THE BIOLOGY AND GEOMORPHOLOGY
OF TROPICAL ISLANDS

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INTEGRATIVE BIOLOGY 158
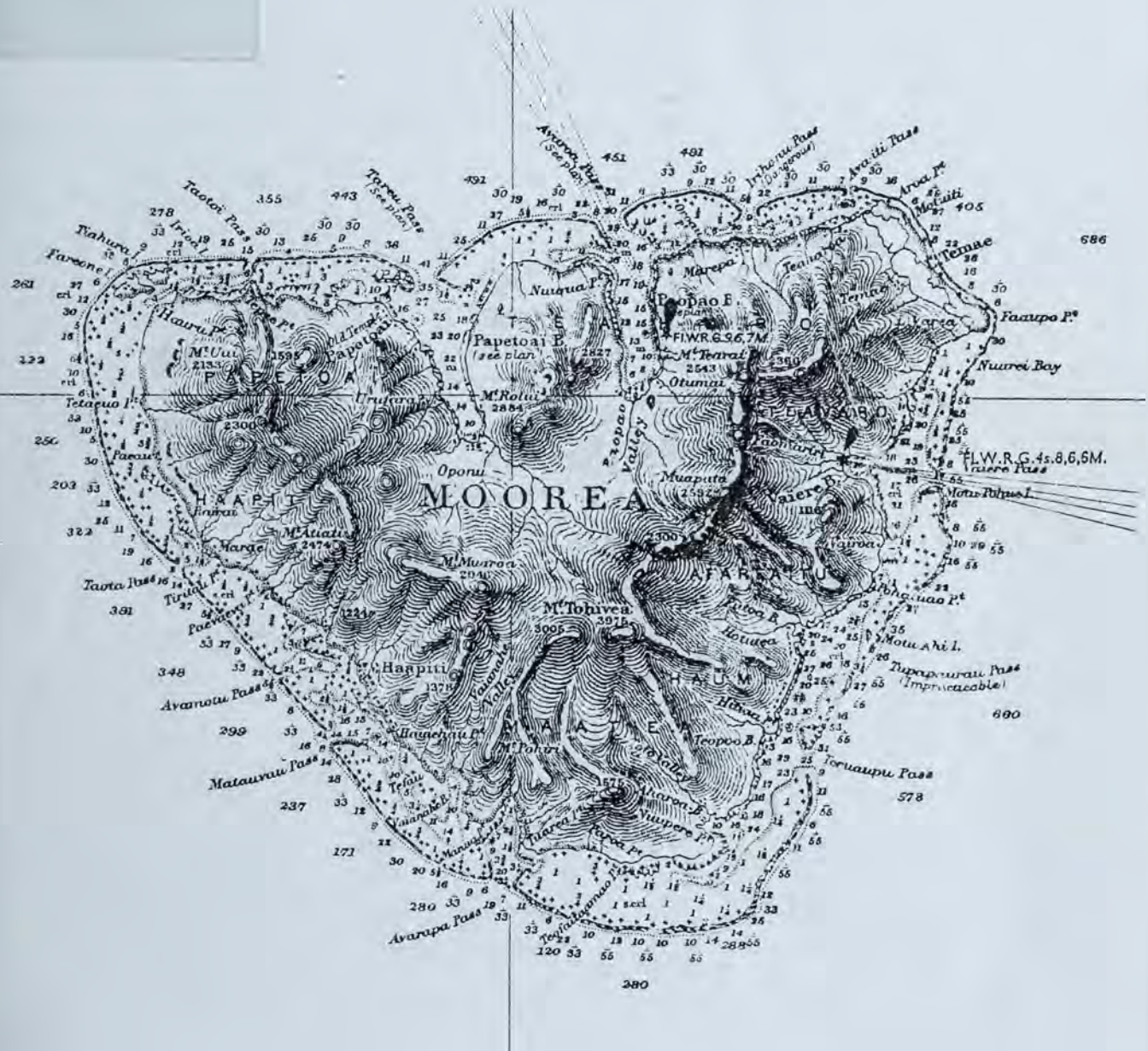
RICHARD P. GUMP BIOLOGICAL STATION, MOOREA
UNIVERSITY OF CALIFORNIA, BERKELEY

STUDENT RESEARCH PAPERS
FALL 1994

THE 1994 MOOREA CLASS. Seated in the front row (from left to right): Healy Hamilton (Graduate Student Instructor), Ina Park, and Cheyenne Laczek-Johnson. Standing (from left to right): Chris Meyer (Graduate Student Instructor), Sarah Kalish, Dan Hahn, Erin Boyd, Tosha Comendant, Rebecca Johnson, Regina (Reggie) Linville, Carolyn Cruz, Elise Grenier, Sarah Jane Rollin, George Wettach, Lia Gaertner, Martha Burford, Stephen Gehlbach, Julie Smith, Jodi Bailey (Graduate Student Instructor), and Frank Murphy (Manager, Gump Field Station).

cat for
Bios

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1994 Moorea Class Reports

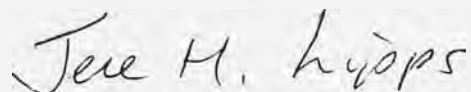## Biology and Geomorphology of Tropical Islands

Environmental Science, Policy and Management 112, Geography 142, Integrative Biology 158, and Interdisciplinary Studies 158

Each Fall Semester since 1991, a unique undergraduate course, "The Biology and Geomorphology of Tropical Islands", has been taught at the University of California, Berkeley's, Richard P. Gump Biological Laboratory on the island of Moorea, French Polynesia. This year, seventeen upper division students from five majors were selected by application and interview to participate in the course. The course offers a good deal more than the biology and geomorphology of an island; it also offers a total immersion experience in another culture, a different climate, unusual foods, close living, and collaboration between each other, Graduate Student Instructors, and Faculty. It is a unique and exceptional experience that has deeply affected the students' lives.

The academic part of the experience began at Berkeley with four weeks of introductory lectures, library research on potential projects, paperwork for travel, and logistics planning. Each student was involved in all of this. Once on Moorea, field trips and lectures introduced the students to the island, its biology, and its geology, as well as some of its history and native peoples. Special field trips to Tahiti, Raiatea, Tahaa, and Tetiaroa were exciting additional study opportunities that exposed the students to the variety of the biology and geology of tropical islands, as well as the local diplomacy. On Tahaa, we were hosted by the Mayor of Tahaa with a fine Tahitian dinner and dance. All of us were involved in the successful proposal to host two Tahaan students at the Gump Station the following month. This interaction, as well as those with French students from Papeete, Tahiti, provided insight for us into other cultures.

The seven-week stay at the Gump Station focused on original research projects, chosen by the students. Each student or pair of students developed and pursued their own projects, with occasional guidance from the instructional staff. The results of this research was presented during a symposium at Berkeley in December and in the papers reproduced in this volume. We are proud of these papers--the students came a long way during this course, from uninitiated university science majors to budding research scientists!

As the instructor-in-charge for 1994, I wish to thank my colleagues who took part in the course. Each is a world-renowned expert in some field of tropical biology or geomorphology-- thus they provided truly outstanding instruction. I thank Professors David Stoddart, Brent Mishler, Vince Resh, and Roy Caldwell, who, along with me, provided not only classroom lectures but field instruction on Moorea. Professors Carla D'Antonio, George Barlow, David Lindberg, and Werner Loher presented lectures at Berkeley. The Graduate Student Assistants, Jodi Bailey, Healy Hamilton, and Chris Meyer, worked hard to provide the logistic and much of the instructional support in the field. Special thanks go to Frank Murphy, Gump Station Manager, and his wife, Hinano, for helpful arrangements and courtesies which gave the class many unique experiences and made the students' lives more comfortable while at the Station. All of us thank Professor Werner Loher, Director of the Gump Station, and the College of Natural Resources, the administrative unit for the Station, for providing the opportunity to conduct this course.

Jere H. Lipps

Jere H. Lipps, Professor
Department of Integrative Biology

The effect of flow rate on hermit crab shell selection in three species of tropical *Calcinus*

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ABSTRACT. Gastropod shells are an extremely important resource for hermit crabs. They use these shells to protect their otherwise vulnerable, soft abdomens. Many factors affect the shell selected by a hermit crab: size, shape, volume, weight, color, and others. This study examined how water flow affects hermit crab shell selection. Population surveys and laboratory experiments were combined to determine if *Calcinus seurati* from a flow environment has a different shell weight to crab weight ratio (weight index) than those from a still environment. It was found that *C. seurati* collected from a high flow site and a still water site differed significantly in their weight indices. Laboratory experiments also showed a significant difference between flow and still treatments. In both cases *C. seurati* selected larger shells in the high flow environment.

