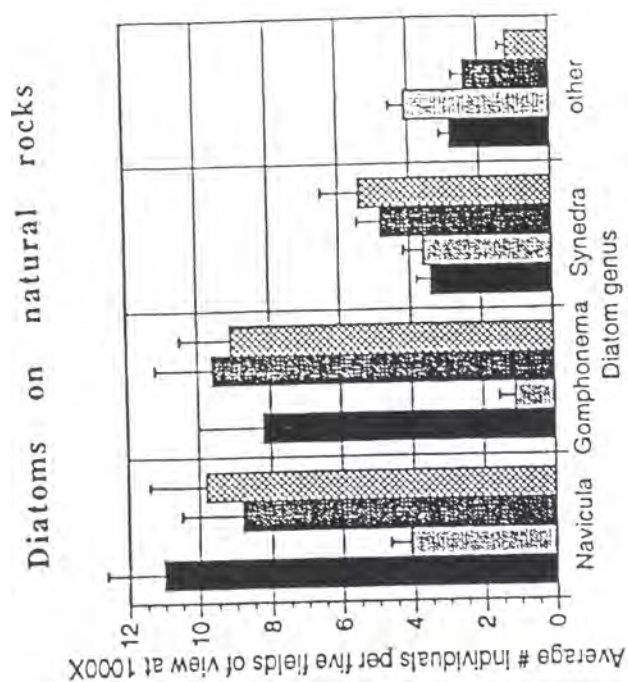


Figure 12: Algal Abundance at Site 3 (Dam/Reservoir)

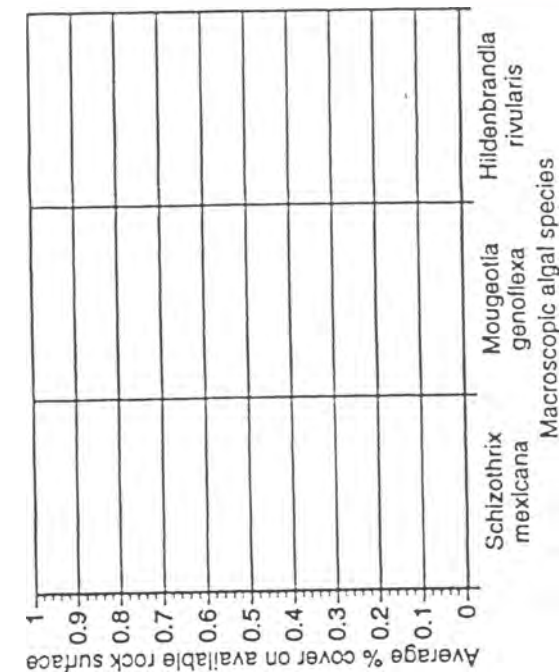


Figure 11: Algal Abundance at Site 3 (Dam/Reservoir)

Figure 12: Algal Abundance at Site 3 (Dam/Reservoir)



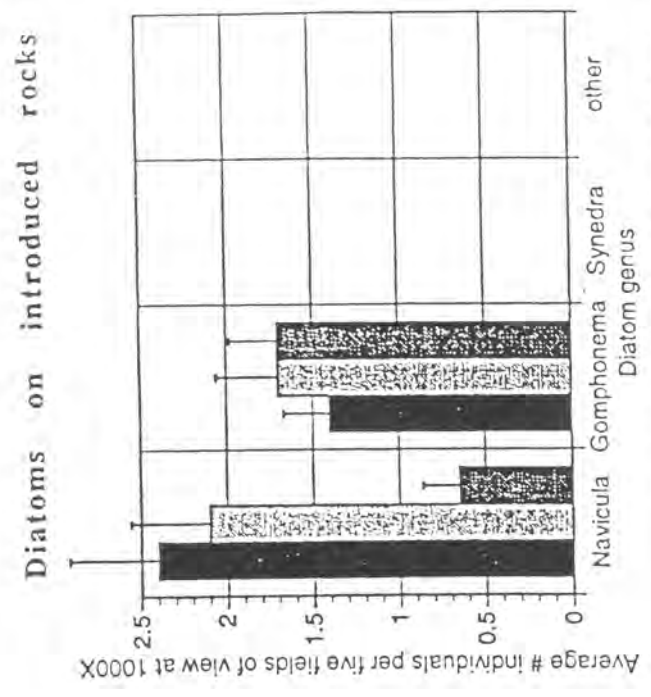
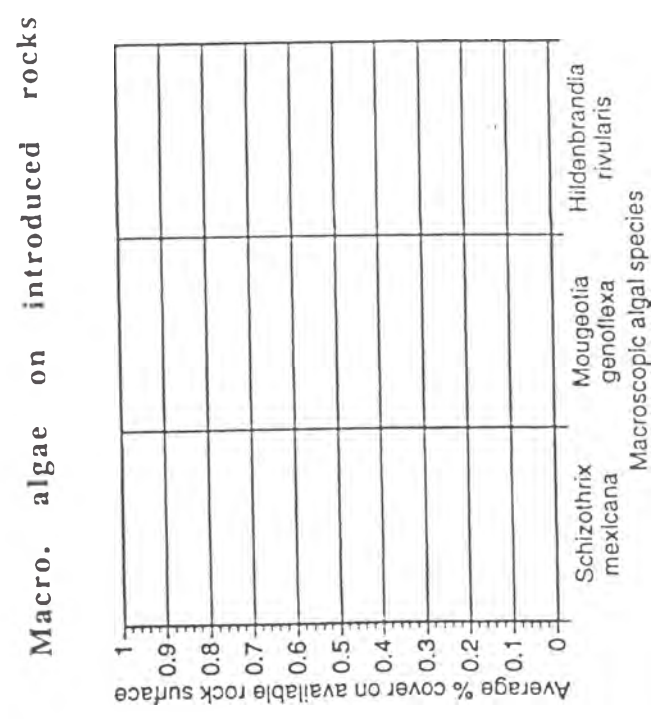
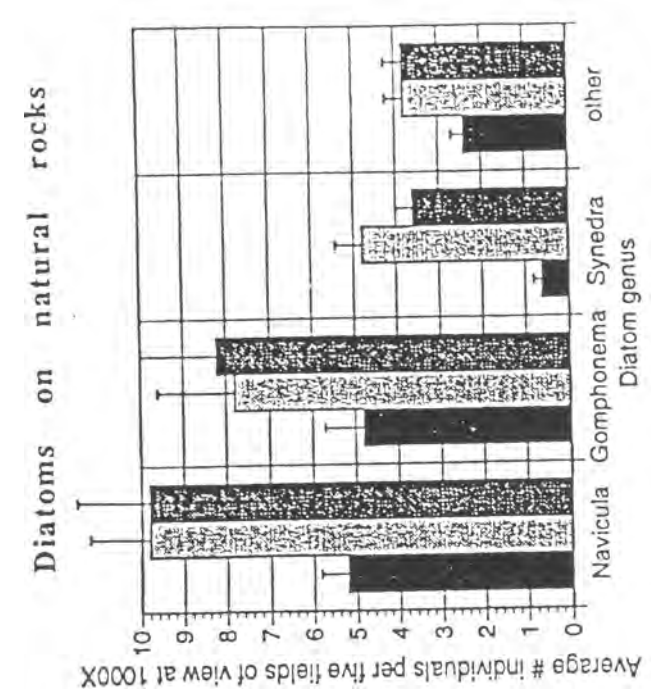
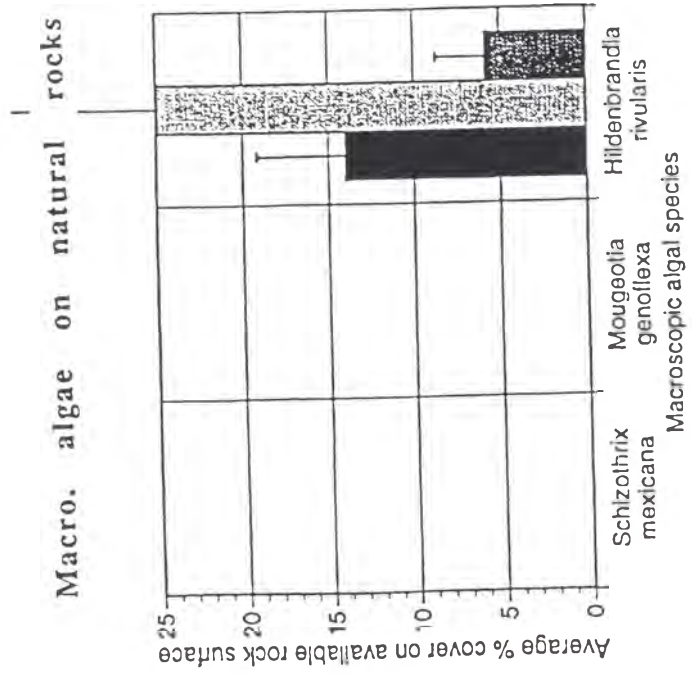


Figure 12

Extended lines=1 standard error (SE)

Figure 13: Algal Abundance at Site 5 (Pineapple plantation/run)