    Calcinus gaimardii and *Calcinus elegans* populations were also surveyed and compared with *C. seurati* survey data. Significant weight index differences were found between *C. gaimardii* and *C. seurati* from the high flow area. No other significant differences were found between species. Regression analyses indicate a correlation between hermit crab weight and shell weight for all three species.

Introduction

Hermit crabs are unique decapod crustaceans that occupy the shells of deceased gastropods or other hollow objects. They have soft abdomens which make them very susceptible to predators and physical stress. Gastropod shells provide protection from predators (Vance, 1972) and reduce the rate of desiccation when the crab is not submerged (Taylor, 1977; Bertness, 1981). Although Hermit crabs need empty shells, Raimondi (1986) found that gastropods have a negative influence on the local distribution of foraging hermit crabs even though they have an overall positive effect on hermit crab abundance in a larger area. The limiting resource for hermit crabs may be gastropod shells (Childress, 1972; Kellogg, 1976; Fotheringham, 1976a) and, thus, the behavioral and environmental determinants of shell selection warrant investigation. Many studies examine the shell selection behavior and the factors (size, color, texture, etc.) that influence the shell selection process (Orians, 1964; Blackstone, 1984; Conover, 1978; Brown, 1993). Other studies investigate intraspecific and interspecific shell fighting, a ritualized way of shell exchange between hermit crabs (Hazlett, 1970; Barron, 1989). No study, however, has looked at the effect of hydrodynamic stress on hermit crab shell selection.

Scully (1979) found that individuals of *Pagurus longicarpus* from two areas had significantly different shell preferences. He attributes this difference to the effects of the environment on growth and/or varying shell preference in response to the physical factors of a given habitat. Direct manipulations of the "physical factors," specifically water energy, were not done. The present study examined the effect of flow rate on the size of shell selected by hermit crabs. Data obtained from population surveys and laboratory experiments were used to determine if *Calcinus seurati* differs in its shell preference (i.e. shell weight to crab weight ratio) depending on water velocity. In addition, the shell weight to crab weight ratio, or weight index, is compared between three species of *Calcinus* (*C. seurati, C. gaimardii, C. elegans*). The size of the shell selected is of consequence to the crab because crabs utilizing shells smaller than optimum have a reduced growth rate compared to those occupying shells of adequate size (Fotheringham, 1976b). And a shell that is

to heavy requires increased energy expenditure by the crab.

Study sites:

There were three field sites on the island of Moorea, French Polynesia (17°30' South latitude, 149°50' West longitude). The first site (station site) was located off of the Richard P. Gump Biological Research Station in Cook's Bay (Figure 1). The second site (Temae site) was off of Fauupo Point, north of Temae public beach on the north west portion of the island (Figure 1). The third site (reef crest site) was located on the reef crest to the east of Avaroa Pass at the mouth of Cook's bay (Figure 1).

At the station sight, water energy was very low with only the occasional perturbation caused by wind induced waves. No high flow or oceanic wave action occurs at this sight. The substrate in this area was predominantly sand and mud with coral rubble and coral boulders littering the bottom.

The Temae sight is unique in that during the high and outgoing tide, unidirectional, rapid flow occurs in a near shore drainage channel. North of the public swimming beach, the reef crest comes very close to the shore, ca. 70m. Waves wash over the reef crest and fill the narrow back reef area. The water then drains from this area south into the more expansive backreef lagoon and finally is expelled from the lagoon via Vaiare Pass (Figure 2 and Figure 3). Substrate in the drainage channel is mainly flat coral pavement with occasional coral heads and coral rubble.

The reef crest site consists of flat bench areas of coralline algae ($1m^2$ - $5m^2$) separated by narrow channels. Although exposed during low tides, waves continually wash over the reef crest. This continuous wave action exposes the hermit crabs, and other reef crest organisms, to rapidly changing hydrodynamic forces. The waves breaking on the reef and then draining off of the reef yield a bi-directional, highly turbulent, flow.
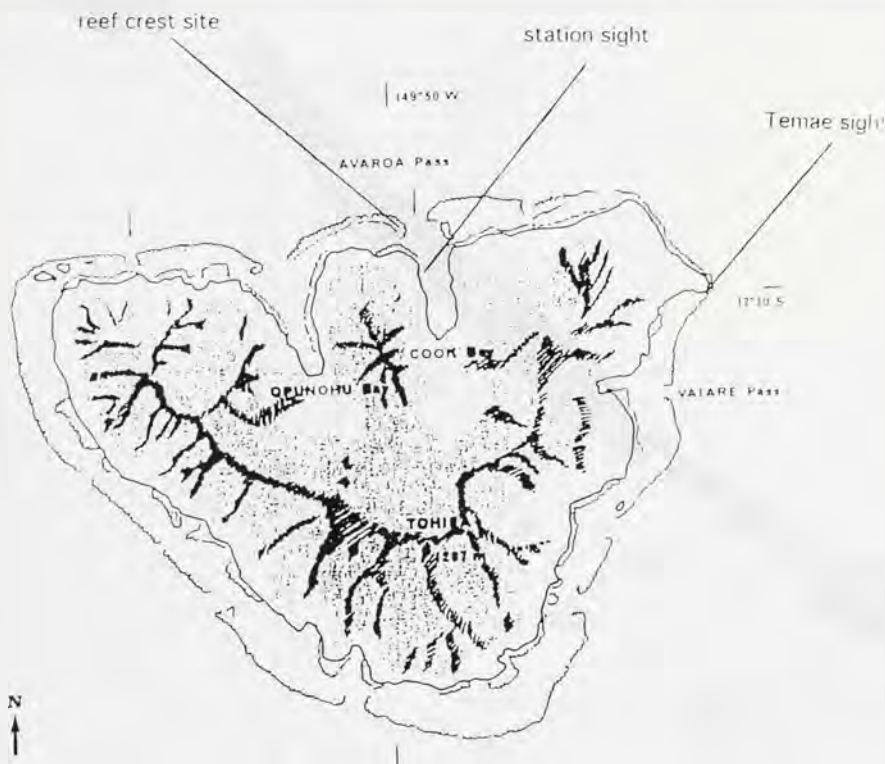
Figure 1. Field site locations on the island of Moorea

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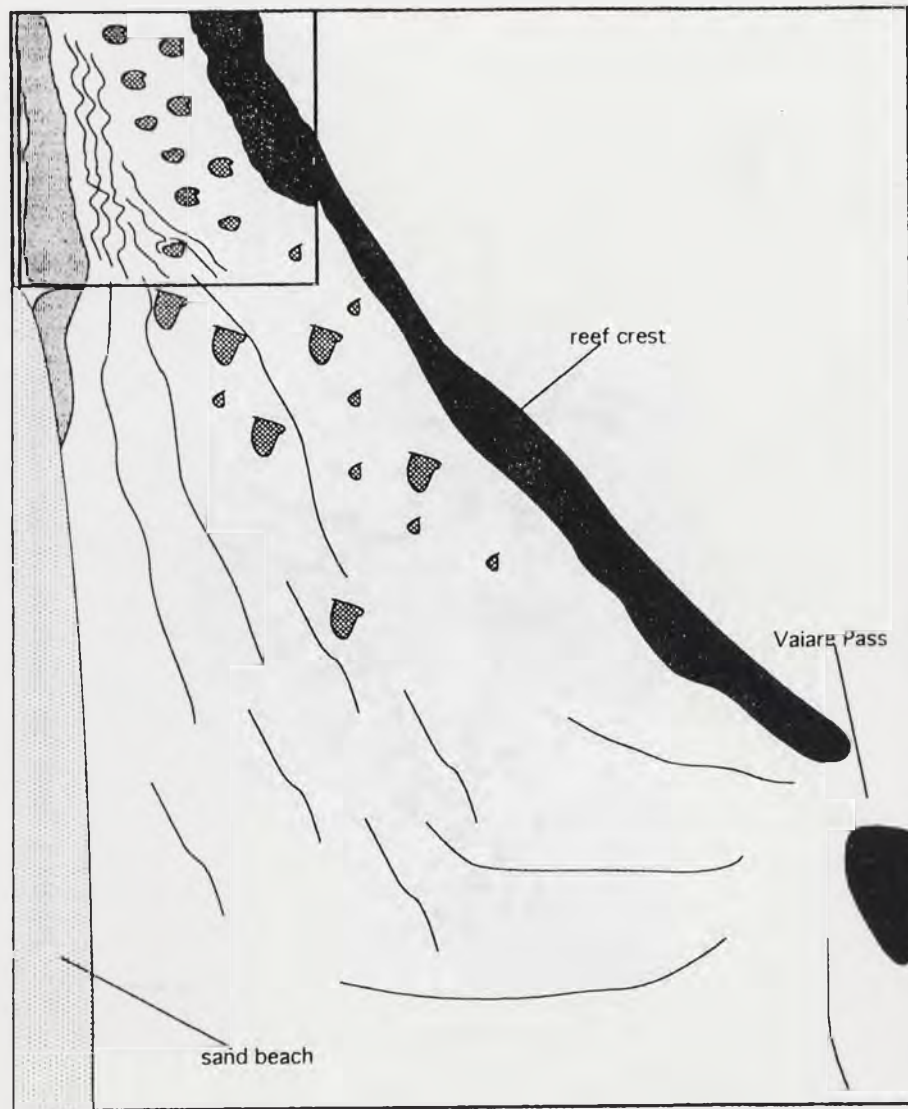
Figure 2. An overhead view of the Temae site.
detail of boxed area is given in fig. 3
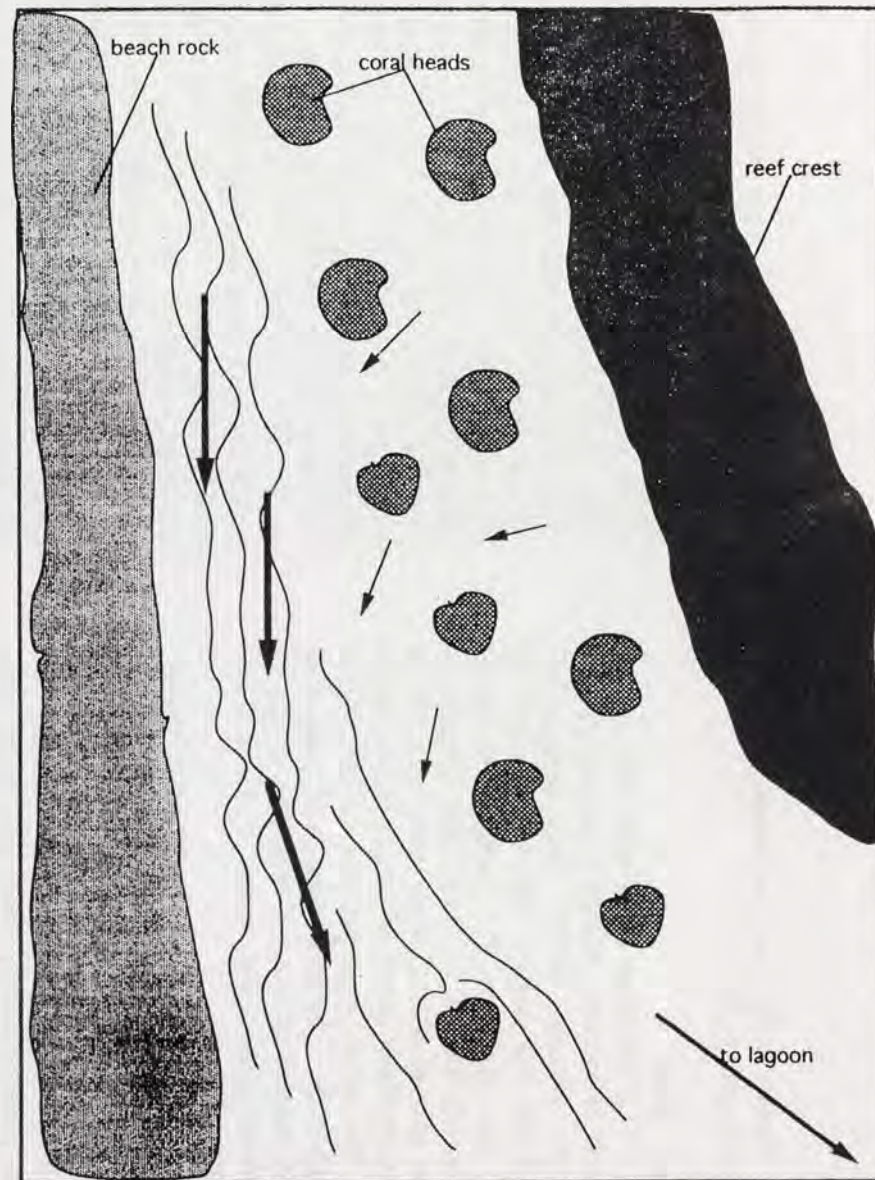
Figure 3. A closer view of the Temae drainage channel.
Arrows designate strength and direction of flow.

Methods and Materials

At the Temae site a 60m line transect was laid perpendicular to the shore line and flow rates were taken at nine points along the transect. Flow rates were measured by placing a 1m length of PVC pipe on the bottom and allowing a neutrally buoyant vial (3.8 cm x 1.3 cm) to float along the top of the pipe while being timed with a stopwatch. At high tide, on two consecutive days, four flow measurements were taken at each of the nine points along the transect. Flow measurements were averaged to give a flow rate at each point.

At all three sites, hermit crabs were collected by searching a belt transect. Due to differing conditions at each site the belt transect varied in its size and the method in which the transect was searched. At the station site *Calcinus seurati* were collected by wading along a 10m x 1m transect in 20 cm to 60 cm of water. All rocks and coral boulders were overturned and searched for hermit crabs. At the Temae sight a 30m x 2m transect was snorkeled in the high velocity drainage channel. *Calcinus seurati* were collected from the coral pavement and off of coral heads at 30 cm to 120 cm depth. A 20m x 1m transect was walked during low tide at the reef crest site. *Calcinus elegans* and *Calcinus gaimardii* were collected from the coralline algae on the top of the reef crest.

Hermit crabs were removed from their shells by applying a flame to the apex of the shell or immersing the hermit crab in warm sea water (40°C). Once removed from the shell, crabs were blotted dry with a paper towel and weighed to the nearest 0.01g. Shells were dried in an air-conditioned room, for at least 24h, and weighed to the nearest 0.01g. Shell lengths and apertures, as well as hermit crab shield length, were also recorded. Due to interspecific variation in gastropod shells, shell weight was used as the determinant of shell size.

Laboratory experiments:

Shell selection experiments were conducted in a flow tank (Figure 4) and a still water tank. The flow tank consisted of
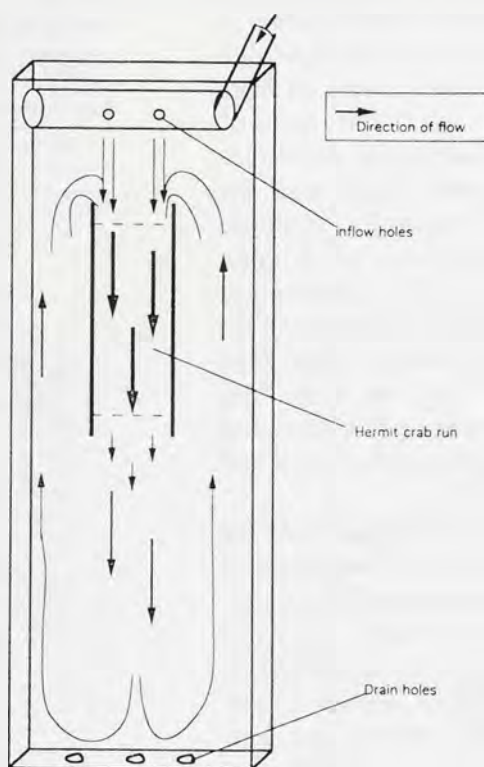
Figure 4. A diagram of the flowtank used in laboratory experiments

a 60 cm x 180 cm tank filled to a depth of 2.8 cm with inflow coming from two 3.2 mm diameter holes drilled in the side of a PVC pipe and outflow from three 2.5 cm holes drilled in the end wall of the tank. To avoid back eddies and maintain unidirectional flow, two 60 cm glass plates were placed 16 cm apart and parallel to each other to provide a "run" which had unidirectional flow. A sheet of sandpaper was glued to the bottom of the run to provide traction and 6.4mm metal screen was placed at the beginning of the run and 35 cm down stream in the run to keep the hermit crabs from escaping during the experiment. A master valve on the inflow enabled control of flowrate. The still water tank measured 20 cm x 50 cm and was filled to a depth of 3 cm. 6.4mm metal screen was used to decrease the working size of the tank to 20 cm x 30 cm: an area similar to the flow treatment.

Calcinus seurati were used in the shell selection experiments. They were removed from their shells by either heating the aperture of the shell with a flame or gently cracking the shell with vice grips. All damaged crabs were discarded and each crab was used only one time. Naked crabs were placed either in the flow tank or the still water tank with a group of seven premeasured shells, all from the family Muricidae, and left for 100 minutes. Shells were selected such that there was at least one shell larger and one shell smaller than the originally occupied shell. Shells were reused from one experiment to the next but alternated between the flow and still treatments. In the flow tank, water velocity was kept between 25 cm/s and 30 cm/s for the duration of each experiment. The occupied shell was recorded at the end of the 100 minute trial.