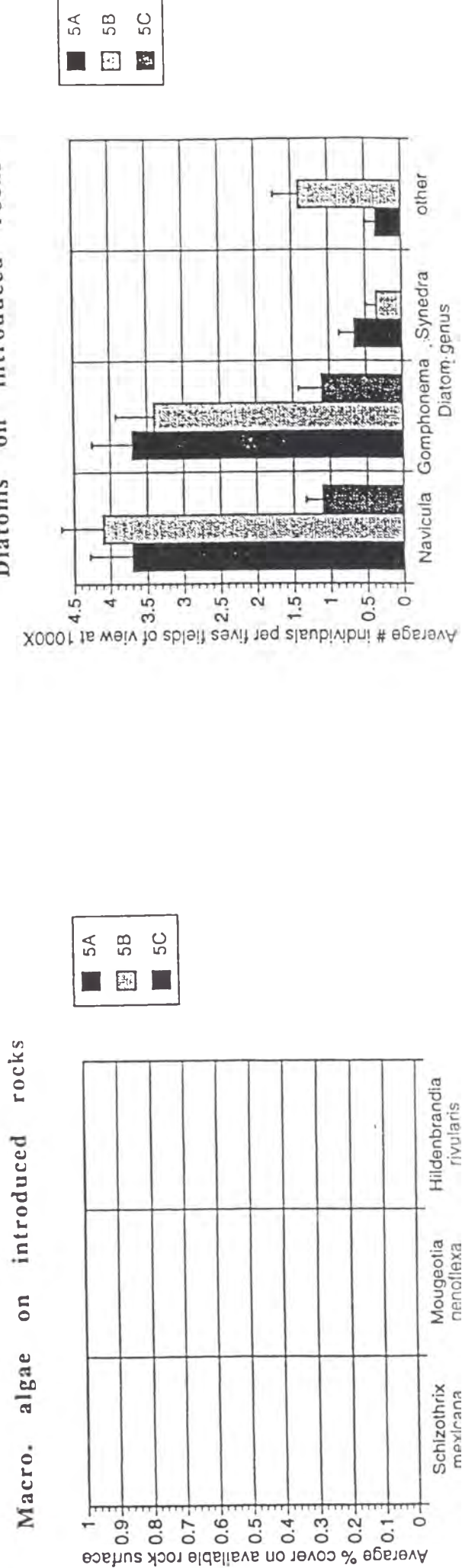
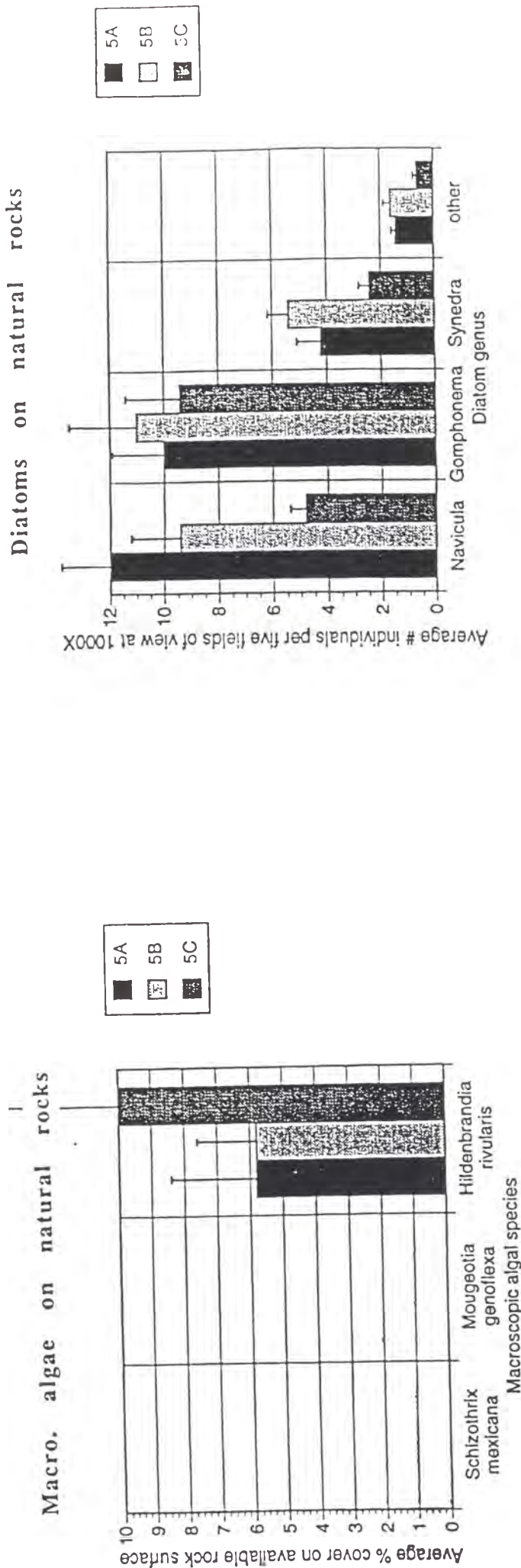




Table 2: Analysis of Variance F-test Values					
	Site 1: Natural canopy removal	Site 2: Canopy removal for farm	Site 3: Dam/reservoir	Site 4: Pineapple plantation/riffle	Site 5: Pineapple plantation/run
Part 1: Sampling of natural algal community					
<i>Schizothrix mexicana</i>		8.52, S			
<i>Mougeotia gonoflexa</i>	0.41, I	1.34, I	9.27, S		
<i>Hildenbrandia rivularis</i>	1.64, I	3.02, I	4.24, S	1.69, I	0.68, I
<i>Navicula</i>	3.18, I	3.44, S	1.50, I	2.30, I	2.45, I
<i>Gomphonema</i>	2.04, I	5.21, S	5.64, S	1.16, I	0.31, I
<i>Synedra</i>	6.83, S	12.85, S	0.78, I	5.16, S	0.79, I
other	0.11, I	7.33, S	1.60, I	2.26, I	1.53, I
Part 2: Sampling of introduced rocks					
<i>Schizothrix mexicana</i>					
<i>Mougeotia gonoflexa</i>		18.69, S			
<i>Hildenbrandia rivularis</i>					
<i>Navicula</i>	1.30, I	0.67, I	6.83, S	4.06, S	3.80, S
<i>Gomphonema</i>	3.85, S	2.64, I	3.05, I	0.73, I	2.48, I
<i>Synedra</i>		5.11, S	2.42, I		2.20, I
other		2.39, I	1.80, I		1.97, I

Table 2 shows the results of the analyses of variance conducted on the abundances of each algal type at each site. The numbers in the table indicate F-test results. Numbers followed by an I were below the critical value (specified using  $\alpha=0.05$  and  $df_1$  and  $df_2$  values representative of each sample size) and statistically insignificant. Those followed by an S indicate statistical significance. Blanks in the table occur where none of the specific algal type was found.

## Discussion

Huang and Boney (1983) noted that during recolonization events, diatoms are the fastest colonists of the algal community, and that they actually inhibit the initial colonization of macroscopic alga. As time goes on, the macroscopic alga are able to colonize and community structure is finally reestablished. This helps to explain the observation that only one set of the introduced rocks was colonized by macroscopic algae (*M. genoflexa*) during the four week period. Meanwhile, diatoms were very successful colonists on the introduced rocks, reaching almost half their natural-rock abundance in the same short period. In almost all cases, taxonomic representation of diatoms on the introduced rocks paralleled that of the natural rocks.

The effects of removed canopy seemed to be manifested in the algal communities of both sites 1 & 2. At site 1, however, the differences in algal type abundance may be too slight to conclude a disturbance effect. *M. genoflexa*, which grows more successfully in areas of high light (Prescott, 1954), was only present in the zone of open canopy, but it covered only .51% of available rock surface. This difference proved to be insignificant based on the AOV test. The low abundance of *M. genoflexa* could be related to the fact that the falling of the Tahitian chestnut tree was a recent occurrence (no detectable rot). There are few light gaps above or below the disturbance zone, and it is likely that there hasn't been ample time to allow for full-scale colonization of the algae.

Only the variation in *Synedra* at this site was statistically significant. As *Synedra* has high light demands (Smith, 1951), this could show a response to the open canopy. However, it is interesting to note that no *Synedra* individuals were present on the introduced rocks, when the rocks at other sites showed significant colonization. Also interesting to note is the fact that, though not AOV-significant, all the algal types were more abundant within the disturbed zone. This could indicate that even the algal types which don't require high light benefit from its presence. The most likely reason for the lack of significant difference between the algal communities at site 1 is the subtlety of the disturbance; the removed canopy has only lowered the percent cover from 85% to 70%. Though this allows twice as much light to reach the stream, the canopy is still basically closed.

At site 2, the effects of removed canopy seem more clearly signified. *S. mexicana* was found only in the zone of disturbance and covered a statistically significant 10% of available rock surface. *Synedra*'s high abundance in the open-canopy reach was also AOV-significant. Because of their high light requirements (Tiffany, 1951; Smith, 1951), these data lend well to the hypothesis that these groups have benefited from the removal of canopy. However, the other light-demanding algae, *M. genoflexa*, was no more successful in the open canopy area. Its abundance here was in fact lower than its downstream abundance. One possible explanation lies in the fact that *S. mexicana* was also present in this stream section. *S. mexicana* has higher photosynthetic rates than *M. genoflexa* (Drouet, 1939) and may thus be able outcompete this less efficient algae. Perhaps the most significant piece of data from site 2 was the presence of *M. genoflexa* on the introduced rocks. It occupied 33% of the available substrate, an amount even greater than its



natural rock abundance. This corresponds with Sze and Boden's (1986) description of algal succession, which describes red alga as the slowest colonist and green alga the fastest (of the macroscopic alga). Perhaps *M. genoflexa* is capitalizing not only on the increase in sunlight, but also on the absence of competition. *Navicula* and *H. rivularis* (though not AOV-significant) were more abundant within the disturbed section. Again, this suggests that even some of those alga tolerant of low light can benefit from the addition of light.