After calculating weight indices for all hermit crabs, t-tests and regression analyses were used to examine differences. Unpaired t-tests, assuming unequal variance, were used to test for a difference between weight indices for *Calcinus seurati* living at the still water station site and the high flow Temae drainage channel. The same test was used to determine if the shell weight to crab weight ratio differed in laboratory flow and no-flow conditions. The datum for one hermit crab in the no-flow treatment was discarded as an outlier. It had a shell weight index double that of the next closest crab in the treatment. Discarding this crab is reasonable because the crab first encountered, and selected, the largest shell available and was apparently unable to move, remaining in the same place for the 100 min. duration of the experiment. Population survey data for *Calcinus seurati* (pooled from both sites), *Calcinus elegans*, and *Calcinus gaimardii* were compared with t-tests to determine if they differed in their shell weight to crab weight ratios. T-tests were also used to compare *C. gaimardii* and *C. elegans* to *C. seurati* from the station site and the Temae site.

Results

Flow rates from the Temae site were found to be highest in the drainage channel and decreased when moving toward the reef crest (Figure 5). The average maximal flow rate near the bottom of the channel was 27 cm/s, coinciding with that found by Goldman (1993), 28 cm/s, using a phosphorescent dye. This estimation was used to set the water velocity in the laboratory flow tank.
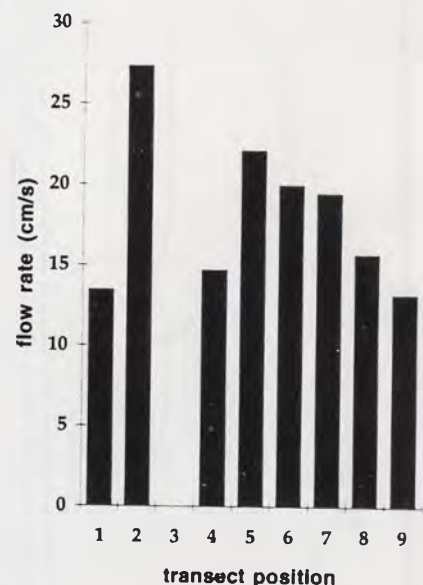
Figure 5. Average flow rates at each of nine points along the Temae transect

A significant difference in the ratio of shell weight to crab weight was found for *Calcinus seurati* collected at the still water station site and the Temae high velocity drainage channel (t-test, p < .003, Table 1). In the flow tank experiments, *C. seurati* selected significantly heavier shells in high flow than in zero flow (t-test, p < .02, Table 2). Mean shell index was very similar in both the population survey and the flow tank experiments for this species (Tables 1 & 2).

Table 1

t-Test (two-sample assuming unequal variances) for Calcinus seurati collected from a still water and a high flow site.

	crabs from station site	crabs from Temae site
Mean	13.49	25.56
Variance	140.33	326.71
Observations	38.00	30.00
Hyp. Mean Difference	0.00	
df	48.00	
t Stat	-3.16	
P(T<=t) two-tail	0.003	
t Critical two-tail	2.01	

Table 2

t-Test (two-sample assuming unequal variances) for *Calcinus seurati* laboratory flow experiments.

	flow tank treatment	still water treatment
Mean	28.65	12.86
Variance	291.00	62.86
Observations	10.00	9.00
Hyp. Mean Difference	0.00	
df	13.00	
t Stat	2.63	
P(T<=t) two-tail	0.02	
t Critical two-tail	2.16	

Table 3

t-Tests (two-sample assuming unequal variances) comparing shell wt. to crab wt. ratios between all species pairs

	C. gaimardii	C. elegans
Mean	16.75	16.36
Variance	124.52	392.58
Observations	31.00	15.00
Hyp. Mean Difference	0.00	
df	18.00	
t Stat	0.07	
P(T<=t) two-tail	0.94	
t Critical two-tail	2.10	

	C. gaimardii	C. seurati
Mean	16.75	18.86
Variance	124.52	254.63
Observations	31.00	68.00
Hyp. Mean Difference	0.00	
df	81.00	
t Stat	-0.76	
P(T<=t) two-tail	0.45	
t Critical two-tail	1.99	

	C. elegans	C. seurati
Mean	16.36	18.86
Variance	392.58	254.63
Observations	15.00	68.00
Hyp. Mean Difference	0.00	
df	18.00	
t Stat	-0.46	
P(T<=t) two-tail	0.65	
t Critical two-tail	2.10	

T-tests did not show a significant interspecific difference between any of the species pairs when *C. seurati* data were combined from the station and Temae sites (Table 3). A significant difference in the ratio of shell to crab weight was found for *Calcinus gaimardii*, but not *Calcinus elegans*, when compared to *Calcinus seurati* from the Temae site (Tables 4 & 5). *C. seurati* from the station site was not significantly different from either *C. elegans* or *C. gaimardii* (Tables 4 & 5). Regression analyses showed a correlation between crab size and shell weight for all three species of hermit crab. For *C. elegans* the correlation was quite high (R^2 = .844, figure 6). For *C. seurati* and *C. gaimardii* the correlation was not as strong with R^2 of .611 and .433 respectively (Figures 7 & 8). *C. seurati* showed slightly better correlation when divided into the Temae site (R^2 = .700, Figure 9) and the station site (R^2 = .622, Figure 10).

$y = 1.0064 + 8.9670x \quad R^2 = 0.844$

Figure 6. Regression analysis of shell weight to crab weight in *Calcinus elegans*.

Table 4

t-Test (two-sample assuming unequal variances) comparing
C. elegans and *C. seurati* (from Temae and station sites)
shell wt. to crab wt. ratios.

	C. elegans	*C. seurati* : Temae site
Mean	16.36	25.63
Variance	392.58	324.73
Observations	15.00	30.00
Hyp. Mean Difference	0.00	
df	26.00	
t Stat	-1.52	
P(T<=t) two-tail	0.14	
t Critical two-tail	2.06	
		C. seurati: station site
Mean		13.51
Variance		140.02
Observations		38.00
Hyp. Mean Difference	0.00	
df	18.00	
t Stat	0.52	
P(T<=t) two-tail	0.61	
t Critical two-tail	2.10	

Table 5

t-Test (two-sample assuming unequal variances) comparing
C. gaimardii and *C. seurati* (from Temae and station sites)
shell wt. to crab wt. ratios.

	C. gaimardii	*C. seurati*: Temae site
Mean	16.75	25.63
Variance	124.52	324.73
Observations	31.00	30.00
Hyp. Mean Difference	0.00	
df	48.00	
t Stat	-2.31	
P(T<=t) two-tail	0.03	
t Critical two-tail	2.01	
		C. seurati: station site
Mean		13.51
Variance		140.02
Observations		38.00
Hyp. Mean Difference	0.00	
df	66.00	
t Stat	1.17	
P(T<=t) two-tail	0.25	
t Critical two-tail	2.00	
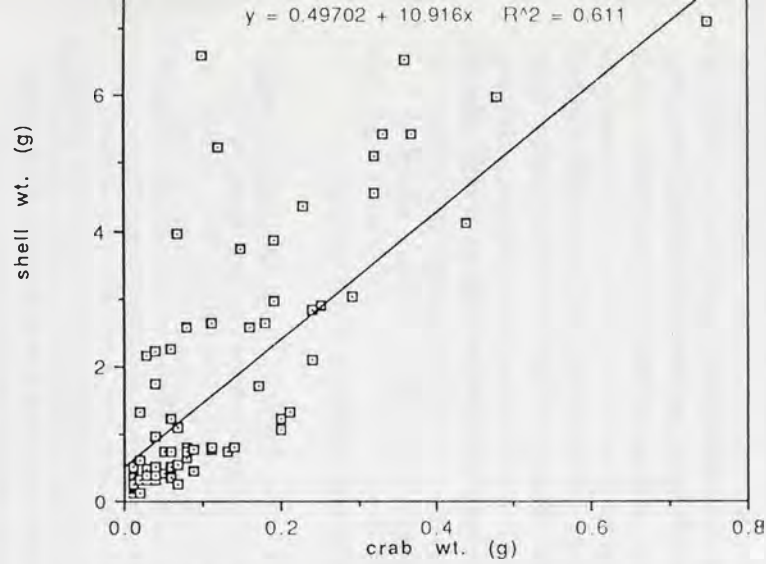
Figure 7. Regression analysis of shell weitht vs. crab weight in *Calcinus seurati*.
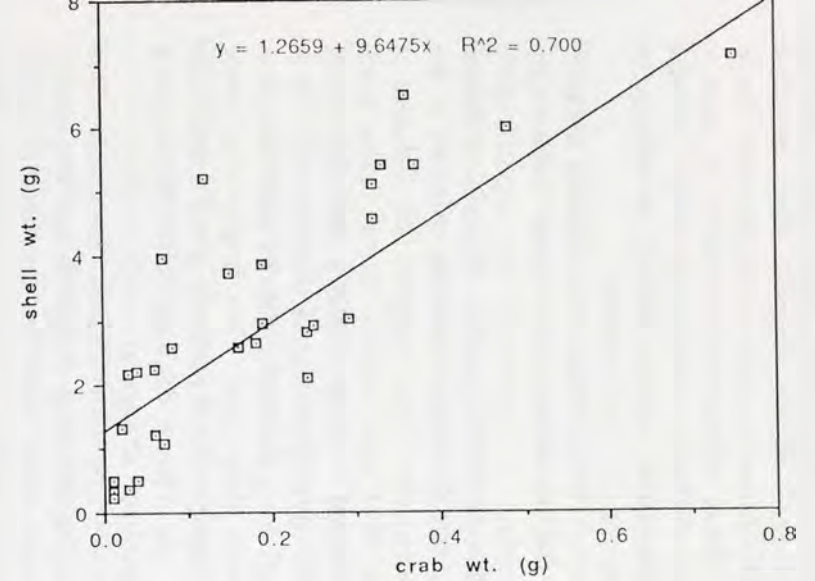
Figure 9. A regression of crab weight vs. shell weight for *Calcinus seurati* from Temae high flow channel.
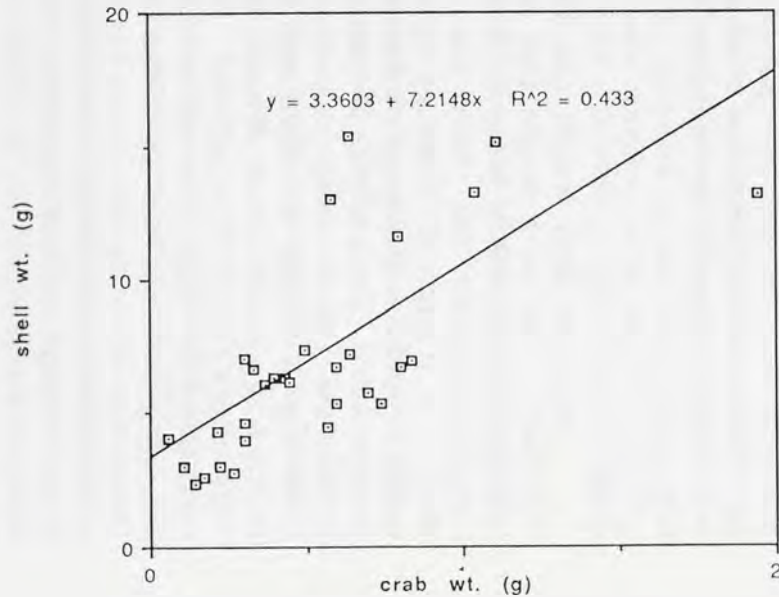
Figure 8. regression analysis of shell weight vs. crab weight for *Calcinus gaimardii*.
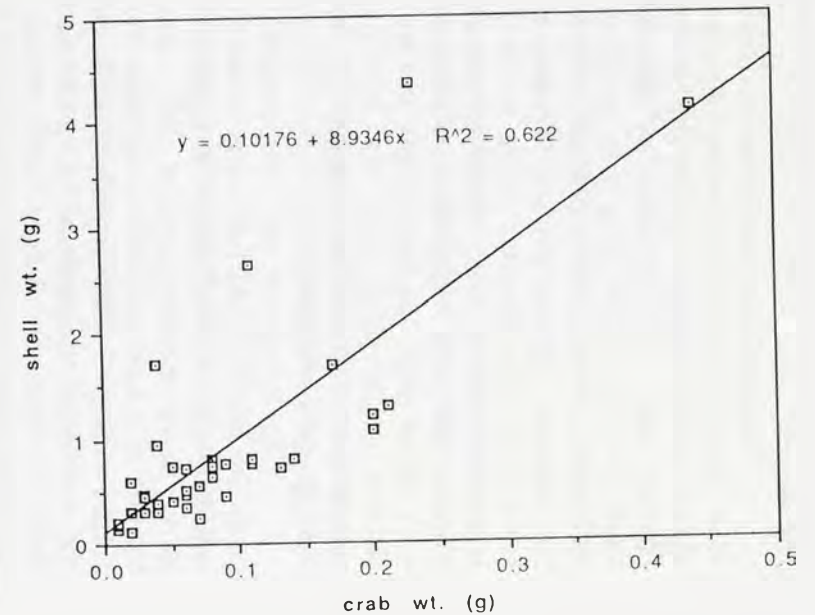
Figure 10. A regression of crab weight vs shell weight for *Calcinus seurati* collected at the station site.

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Discussion

The results of population surveys show that *Calcinus seurati* selects heavier shells when exposed to flowing water (Temae site). The selection of heavier shells in flow is not simply a result of differential availability of shells in the two habitats. This is evident because, in laboratory experiments, crabs in both treatments had the same shells to choose from and the mean weight indices coincide with those from the population survey. Hermit crabs must then be actively selecting for heavier, or larger shells, in the high flow environment.

The occupation of a heavier shell could be beneficial to the hermit crab in several ways. Since it takes more force to move more massive objects, the extra weight of a heavier shell could help the hermit crab to avoid being dislodged from the substrate. Concomitantly, a heavier shell is typically larger and thicker providing more protection for the crab if it were dislodged and tumbled down current. Since shell size and shell weight are closely related to each other it is difficult to distinguish if on factor is more important to the hermit crab than the other. By making shells of the same size heavier or lighter (by attaching weights or attaching styrofoam) it would be possible to determine if the crab is selecting for a particular weight or a particular size of shell.

Increased shell weight also has drawbacks. The extra weight that can help to hold the crab in place in strong current can hinder the crab's ease of movement. A larger shell means a higher energy expenditure is required by the crab to move about. There is then a trade off between shell size and energy expenditure. If the crab is to gain any advantage by having a larger shell it must diminish the extra energy cost of the larger shell. For crabs living in a high flow environment this energy cost may be compensated for; the current will bring food to the hermit crab and decrease the amount of movement it must undergo to obtain comestibles. This same advantage would not be gained by crabs in still water which must actively forage. Hence, hermit crabs in flow environments may select heavier shells without substantial increases in energy expenditure while gaining added protection and the ability to remain in contact with the substrate.

Weight indices are similar for each of the three species of Calcinus as shown by t-tests. *C. gaimardii* is significantly different from *C. seurati* collected at Temae but not different than those collected at the station site. This suggests that the area of the reef crest where these crabs were collected is more similar to the station site in its hydrodynamic factors, that is, if flow is playing the major role in shell selection. These data may also imply that only extreme cases of hydrodynamic stress, such as the Temae drainage channel, cause a significant change in weight indices.

The correlation between crab weight and shell weight is not surprising. Larger crabs would be expected to utilize larger shells. This correlation does, however, illustrate that hermit crabs are actively seeking a shell of appropriate size and not just taking shells at random.

More extensive work needs to be done to determine the factors that influence a hermit crab's shell selection under different levels of hydrodynamic stress. Laboratory manipulations of shell weights, sizes, species of shells offered, and a wide range of flow conditions are all necessary to determine the shell selection behavior of crabs living in high flow, or other high energy, environments. Field manipulations, including caging experiments, would also be valuable in determining the effect of hydrodynamic forces on shell selection.

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Food Preferences of Juvenile *Octopus bocki*

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ABSTRACT. *Octopus bocki*, a pygmy species, has been documented to occur in Fiji and the Philippines. This species was collected around the island of Moorea, French Polynesia at depths from 0 to 30 m. Relative food preferences were observed in the laboratory. Crustaceans, as with many octopuses, were the preferred food. *O. bocki* showed relative preference for small sized galathoidean crabs and stomatopods over alpheus and xanthids. Paguriodea, bivalves, gastropods, echinoderms, fish, and sipunculids were not preferred. Galathoidean crabs of carapace width 1.5 mm to 7 mm were preferred over those 7.5 mm to 10 mm.

Introduction

Most large octopuses are generalists feeders, with a preference for one or more crustacean and/or molluscan species (Wells, 1969; Ambrose, 1982, 1984; Hartwick et al., 1981; Smale and Buchan, 1981; Ambrose and Nelson, 1983; Boletzky and Hanlon, 1983; Iribarne et al., 1991). They forage with the use of chemotactic and tactic senses (Wells, 1969; Mather, 1991; Mather and O'Dor, 1991). Prey attack is directed with the use of acute vision (Wells, 1969).