The algal community at site 3 revealed perhaps the strongest correlations with disturbance effects. At site 1A (reservoir), only *M. genoflexa* of the macroscopic alga was found, covering 9.01% of the available substrate. It was on portions of protruding rocks that *M. genoflexa* was growing. Perhaps the absence of competition from other macroscopic species and its tolerance for a wide range of currents allowed this species to grow successfully on available substrate. Note, however, that the abundance of *M. genoflexa* was lower than that occurring above and below the disturbance. This may reflect the fact that even the portions of protruding rock were covered with sporadic patches of sediment. The AOV-significant lack of *H. rivularis* in the reservoir corresponds with its habitat requirement of rapid, turbid waters (Smith, 1933).

In the falls section, meanwhile, *H. rivularis* was present while *M. genoflexa* was absent. This again corresponds with the habitat demands of these species. In fact, *H. rivularis* was almost 100% more abundant in the falls than it was in the upstream and downstream sections, suggesting that the more turbulent water has enhanced its growth. The lack of *M. genoflexa* in this section was also statistically significant, corresponding with its intolerance of excessively rapid waters (Tiffany, 1951). Diatoms were far less abundant in the falls (though only *Gomphonema*'s variation proved AOV-significant), suggesting that the constant scouring forces don't allow significant colonization. In fact, no diatoms were found on the inserted rocks within this section while approximately .30 ind./field of view were found on all three of the other rock sets. Strangely, *Synedra*, which because of its size, should be most susceptible to scouring, was approximately equal in abundance in all four subsites. In general, diatoms were most abundant in the reservoir. This suggests that their wide tolerance of currents and substrate type (Tiffany, 1937; Smith, 1933) and the lack of scouring forces has allowed for greater colonization.

At sites 4 & 5, the data revealed no obvious patterns; there was no detectable effect on the algal community. At site 4, *H. rivularis* was the only macroscopic species present, and it was most abundant in the disturbed zone. It was less than half as abundant in the downstream section, but this most likely can't be attributed to the presence of toxins, since the species was successful in the disturbed zone. Diatoms were, however, clearly less abundant in the disturbed section; they were approximately half as abundant in this section as they were in the upstream and downstream sections. Perhaps the chemicals from the herbicides and pesticides were having an effect within this zone. Though the exposure to toxins is brief, it is within the disturbed zone that the exposure would be the most concentrated. At the downstream section, the chemicals would be slightly more dilute, lessening their impact. However, this hypothesis is confounded by Darley's (1982) observation, mentioned in the introduction, that diatoms are generally the least susceptible of the alga to presence of pollution and toxins.



At site 5, again little effect on the algal community was found. *H. rivularis* was actually most abundant in the downstream section. In addition, the presence of diatoms was fairly consistent throughout the sites. Although the pineapple plantation is causing increased sedimentation and an influx of toxins, these disturbances seem to have little effect on the algal community. Perhaps this can be attributed to the fact that the Mahaerua River has a relatively fast current (table 1), preventing significant sedimentation from accumulating and preventing prolonged exposure to toxins. A study of the pools along this stream section may indeed demonstrate a disturbance effect, but there were few pools within the vicinity of the plantation. As the sedimentation analysis revealed, there was no detectable sediment in the riffle sections and only minor sedimentation in the runs (3% above, 8% at and 14% below).

### Conclusions

The quantitative assessment of the algal communities at sites 1-5 suggest that disturbance has affected algal species composition and abundance only at the sites of removed canopy and the site of the dam. At these sites, the distributions of the macroscopic species seem to conform to their respective habitat requirements. At sites 1 and 2, the effect of added light enhancing the entire algal community, especially *S. mexicana* and *M. genoflexa*, was apparent. At site 3, the effect of stagnant waters limiting *H. rivularis* and turbid waters limiting *M. genoflexa* was also apparent.

The diatom community of Moorea didn't reveal such clear patterns. One possible reason is that the diatoms of Moorea's streams are generally less specific in habitat association (Smith, 1951). Another reason could be that the diatoms were quantified only on the genus level. It is possible that a study on species abundance could have reflected a disturbance impact. While the diatom genera and even the dominant species within each genus were easily distinguished, the quantification of the less abundant species was very subjective. Nonetheless, the diatoms did show some interesting distribution patterns which may well represent disturbance effects. In particular, the distributions of *Synedra* seemed to correspond with its high light requirements. Also, though there was little statistical significance to infer causation, both *Navicula* and *Gomphonema* were more abundant in open canopy areas. At the site of the falls, the low abundance of diatoms supports the hypothesis that the scouring forces of the water limit colonization.

Part 2 of the experiment, the sampling of ~~the~~ inserted rocks, seemed to function only as a means to assess the initial stages of diatom colonization. As the figures reveal, diatom abundance on the introduced rocks corresponded well with their natural rock abundances. Four weeks is clearly not long enough an interval to allow establishment of the natural algal community structure. Again, I refer to Huang and Boney (1983) who noted that initial recolonization by diatoms inhibits recolonization by macroscopic alga. Sze and Boden (1986) also explained that in recolonization events, red algae, because of its slower growth rates and lower photosynthetic levels, is a late successional form and is usually the last of the alga to reestablish its normal community levels. This explains why *H. rivularis* was so consistently abundant within all of the sites yet failed to colonize the inserted rocks in four weeks' time. The fact that macroscopic alga require a longer period to recolonize habitat

heightens the implications of *M. genoflexa*'s colonization of site 2A's rocks. Perhaps only with such a high input of light was this species able to colonize these rocks in such a short time period. Effects of disturbance could also have been made more clear if the sample sizes had been larger; 10 rocks per site for macroscopic algae and five rocks for diatoms may have been too small to detect a reaction to disturbance. This is especially true for the introduced-rock sampling, where the sample size was only three.

It will be interesting to observe the degree of colonization on these rocks at future dates. One would expect an equilibrium to be reached, where the species composition and abundance occurring on the rocks corresponds with that of the natural community surrounding them. It is important that other communities within the larger stream community are studied in similar fashion. Eventually, a full picture of the stream community can be established, and one can determine the impact of stream disturbance. This information would ideally be put to use on Moorea and in other locations to ensure the long-term health of the stream community.

### Acknowledgments

For assistance with the identification of the macroscopic algal species, I thank P. Silva of the University of California Herbarium, Oakland, California. D. Erman of the University of California Forestry and Conservation Department supplied the equipment to conduct the Winkler method and was very helpful in giving information and advice concerning the study of freshwater communities. I thank the French Research Station on Moorea for the use of their balance and for the generous sharing of their library material, without which I would not have been able to identify the freshwater diatoms of Moorea. C. D'Antonio of the University of California Integrative Biology Department was especially helpful with the logistics and methodologies of the experiment. The hours of time given by S. Siegel provided the stream profiles and graphical presentations for the experiment. Last, I thank L. Vaughan for his help in receiving permission to conduct work at my sites and for his never-ending input and support for this project.

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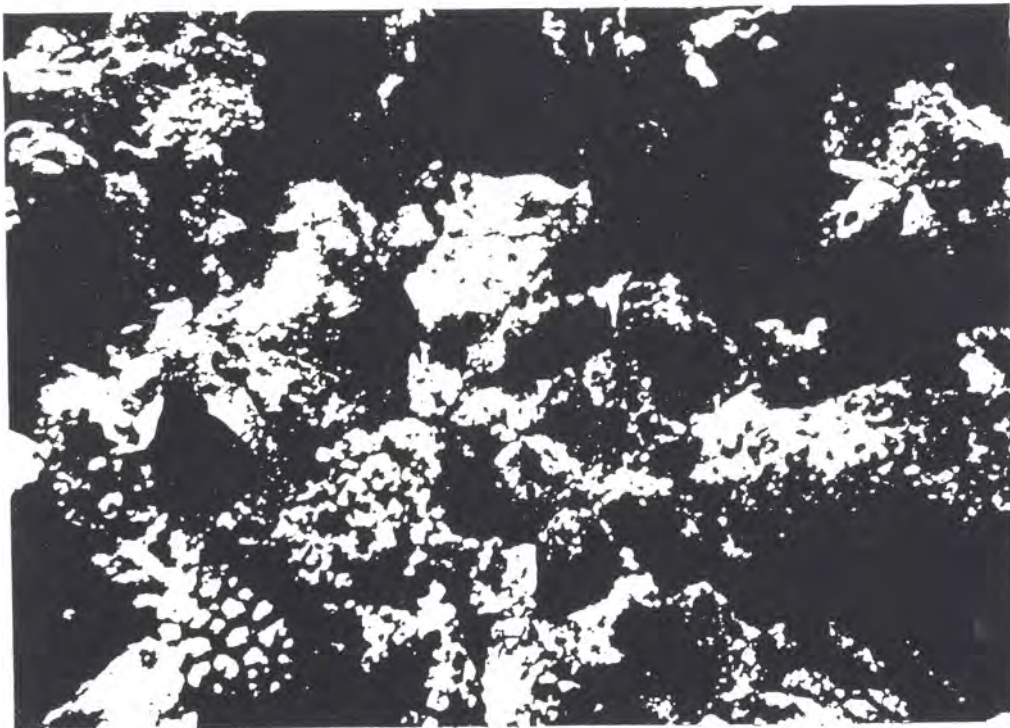
Appendix 1: Table of Natural Algal Community Sampling Data