Smaller individuals tend to have a more limited range of prey. The lack of strength and mechanical advantage lowers the mean prey size of octopi in the field (McQuaid, 1994). It has also been suggested that young octopi prey upon a particular type of food instinctually, then learn to eat other things (Wells, 1969).

The ability of an octopus to eat a particular prey item seems to be based on octopus to prey size ratios, and tendency for the octopus to drill with the use of their modified radula (Wells, 1969). *O. membranaceous*, for example, apparently can not or will not drill and are therefor limited, in their bivalve consumption, to those mussels and clams small enough to pull open (Lam & Chiu, 1983). There are also chemicals associated with some crabs (Iribarne, 1991) and gastropods (Thompson, 1960; Ambrose et al., 1979) that may make them more or less attractive (Schmitt, 1982).

Sometimes mistaken for juveniles, pygmy octopi are fully mature at a much smaller size, and have much shorter life spans (Forsythe, 1984; DeRusha et al., 1987). The feeding behavior of pygmy species is almost completely unstudied. Their foraging is probably limited at least somewhat by size. *Octopus tehuelchus*, a South American pygmy species, is capable of eating a variety of prey items, but chooses to eat (a limited range, a few, a subset).

Octopus bocki, an Indo-Pacific pygmy species, was described after a single specimen collected in Fiji by Dr. Sixten Bock (Adam, 1941, 1945). M. D. Norman collected *O. bocki* in the Philippines (in press), and has identified specimens collected in Moorea, French Polynesia as such (Wong, personal communication). No work has been published on the natural history of this species other than range.

This study is a preliminary survey to determine: if *Octopus bocki* occurs in a variety of locations around Moorea, or if it is limited to a particular area of the island; what type of prey juvenile *O. bocki* prefers; and whether it prefers one size class of galathoidea crab over another.

Materials and Methods

Site description:

Moorea, Tahiti is a high island of the Society Archipelago. It is encircled by

a barrier reef and is located at 17°30' South Latitude, 149°50' West Longitude. Octopi were collected at several sites around the island where coral rubble was abundant. Site 1 (Figure 1 and Table 1) is where collection of most octopi took place, on the ridge crest to the west of Cook's Bay. Animals were also collected at sites 2 through 8.
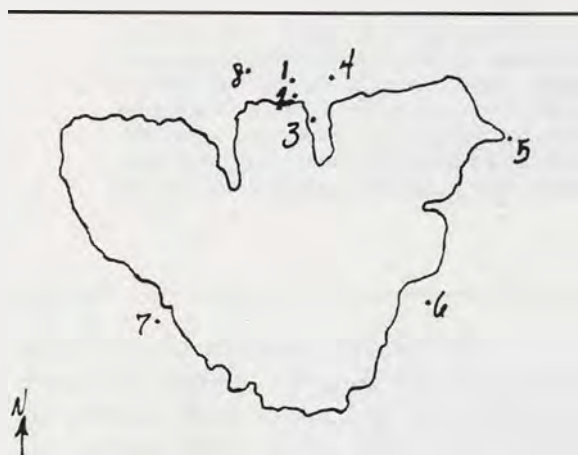
Figure 1. Octopus collection sites on Moorea, French Polynesia.

Octopus collection:

Coral rubble boulders ranging from 30 cm x 13 x 40 to 90 cm x 30 x 50 were placed in 20 gallon black plastic trash cans and allowed to drain for 10 to 30 minutes. Rocks were then removed from trash cans and the remaining water and cobble examined carefully for octopi.

Subtidal rocks were collected on snorkel and handed to an assistant in a skiff where trash cans were waiting. Rocks from 30 m were gathered on SCUBA and brought to the surface in mesh bags via lift bags. Rocks were then quickly transferred into waiting trash cans.

Prey collection:

Prey was collected from coral rubble boulders approximately 30 x 30 x 40 cm gathered at sites 1 and 3. Three to four rocks were broken for each feeding session with a mallet and harvested of all macro organisms. Food items included in the study were those found in the same rocks as the octopi: crabs, shrimp, and stomatopods, sea urchins, tube worms, scallops, fish, and gastropods.

Laboratory maintenance of animals:

Test octopi were kept individually in 16 oz opaque white plastic cups, covered by lids, but not sealed. Water was changed in the cups every other day. Animals were fed approximately twice weekly, with water changed following feeding or if the animal inked. Individuals selected for the experiment were of the smallest size category: 4.5 to 7 mm mantle length.

Feeding Process - Prey Selection:

Prey were selected by size and variety and tested for palatability. A variety of crustaceans were tested. Selected individuals were apparently healthy, with undamaged exoskeletons and all pincers intact. Crabs were measured by their maximum carapace width, and shrimp, from head to end of tail. Groups tested were: 3.5 mm carapace width xanthids (mud crabs); 10 to 12 mm

Table 1. Octopus collection sites and depths.

Site location	Site (#)	Sample minimum	Sample maximum
Ridge crest west of Cook's Bay	1	0.0	1.0
Fringing reef west of Cook's Bay	2	1.0	1.5
In Cook's Bay around the Gump Field Station	3	0.0	1.5
Back reef east of Cook's Bay	4	2.0	7.0
Reef crest at Temae, west of island	5	0.5	1.0
Back reef near motu of Ahi, west of island	6	3.0	4.0
Outside of a mangrove	7	0.5	1.0
Fore reef between Apunahu and Cook's Bays	8	27.0	30.0

Gonodactylus (mantis shrimp); paguroidea (hermit crabs) in 4 to 6 mm *Terebra affinis* shells; and 6 mm alpheus (snapping shrimp).

Three bivalves, measured by maximum valve dimension, were tested: 7 mm clams, 13 to 15 mm scallops; 10 to 12 mm solenidae, or razor clams; as well as 6 to 7 mm Vexillum (Costellaria) rosea, a neogastropod snail. Two types of echinoderms were tested: 4 mm test width *Echinometra mathaei*, a sea urchin; and 4 mm center to arm tip bat star (asteroidea). One variety of goby, a 8 to 10 mm fish, was tested; and sipunculids 4 to 5 mm were tested. Both were commonly found incidentally with octopus collection.

One group of crustaceans was tested more extensively, the galathoidea (porcelain crabs). These were divided into size classes to the .5 mm. 1.5 mm to 10.0 mm crabs were tested. Individuals were selected that had two intact claws and relatively light body armor. It was recorded which apparent species, A through H, were given at feeding time.

Feeding:

Octopi were fed one small crustacean, then deprived of food for 48 hours. Feeding took place between 8 and 10 p.m. Potential prey were individually dropped into the cups with the octopi , and removed 10 to 12 hour later. Retrieved crabs were put into one of three categories: alive, dead, or eaten. The 'eaten' category included those animals appearing partially or entirely consumed. A minimum of six repetitions for each prey category were tried.

Results

Octopus bocki were found at all sampled sites, at depths ranging from 0-30m (Figures 1 and 2). Animals ranged in size from 4.5 to 21 mm mantle length. The largest individual was a 21 mm female with eggs. Five other types of octopus were also collected: *O. cyanea*, a large species and *O. wolfi*, another pygmy. Three were of unknown species: a light gray variety found subtidally in sandy areas, and two others

found deeper, a light colored type with large papilla, and an orange speckled variety.
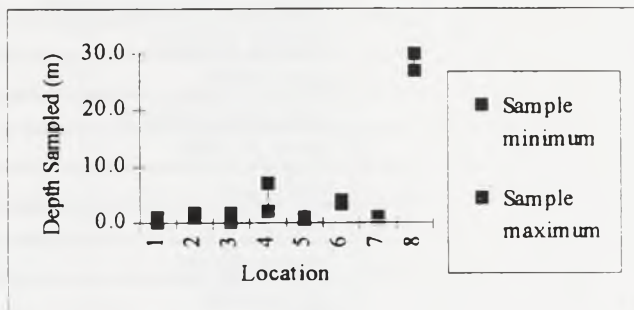
Figure 2. Depths where octopi were collected.

O. bocki attacked some prey items when first introduced and others later in the trial period. Exoskeletons of crustaceans were not consumed, rather the soft internal tissue was pulled out. Results of preference tests are summarized in tables 2 and 3 and in figures 3 and 4. Only crustaceans were consumed. All mantis shrimp tested were eaten. 38% of mud crabs tested, and 67% of snapping shrimp offered were also eaten. No hermit crabs were consumed. No calms, scallops, razor clams, snails, sipunculids, urchins, star fish, nor fish were eaten.

Small sizes of porcelain crabs offered were eaten: 100% of those 1.5, 2.5, 4.5, 5.0, and 6.0 mm were eaten. Of those: 2.0 mm, 89% were eaten, 11% were dead; 3.0 mm 90% were eaten, 10% were dead; 3.5 mm, 90% were eaten, 10% were dead; 4.0 mm, 86% were eaten, 14% were dead; 5.5 mm, 88% were eaten, 13 % were dead; 6.5 mm, 83 % were eaten, 17% were not eaten; 7.0 mm, 83 % were eaten, 17% were not eaten; and 7.5 mm, 17 % were eaten, 66% were not eaten, and 17% were dead. Large sizes of porcelain crabs were not eaten: 100% of those 8.0, 8.5, 9.5, and 10.0 mm were not eaten. 67 % of crabs 9.0 mm were not eaten, 17 % were dead.

Table 2. Prey offered to octopus

Prey type	Number Offered	Number Eaten	Number Not Eaten
2.5 mm porcelain crabs	12	12	0
8.0 mm porcelain crabs	6	0	6
mantis shrimp	6	6	0
mud crabs	6	2	4
snapping shrimp	6	4	2
hermit crabs	6	0	6
scallops	6	0	6
clams	6	0	6
boring clams	6	0	6
sipunculid	6	0	6
urchin	6	0	6
star fish	6	0	6
fish	6	0	6
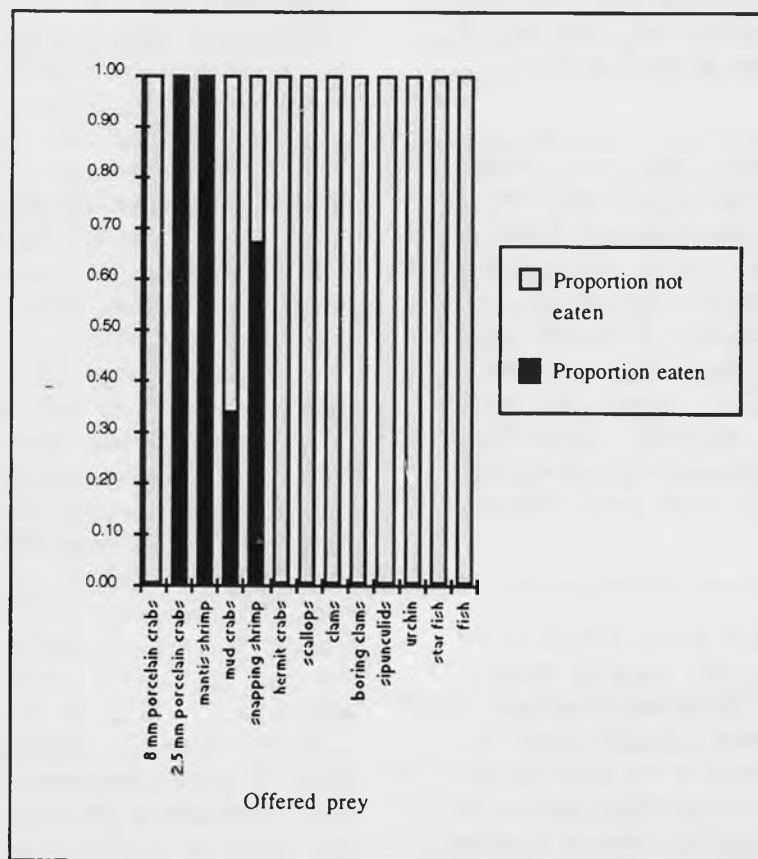
Figure 3. Potential prey offered to octopus.

Table 3. Galathoidea crabs offered to octopus.

Size of Crab (mm)	Number Offered	Number Eaten	Number Not Eaten	Number Dead
1.5	7	7	0	0
2.0	9	8	0	1
2.5	12	12	0	0
3.0	10	9	0	1
3.5	10	9	1	0
4.0	7	6	0	1
4.5	6	6	0	0
5.0	6	6	0	0
5.5	8	7	1	0
6.0	5	5	0	0
6.5	6	5	1	0
7.0	6	5	1	0
7.5	6	1	4	1
8.0	6	0	6	0
8.5	6	0	6	0
9.0	6	0	5	1
9.5	6	0	6	0
10.0	6	0	6	0
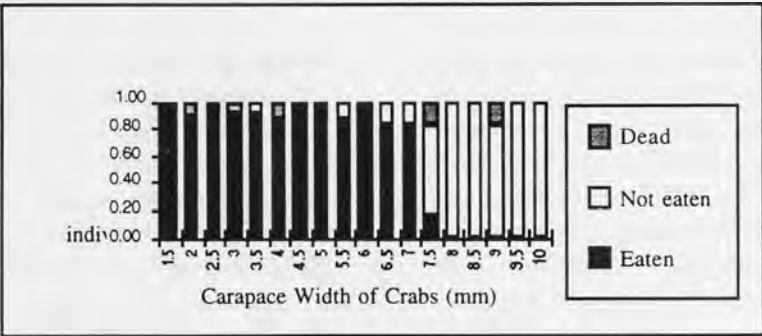
Figure 4. Galathoidean crabs offered to octopus.

DISCUSSION

Range:

Octopus bocki was found at all collection sites, which ranged from 0 to 30 m (Figures 1 and 2). Their population is able to withstand predation and utilize food resources at all sampled depths and in a variety of locations around Moorea.

Feeding:

The results of feeding tests indicate relative preference for crustaceans over molluscs, echinoderm, fish, and sipunculids (Figure 3). Porcelain crabs 1.5 mm to 7.5 mm were preferred over those 8.0 mm to 10 mm (Figure 4). These are relative preferences under the given controlled conditions. Juvenile O. bocki may be capable of consuming molluscs, echinoderms, fish, or

sipunculids. However, the species and sizes tested were not preferable under those conditions.

In recording preference test results, I considered the condition of items offered for each trial. 'Eaten' prey were those whose soft body parts were at least partially consumed. Potential prey collected alive at the end of the experiment were considered 'not eaten.' The octopus may not have attempted to eat these animals, for example, if the prey item was too big, or was chemotactically undesirable. The octopus might also have grabbed the item and rejected it, or unsuccessfully attacked the item.

Prey recorded as 'dead' at the end of an experiment, might have died because of damage in collection, they could have died 'natural' deaths, or the octopus could have killed the animal and not eaten it. It is possible that partial consumption of these 'dead' animals did take place and went undetected. It is also possible that some 'dead' prey were scavenged by the octopus, however, attacks on most prey were observed.

Crustaceans:

Crustaceans not eaten during experiment might have survived because they evaded the octopus. 33% of mud crabs tested were not eaten and snapping shrimp were not eaten in 62% of trials. If 6 mm snapping shrimp are not well within an 'easily consumable' size range, they might have been able to defend themselves with their chelipeds from predation. Snapping shrimp are also fast swimming animals that swam away when attacked. Mud crabs also are fast swimming, and could have evaded the octopus. Results of these tests indicate that juvenile bocki are capable of eating these size classes of these animals, but don't always. This could be because they are not highly preferred prey, or because they are just not as successful predators of these prey, i.e., *O. bocki* is unable to catch them.

Porcelain crabs that were not eaten might also have defended themselves well enough to avoid being consumed. As more than one species of galathoidean crab was used for size preference tests, it is possible that some species of these crabs were more palatable than others (Thompson, 1960; Cates and Orians, 1975; Ambrose et al., 1979; Schmitt, 1982; Iribarne et al., 1991). However, the same species of crab used for large crab tests (species H) was the same as some of the smaller crabs that were eaten. It is possible that these smaller individuals had not yet developed the character making them unpalatable; or that they were categorized incorrectly as the same species.

Hermit crabs were not preferred prey in this study. Hermit crabs tested might have been more preferred, had they been in smaller shells. Kobayashi (1986) found that a given sized hermit crab is more preferred as a prey item when it is living in a tight-fit shell. Because hermit crab to shell size was not controlled, this test may not be informative about true juvenile *O. bocki* preference for hermit crabs. One naked crab was tried under experimental conditions, and was eaten, so the crabs themselves must be edible by juvenile *O. Bocki*.

Molluscs:

Scallops, clams, and razor clams were not eaten. There are two ways that octopi eat bivalves: prying or drilling. Not all species of octopi equally use drilling when they feed. This may be a learned behavior (Arnold and Arnold, 1969; Wodinsky 1969; Wells 1978). The juvenile *O. bocki* tested might also tend not to drill or have learned how, yet, and/or are not strong enough to open bivalves of tested sizes. Predator to prey size ratio limits the predation of octopus on bivalves to those that can be pried open (McQuaid, 1994). Ability to drill might limit predation on gastropod mollusks as well. Distastefulness might limit consumption of gastropods that might otherwise be crushed or pulled out of their shell (Wells & Wells, 1970; Ambrose et al., 1979; Iribarne et al., 1991).