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	Site 1: Natural canopy removal						Site 2: Canopy removal for farm						Site 3: Dam/reservoir						Site 4: Pineapple plantation/rifle				Site 5: Pineapple plantation/run								
	1A		1B		1C		2A		2B		2C		3A1		3A2		3B		3C		4A		4B		4C		5A		5B		5C
	(at)	(above)	(above)	(below)	(below)	(below)	(at)	(at)	(above)	(below)	(below)	(res.)	(falls)	(above)	(below)	(at)	(at)	(above)	(below)	(below)	(at)	(at)	(above)	(below)	(at)	(at)	(above)	(above)	(below)		
Macroscopic algae species (average % cover on available rock surface) [SE in brackets, n=10]																															
<i>Schizothrix mexicana</i>	0	0	0	0	0	0	10 [3.6]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mougeotia genoflexa</i>	0.51 [.25]	0	0	0	0	0	27 [5.6]	21 [4.6]	28 [3.1]	28 [3.1]	28 [3.1]	11 [4.8]	0	15 [2.5]	20 [3.4]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hildenbrandia rivularis</i>	5.9 [1.2]	4.7 [2.2]	4.1 [.69]	4.1 [.69]	4.1 [.69]	4.1 [.69]	28 [9.1]	11 [3.0]	16 [2.8]	16 [2.8]	16 [2.8]	0	9.3 [6.6]	3.5 [.71]	4.6 [1.4]	14 [5.2]	25 [11]	5.8 [2.9]	5.8 [2.9]	5.8 [2.9]	5.8 [2.6]	5.8 [2.6]	5.8 [2.6]	5.8 [2.6]	5.8 [2.6]	5.8 [2.6]	5.8 [2.6]	5.8 [2.6]	5.8 [2.6]	5.8 [2.6]	
Diatom genus presence (average # individuals per 5 fields of view=1 rock at 1000X) [SE in brackets, n=5]																															
<i>Navicula</i> (7 spp. present)	7.2 [1.4]	4.2 [.85]	4.6 [.45]	4.6 [.45]	4.6 [.45]	4.6 [.45]	12 [2.1]	7.8 [1.1]	8.8 [1.4]	8.8 [1.4]	8.8 [1.4]	11 [1.6]	4.1 [.58]	8.8 [1.7]	9.8 [1.6]	5.2 [.63]	9.8 [1.4]	9.8 [1.7]	9.8 [1.7]	9.8 [1.7]	9.8 [1.7]	9.8 [1.7]	9.8 [1.7]	9.8 [1.7]	9.8 [1.7]	9.8 [1.7]	9.8 [1.7]	9.8 [1.7]	9.8 [1.7]	9.8 [1.7]	
<i>Gomphonema</i> (4 spp. present)	6.6 [1.1]	3.4 [.49]	4.4 [.85]	4.4 [.85]	4.4 [.85]	4.4 [.85]	3.6 [.94]	12 [2.2]	9.6 [2.1]	9.6 [2.1]	9.6 [2.1]	8.2 [1.8]	1.1 [.45]	9.6 [1.6]	9.1 [1.4]	4.8 [.90]	7.8 [1.8]	8.2 [1.8]	8.2 [1.8]	8.2 [1.8]	8.2 [1.8]	8.2 [1.8]	8.2 [1.8]	8.2 [1.8]	8.2 [1.8]	8.2 [1.8]	8.2 [1.8]	8.2 [1.8]	8.2 [1.8]	8.2 [1.8]	
<i>Synedra</i> (1 spp. present)	1.4 [.38]	0	0.61 [.15]	0.61 [.15]	0.61 [.15]	0.61 [.15]	11 [1.2]	0	2.8 [.45]	2.8 [.45]	2.8 [.45]	3.4 [.40]	3.6 [.58]	4.8 [.67]	5.4 [1.1]	0.61 [.20]	4.8 [.62]	3.6 [.40]	3.6 [.40]	3.6 [.40]	3.6 [.40]	3.6 [.40]	3.6 [.40]	3.6 [.40]	3.6 [.40]	3.6 [.40]	3.6 [.40]	3.6 [.40]	3.6 [.40]	3.6 [.40]	3.6 [.40]
other (6 spp. present)	1.6 [.20]	1.1 [.27]	1.1 [.21]	1.1 [.21]	1.1 [.21]	1.1 [.21]	3.2 [.36]	0.41 [.15]	0.61 [.20]	0.61 [.20]	0.61 [.20]	2.8 [.30]	4.1 [.45]	2.4 [.34]	1.2 [.23]	2.4 [.30]	3.8 [.42]	3.8 [.45]	3.8 [.45]	3.8 [.45]	3.8 [.45]	3.8 [.45]	3.8 [.45]	3.8 [.45]	3.8 [.45]	3.8 [.45]	3.8 [.45]	3.8 [.45]	3.8 [.45]	3.8 [.45]	3.8 [.45]

Appendix 2: Table of Introduced Rock Sampling Data																
	Site 1: Natural canopy removal			Site 2: Canopy removal for farm			Site 3: Dam/reservoir				Site 4: Pineapple plantation/rifle			Site 5: Pineapple plantation/run		
	1A (at)	1B (above)	1C (below)	2A (at)	2B (above)	2C (below)	3A1 (res.)	3A2 (falls)	3B (above)	3C (below)	4A (at)	4B (above)	4C (below)	5A (at)	5B (above)	5C (below)
Macroscopic algae species (average % cover on available rock surface) [SE in brackets, n=3]																
<i>Schizothrix mexicana</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mougeotia genoflexa</i>	0	0	0	33 [10]	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hildenbrandia rivularis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diatom genus presence (average # individuals per five fields of view=1 rock at 1000X) [SE in brackets, n=3]																
<i>Navicula</i> (5 spp. present)	3.1 [64]	1.1 [24]	2.7 [53]	4.4 [92]	3.7 [51]	3.4 [64]	3.7 [52]	0	2.4 [41]	2.1 [35]	2.4 [52]	2.1 [46]	0.65 [21]	3.7 [58]	4.1 [58]	1.1 [23]
<i>Gomphonema</i> (3 spp. present)	1.1 [24]	0.35 [15]	1.4 [27]	1.1 [24]	2.7 [48]	3.1 [57]	0.65 [21]	0	2.1 [43]	2.4 [53]	1.4 [27]	1.7 [36]	1.7 [28]	3.7 [55]	3.4 [52]	1.1 [32]
<i>Synedra</i> (1 spp. present)	0	0	0	1.4 [34]	0	0	0.65 [21]	0	0	0.65 [31]	0	0	0	0.65 [21]	0.35 [15]	0
other (4 spp. present)	0	0	0	0.65 [21]	0	0.65 [21]	0.35 [15]	0	0.35 [15]	0	0	0	0	0.35 [15]	1.35 [34]	0



Territory Structure and  
Aggregated Behavior  
of Damselfish  
(*Stegastes nigricans*)  
on Moorea, French Polynesia



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IB 158, Fall 1992



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Abstract

A study was conducted on the damselfish, *Stegastes nigricans*, on the back reef of the island of Moorea (17° 30' S, 149° 50' W) between 8 October 1992 and 21 November 1992. These fish aggregate in groups of varying size and selectively defend algal mat territories against both conspecific and heterospecific intruders. Sizes of 16 territories were mapped using perimeter point and transect methods, and a correlation was found between fish density and algal mat surface area. Behavioral data in the form of time/energy budgets were also collected. Time/energy defense indexes were recorded from sites of varying size, in both inshore and offshore habitats. Data indicate that territory size has little to do with amount of time individuals spend on defense; however, variation does occur with regard to location. Inshore territories have fewer intrusions, both conspecific and heterospecific, than their offshore counterparts. It is expected that inshore territories, therefore, would have a lower population density per unit area due to decreased competitive pressure. However, slope analysis of the density regressions for these two regions does not show the expected significant difference. It was concluded from these data that intraspecific pressures likely have a greater influence on population density for a given territory.

Introduction

Damselfish of the family Pomacentridae are among the most territorial animals on coral reefs (Harrington et al, 1990). Pomacentrid fishes "farm" algal territories (Lassuy, 1980), which they aggressively defend against conspecific and heterospecific intruders alike (Itzkowitz, 1990). Resources defended include food (Losely, 1982;

Thresher, 1976; Brawley and Adey, 1977, and others), shelter (Thresher, 1976), mating territories (Itzkowitz, 1977), and nesting sites (Myrberg and Thresher, 1974). The Dusky Gregory damselfish (*Stegastes nigricans*), found commonly in the lagoons of Moorea, aggregate in territories that provide food (in the form of "farmed" algal mats), shelter, and a spawning site.

*S. nigricans* territories in Moorea can be categorized into three distinct habitats, as defined by Klumpp et al, (1989): (1) zones of relatively high topographic relief among massive coral substrata, (2) areas of low coral ledges, and (3) branching *Acropora* thickets. Population counts from my field work indicate densities range from 1 to greater than 100 fish per territory.

At the lagoon off motu Temae, on the north-eastern side of the island (Figure 1), there are two distinct habitats where damselfish are found: those found inshore (less than 50 m from shore) are comprised of sparse substrata with low diversity of fish species; in contrast, the offshore regions (greater than 150 m from shore) offer greater relief and higher species diversity (Figure 2).

Territories can be characterized in terms of two dimensional living space, and in terms of actual surface area, by taking into account the topography (three-dimensional). The latter value is related to the food productivity of a given area, as algal mats are fairly uniform, and cover nearly all dead coral surfaces within a territory. It is expected that a better correlation will be noted between fish density and this measurement.

Fish densities in conjunction with behavioral observations will be used to compare inshore and offshore habitats, and small and large territories. It is hypothesized that fish of the inshore habitat will be less densely distributed due to decreased heterospecific competition for resources, and that fish within these territories will expend less energy defending when compared to their offshore counterparts. Also it is hypothesized that fish of small territories will spend a greater proportion of their energy defending against heterospecific intruders, while those of the large territories will have more time to devote to conspecific territorial disputes.

### Methods and Materials

Damselfish were studied at Temae reef on the north east corner of Moorea (17° 30' S, 149° 50' W) between 8 October 1992 and 21 November 1992. A total of 16 territories were studied: eight inshore, and eight offshore. All fell into the type 1 category, as defined by Klumpp et al (1989). The 16 study sites were chosen non-randomly, on the basis of size variation and ease of mapping.



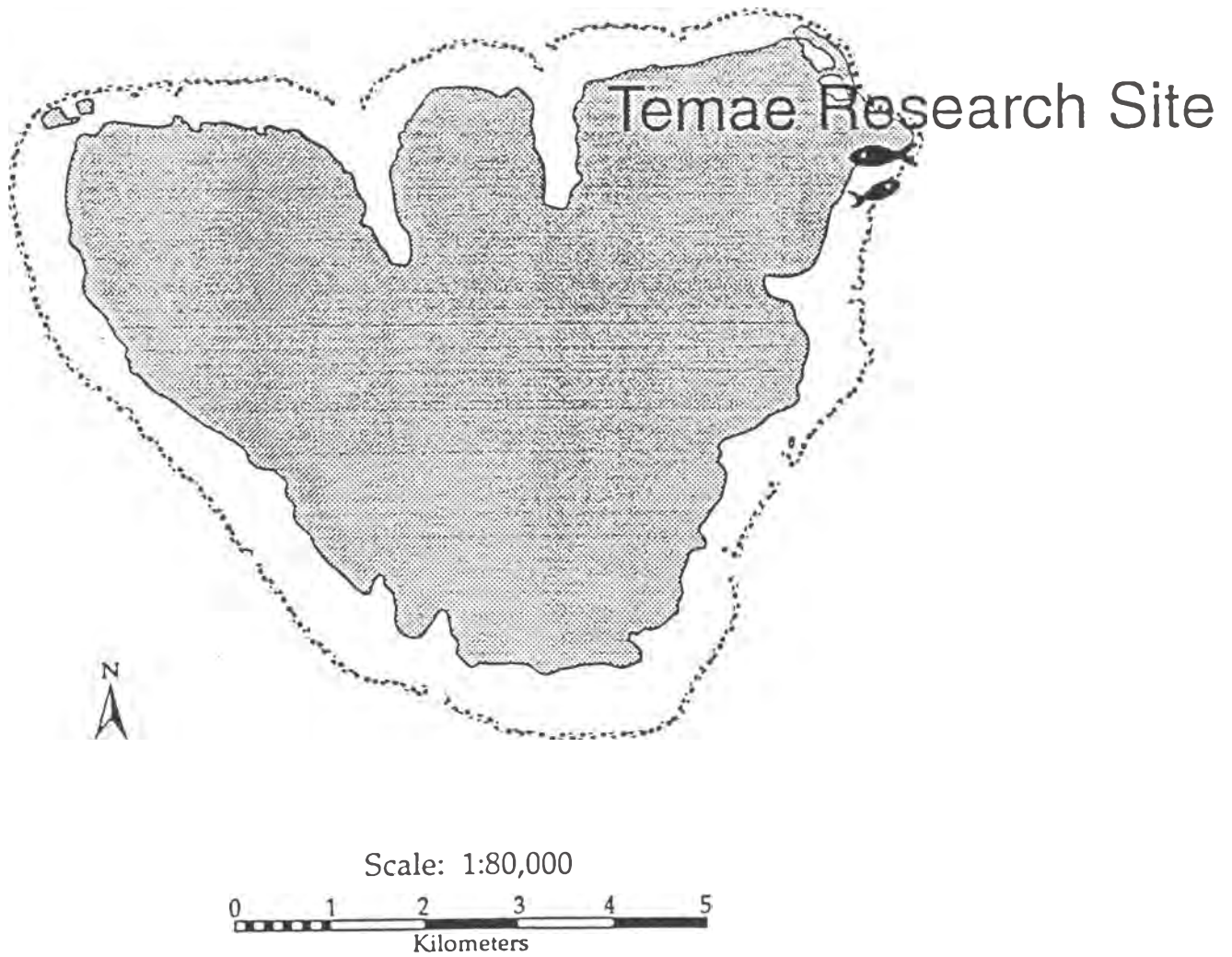
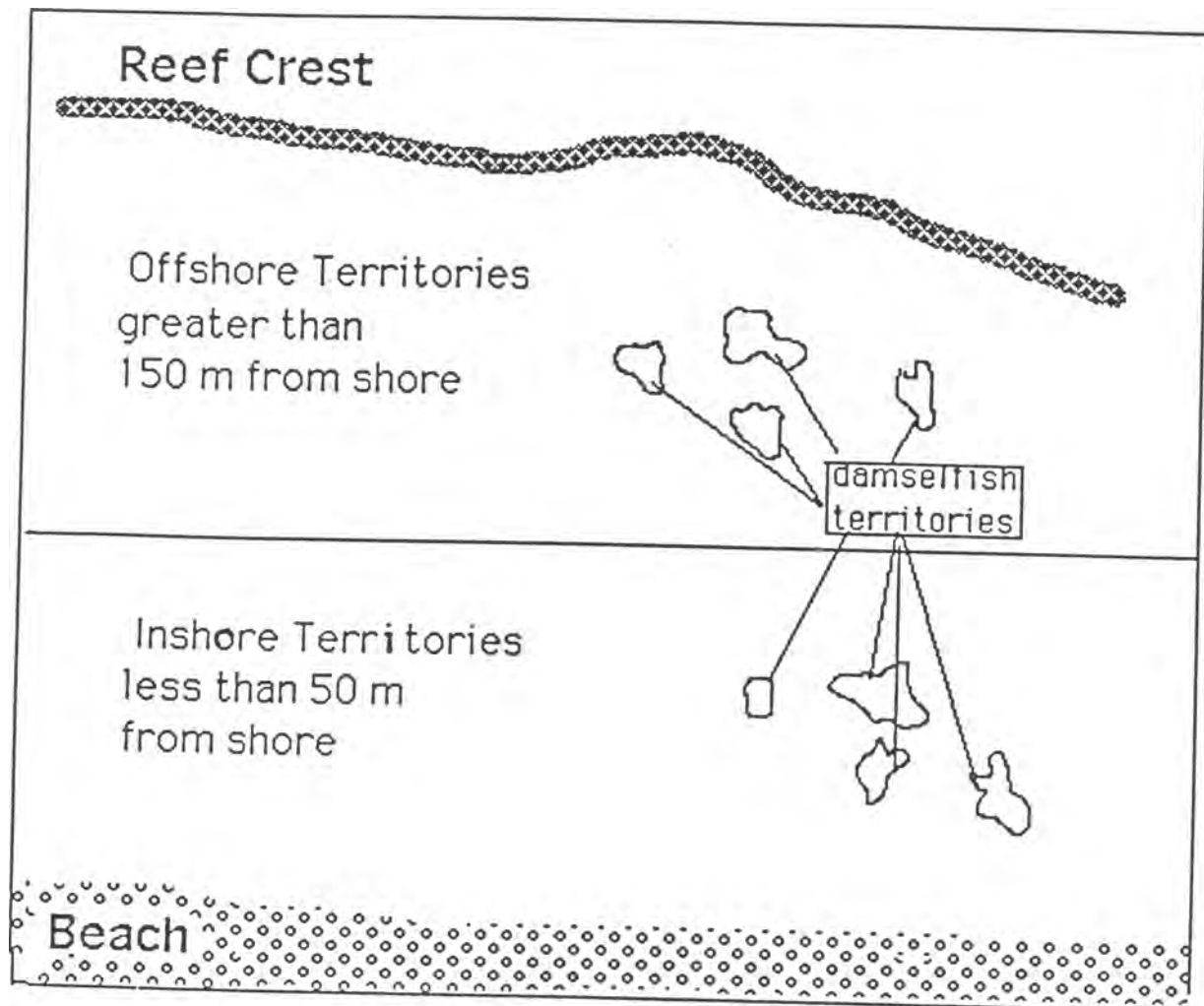


FIGURE 1: STUDY SITE LOCATION



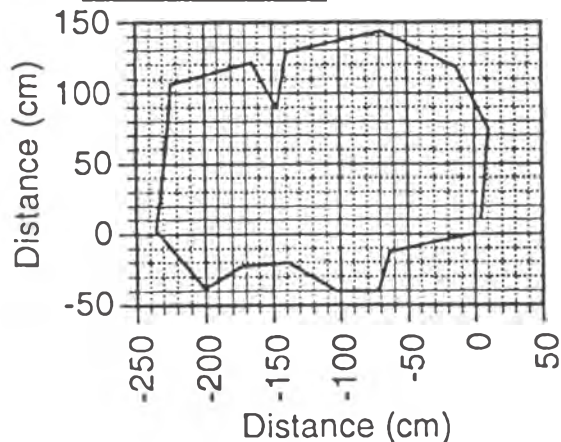


Representation  
of Temae  
Research Site

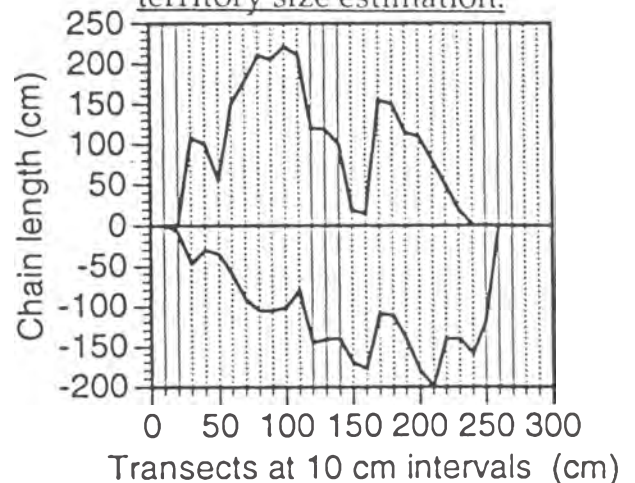
FIGURE 2

Territories were defined by three components: areas covered by algal turf (Brawley et al, 1977), furthest points of feeding, and boundaries in which the resident patrolled (Harrington et al, 1990), all of which were correlated to the same area. Since it was unknown how damselfish actually perceive their own territories, sizes were measured using two alternate methods. Method 1 consisted of polar coordinate perimeter mapping, giving estimations of two dimensional area only (Figure 3). This measurement corresponds to living space in a single plane, with regard to territorial defense. Method 2 was employed to measure topographic surface areas of territories using chain (2.5-cm link) transects (Klumpp et al, 1989). This second method assumes that damselfish define their territory by algal mat area. Transects at ten-centimeter intervals were run in straight lines across the surface contour of each territory (Figure 4).

**FIGURE 3:** example of polar coordinate method of territory size estimation.



**FIGURE 4:** example of transect method of territory size estimation.



Fish counts were made periodically during mapping, and again immediately after mapping was complete. Maximum values were used.

Behavioral observations were made over a two week period, and were used to construct time budgets for fish in different sized territories. Because it had been observed that *S. nigricans* diurnal activities vary with time (Galzin, 1985), data collection began at the same time each day, with order of observations alternated to minimize bias. Territories were divided into four size designations: small (2-4 fish), medium (7-8 fish), large (12 fish), and massive

(greater than 17 fish). Eight classes were then defined by the four size designations applied to both the inshore and offshore. Eight damselfish from each class were then observed for five minutes each, for a total of 64 fish observed (Table 1). Care was taken to observe each fish only once, so fish from several territories were used for the small and medium size classes.

TABLE 1: Behavioral Observations

Class #	# Fish	Class Designation	Location	# Fish Observed
1	2-4	small	inshore	8
2	7-8	medium	inshore	8
3	12	large	inshore	8
4	> 17	massive	inshore	8
5	2-4	small	offshore	8
6	7-8	medium	offshore	8
7	12	large	offshore	8
8	> 17	massive	offshore	8

TOTAL FISH OBSERVED = 64

*S. nigricans* exhibited defensive behavior, in which both conspecifics and heterospecifics were driven out of a territory. Three types of defensive behavior were defined and recorded as numbers of events: Erection of dorsal spines (denoted E) was the first show of aggression toward an intruder (and usually resulted in a chase). In the second response, called a short chase (S), the damselfish chased an intruder to the edge of the territory only. The third response, the long chase (L), consisted of a chase event that continued beyond the territory boundary. These categorized number counts were transformed into time/energy indices by multiplication with coefficients 1, 2, 3 respectively. The coefficients were chosen because observations indicate that (S) takes roughly twice the time (and substantially more energy) as (E), and (L) takes approximately three times that amount on average.

### Results

Density regressions were generated of area versus number of fish for each territorial characterization (Figure 5a,b).

Fig. 5a: density regression ,Method 1,  
(polar coordinate, all 16 sites)

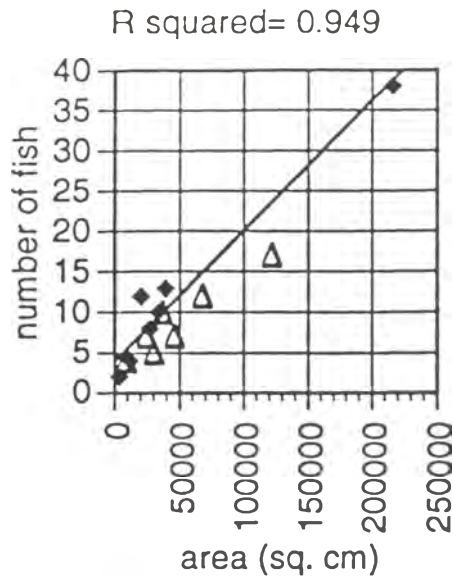


Fig 5b: density regression for transect  
maps, Method 2, all 16 sites

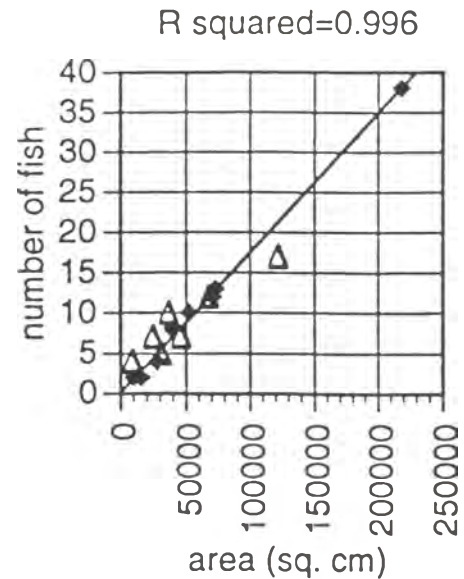


Fig 5c: density regression, inshore

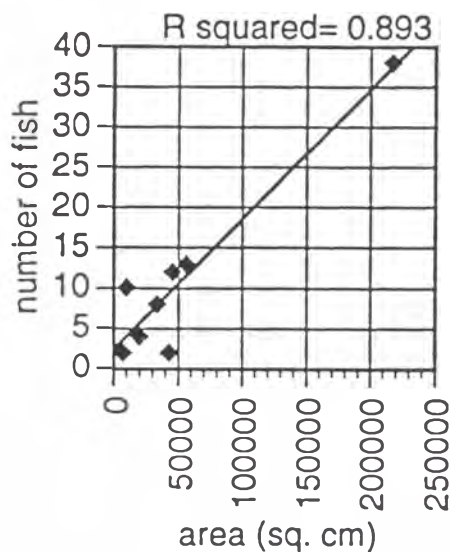
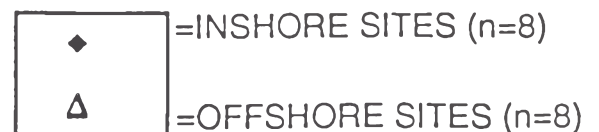
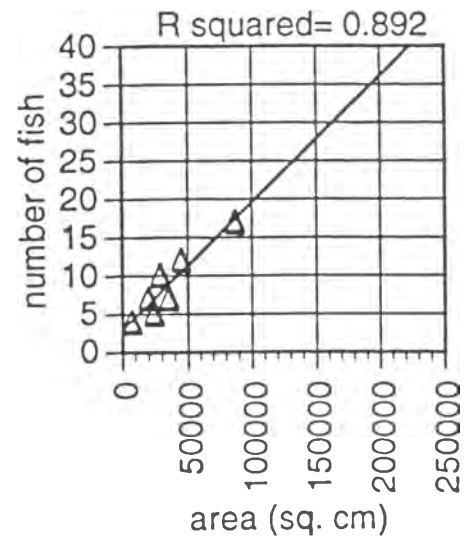


Fig. 5d: density regression, offshore



**FIGURE 5:** Fish density plots comparing mapping  
techniques and inshore vs. offshore sites.



FIGURE 6: Time/energy territorial defense—breakdown by species  
 index= sum of 1X(E), 2X(S), and 3X(L)

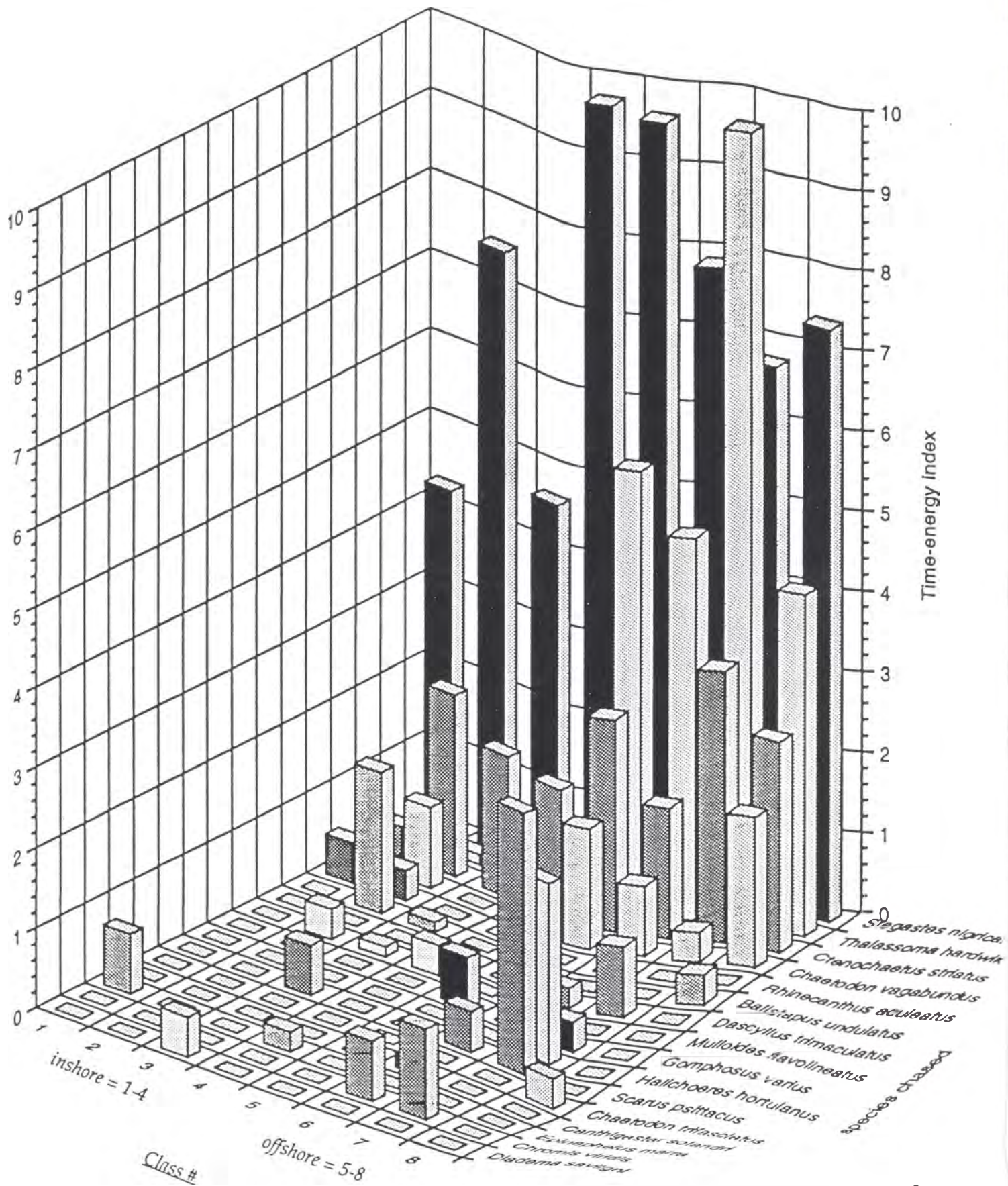
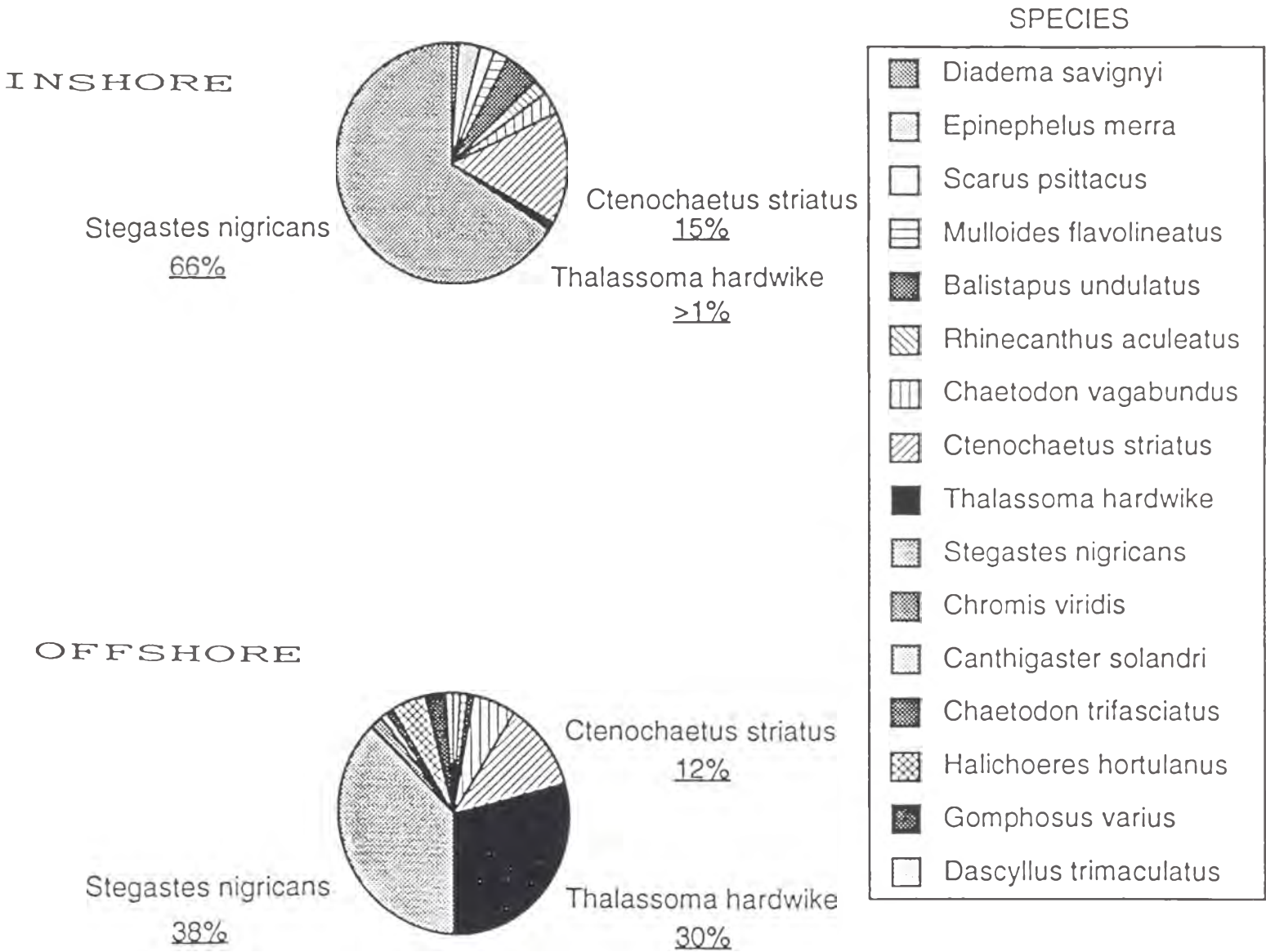




FIGURE 7a and 7b :

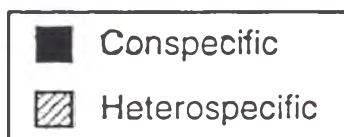
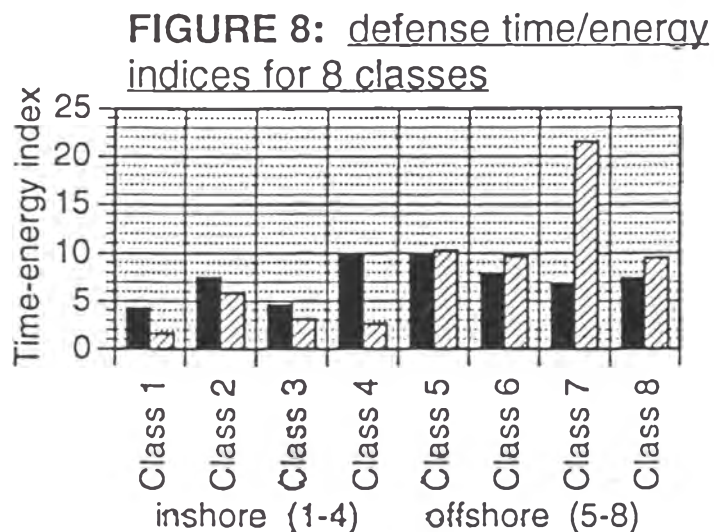
Percent of Aggressive Responses  
Against Intruders of  
Various Species



The  $R^2$  values indicated a better fit using the transect method by an  $R^2$  difference of 0.047. Since this was not significantly different, all subsequent observations, therefore, were analyzed incorporating the results of the average of these two methods.

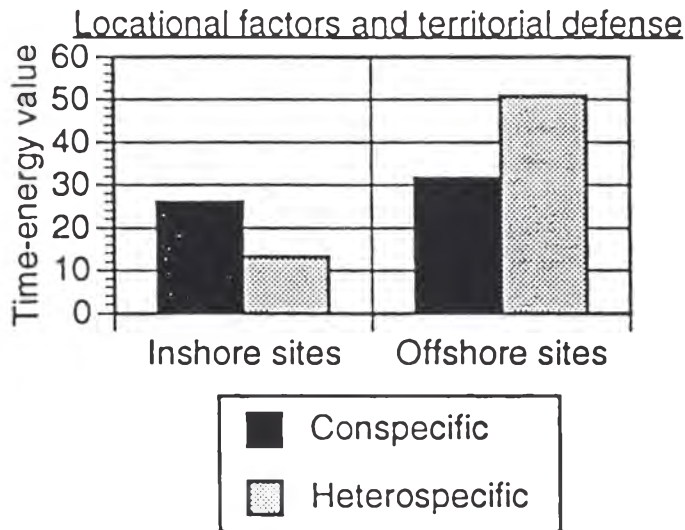
To compare fish density in the inshore and offshore sites, separate density regressions were plotted (Figure 5c,d), and an  $R^2$  difference of 0.001 was calculated. The slopes of the regressions were compared (Zar, 1984) and found not to be significantly different ( $t=1.613$ ,  $p(2\text{-tailed}) > 0.05$ ,  $n=8$ ). Although there was no detectable difference in densities between inshore and offshore sites, behavioral differences were observed.

The defense behavior data were collected on 64 fish (eight fish in eight classes, Table 1) and adjusted as follows: erect dorsal fin counts, short chases, and long chases were multiplied by coefficients 1, 2, and 3 respectively. The adjusted data was a better indication of relative energy output for each defense response as it normalized time, and allowed the data to be totalled as a single Time/Energy index. Figures 6 and 7 are a breakdown of the relative Time/Energy spent defending against each species of fish. For simplicity in later analysis, this data was lumped into two categories--conspecific and heterospecific. (Figure 8)



The plot of conspecific vs. heterospecific defense (Figure 8) shows a pattern of greater time/energy of conspecific defense on the inshore territories, and greater heterospecific defense on offshore territories. *Wilcoxin's signed ranks test* was applied ( $p(2\text{-tailed})=0.125$ ,  $n=8$ ), and found to be non-significant, possibly due to the small sample size. A clear difference, however, is evident in Figure 9 (cumulation of Fig.8). Viewed in this fashion, inshore damselfish spend much less time/energy defending against heterospecific intruders than their counterparts in the offshore territories. Conspecific defense increases slightly in offshore sites, but this increase appears to be less important.

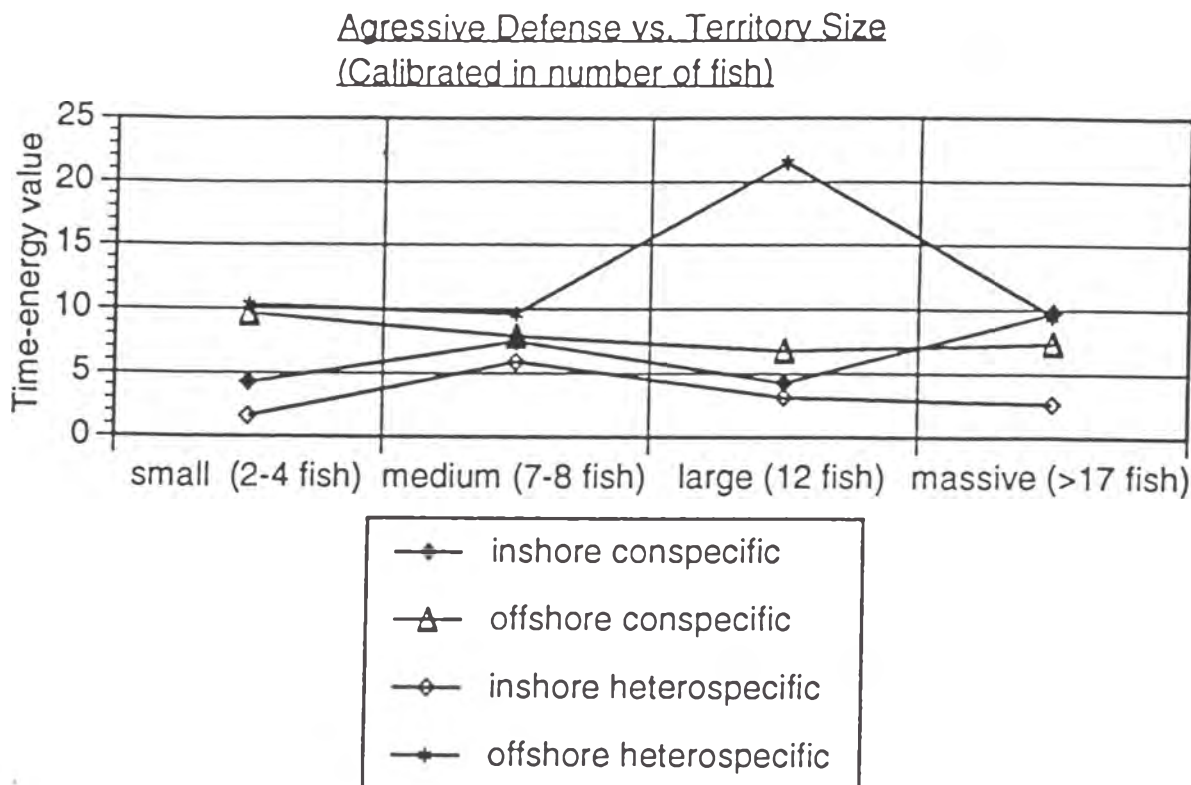
FIGURE 9



When time/energy data was plotted against territory size class, no discernable increase or decrease was noted in slopes (Figure 10). In fact, with the exception of the one point on the "offshore heterospecific" line (caused by a single large school of fish invading the territory), the points all form relatively horizontal lines, indicating consistency between territory size, and time/energy expenditure for defense.

The linear relationship indicated by Figure 10 suggests that territory size is not an independent variable. Therefore, another set of statistical tests (standard t-tests) were run on data from Figure 9, with territory size normalized by averaging the 32 observations for both the inshore and offshore. By increasing the "n" value, a significant difference was measured between heterospecific defense in the inshore and the offshore sites ( $t=2.327$ ,  $p(2\text{-tailed})<0.05$ ,  $n=32$ ). However there was still no significant difference in conspecific defense with regard to the two locations.

FIGURE 10



### Discussion

Fish density was strongly, positively correlated with living space (ie food productivity). Sammarco and Williams (1982) claim to have found a correlation between territory size and density of the threespot damselfish (*Eupomacentrus planifrons*), by taking only length and width measures of the territories. It is unlikely that two linear measurements could accurately portray the undulating topographic surface area of damselfish algal lawns. Furthermore, they inferred from this that "damselfish which occur in aggregations are able to defend larger territories together than they would when occurring alone." Data from my study indicate a strong linear correlation between density and algal mat size (Figure 5), and thus seems to refute this statement. Indeed, except for one anomaly, fish in single-fish territories were found to defend proportionally the same size areas as fish in 17-fish territories.

Behavioral data indicates that fish in large territories spend nearly as much time defending against intruders as fish in small territories (Figure 10). While Sammarco and Williams' statement about the efficiency of group defense has great intuitive appeal, it appears that competing heterospecifics randomly roam the back reef in search of food, and probability specifies that they encounter large damselfish territories more frequently, thus violating the assumption that all territories are invaded equally.



Manipulative experiments performed by Williams (1981) indicate that damselfish territories remained stable even when two species of competitors (*Diadema antillarum* and *Echinometra viridis*) were excluded. This is in agreement with my observations that inshore and offshore territories, with differing levels of intrusions, remained analogous with regard to size (slope analysis, Fig.3,4).

So then, what controls fish density in damselfish territories? It is probable that strong intraspecific pressures are the cause, placing upper limits on density, with space (ie. food resources) as the limiting factor. A past study conducted by Roberts (1987) concluded that food resources are not limiting to damselfish densities. More recently, observations by Klumpp et al (1989) on *Stegastes apicalis* (which exhibit aggregated colonies similar to *S. nigricans*) disagreed with Roberts' conclusion, and suggested the topic warranted further investigation. According to Klumpp, the very "fact that damselfish defend their algal mats suggests the importance of interference competition." My data indicates intraspecific aggression was, in nearly all cases (Figure 6), greater than that displayed against any other single species of intruder. This is further documented by Myrberg and Thresher (1974), and Brawley and Adey (1977). Inshore, offshore, small, and large territories all had proportionally equivalent ratios of fish density and territory size, even while the number of heterospecific intrusions varied significantly from inshore to offshore. Observations were also made of sick and wounded damselfish being driven away from territories. All these facts tend to support the theory that intraspecific competition is of greater importance than interspecific competition for the structuring of *S. nigricans* territories.

Some researchers (Potts, 1977) have suggested that damselfish bite and kill live coral polyps to increase algal mat surface area, and therefore increase productivity. While this was not observed with *S. nigricans*, fish were seen dragging dead *Acropora* branches into their territories, presumably to provide additional surface area for algal colonization. These observations seem to indicate that *S. nigricans* may have some control over their environment.

Further investigation on a larger scale involving manipulative experiments is needed to truly understand the complex social behavior of the damselfish *Stegastes nigricans*. The importance of territorial damselfish is only beginning to be appreciated. *S. nigricans* is a major supplier of food to other reef fishes and invertebrates alike, and is likely a major force in the maintenance of species diversity on the coral reef.



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