Echinoderms:

Sea urchins and starfish are not a common prey item of octopi. If they are capable of breaking them open, at this size there would be very little matter of nutritional value.

Fish:

All feeding trials with gobies, with octopus of all size classes, failed. This variety of fish is probably not eaten, as it is extremely common in the same habitat. Fish are often not eaten by octopuses because they apparently have difficulty catching them (Wells, 1969). These gobies, however, were not fast moving.

The species of each prey type tested, however, may not represent the preference of juvenile *O. bocki* for that entire group of animals. There may be other species of molluscs and fish, for example, highly preferred although not tested.

Feeding in nature:

Food preference is one component of many determining the natural diet of an octopus. There are a number of other biotic and abiotic factors affecting what an octopus consumes, including: the relative abundance of potential prey, and prey habitat, range, and behavior; behavior of the octopus, and ability of the octopus to eat a given prey item.

There is no available data on relative abundances of the potential prey used in this study. It was noted, however, during collection, that there seemed to be a great abundance of these species tested. It is possible that most preferred prey items were not found in rocks abundantly, and therefor not tested. This could be a result of octopus predation. The habitat and behavior of prey items could also determine how often they are eaten.

Octopus bocki seem to be, at the beginning of their lives, somewhat specialized predators. They appear to prefer a fairly narrow range of food items. To determine whether this is truly due to preference, or if juvenile *O. bocki* are capable of feeding only on this small range, more data are needed. Further studies with a range of hungriness, closer evaluation of crab remains, and a larger sample would help determine what these apparent limits are caused by. It is possible, for example, that a hungrier octopus will eat larger crabs, that it otherwise would not risk the possible damage in battle. Another possible reason to attack larger crabs, would be that they simply need more nutrition. Such reasoning by this animal seems unlikely. Testing these two hypotheses might reveal whether results of this study reflect preference, or ability limitations of these juvenile octopuses.

As adult *O. bocki* may have completely different prey preferences than juveniles. They might eat a larger variety of food than juvenile individuals because they have learned to eat other prey types, or because they can handle larger animals. Their role in the community as predators could be much different that of juveniles.

Community interactions:

It has been suggested (Hughes, 1980; Schoener, 1987; McQuaid, 1994) that patterns of prey preference might be based on natural selection pressures to maximize fitness. This might mean maximizing energy return or minimizing exposure of octopus to predation while foraging (Abrams, 1982; McQuaid, 1994). Considering the abundance and variety of potential octopus prey, availability of prey probably does not limit the populations of either the octopus or the prey. Other factors affecting such things as recruitment success may have much greater affects on *O. bocki* populations. The relationships of co-occurring octopus species ecologically and evolutionarily might also be of great importance for the feeding behavior of *Octopus bocki*.

Acknowledgments

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Masking Behavior and Distribution of the Tropical Sea Urchin
Tripneustes gratilla

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ABSTRACT. Masking behavior of many animal phyla has been described but the underlying mechanisms prompting this behavior are poorly understood. This study investigates the distribution and masking behavior of the tropical sea urchin, *Tripneustes gratilla* on Moorea, French Polynesia. In the "islet reef", *T. gratilla* has an aggregate diurnal distribution. During the day, individuals occupy the floor of the "islet reef" and during the night urchins occupy peaks that protrude above the substrate surface. This climbing behavior was also displayed during laboratory studies. We infer that this behavior helps the animal minimize the effects of damaging light during the day while maximizing the effects of flow during nocturnal foraging.

Laboratory experimental results provide evidence that masking behavior is positively correlated with light intensity. Field observation results suggest that masking behavior is significantly greater during the day than at night. Masking during sunny days tended to be greater than during cloudy days but the differences were not statistically significant. Field observation results suggest that there is no correlation between speed of flow and weight of cover carried. However, field transplantation experiments of urchins to different flow regimes provides evidence that flow speed is positively correlated with weight of cover carried. Field studies provide evidence that the urchins are truly camouflaged because their cover represents a random sample of their environment. Since predation pressure (other than from humans) was minimal our study found that varying degrees of masking did not effect survival. This study implies that covering behavior is not a response to one environmental cue but may be simultaneously influenced by many factors.

Introduction:

Aquatic organisms are influenced by a variety of environmental factors. The difficulties in dealing with the complexity of interactions of these many factors have led some to seek correlations between single factors and some ecological response. One such response is the covering or masking behavior of the caddis flies, crabs (of the genera *Hyas*, *Maia*, *Pisa*, *Inachus*, *Dromia*, and *Stenorhynchus*), gastropod mollusks (for example, *Xenophora*), and sea urchins (Portmann, 1959). These organisms have a variety of mechanisms for masking, ranging from the weaving of scraps of shells and gravel into a protective covering to using specialized appendages to hold the mask over their body. In the case of sea urchins, the behavior is performed by the tube feet. The feet at the base of the urchin's test extend until coming into contact with loose material. Each tube foot contracts, as to pull the material firmly against the tips of the primary spines, which are then moved aborally. The spines act on a "crowbar" principle, levering the material upwards, aided by their roughened surfaces and the action of the more aborally situated tube feet. Upon reaching the aboral surface the materials are held in place by the underlying tube feet. Light floating or suspended objects may be seized directly by the aboral tube feet (Millott, 1956). Masking behavior in these and other organisms has been well studied by scientists due to its possible selective advantages; it has been suggested as an adaptive response to one or more of the following factors:

Flow:

Water motion can be a significant factor directly or indirectly affecting the abundance, behavior and morphology of benthic organisms (Reidl, 1971). Direct effects include dislodgment as a result of exposure to strong waves and surge (Shelton and Robertson, 1981). Indirect effects include reduction in activity, such as grazing, during periods of high flow (Dance, 1987; and Ogden 1989). Behavior of

organisms in high flow environments requires a compromise between minimizing and maximizing the effects of flow. Marine organisms such as urchins depend on moving fluid for food, replenishment of calcium carbonate ions for skeleton construction, waste removal, and gamete dispersal (Russo, 1977). Moving fluid can also be detrimental to urchins. In addition to dislodgment, high turbulence and drag can cause spine breakage (Harvey, 1956). Covering behavior has been hypothesized as a means of achieving ballast in urchins to counteract these negative effects of flow. This behavior has been described as early as Pliny (23-79 A.D.) in his *Natural History* (translation by Bostock and Riley) and depicted in legends by many other writers, including *Camerarius* in 1654 (Harvey, 1956). Both believed the covering behavior was a response to high flow and that it prevented the urchins from rolling around and wearing away their spines. However, to our knowledge, no research has been published in this area.

Light Avoidance:

The light in the sea depends on depth, time of day, season, and weather conditions. For a mobile marine organism, there is a condition of light most suitable to its well being, and the organism is maintained in this quality of light by its internal mechanisms. If the organism is exposed to excessive light, the animals' photochemical reactions cause it to avoid the light source, either through fleeing responses, seeking refuge, or covering behavior (Stephenson and Stewart, 1955). Much research has been conducted concerning sea urchins' sensitivity to light. In general, they are negatively phototrophic, and it has been found that urchins display light avoidance behaviors typical of other marine organisms (Mortensen 1927; Millott 1955, 1956; Lewis, 1958). Covering behavior is common in the echinoids, with over 16 known species displaying this behavior. Research has demonstrated that changes in both intensity and levels of light are important variables in the covering response (Millott, 1956). Furthermore, urchins react faster to ultraviolet light than to white light, from

which the ultraviolet has been filtered (Sharp and Gray, 1962).

Predation/Camouflage:

Camouflage is widely utilized throughout the animal kingdom for concealment and protection from predation (Cott, 1940). Concealment may be achieved through cryptic camouflage involving color, form, and behavior. For the "masking" organism, the camouflage, or masking material is derived directly from the organism's environment (Stephenson and Stewart, 1955). The mask allows it to completely merge with its background without paying the expense of producing cryptic coloration, which may not truly protect the organism (Feltmate, 1989). In sea urchins, covering behavior has been interpreted as a means of advantageous concealment, both from predators and potential prey (Portmann, 1959 but Millott, 1956). To our knowledge there have been no studies that provide evidence for this hypothesis.

Since the covering behavior in urchins is poorly understood and previous work does not provide complete and definitive proof that this behavior is truly an adaptation, (Brandon, R., 1991) the present study aims to provide a more thorough investigation of this behavior in the tropical sea urchin, *Tripneustes gratilla.* This urchin is widely distributed throughout the Indo-Pacific, occurring as far west as Madagascar and East Africa and as far east as the Hawaiian islands, with northern and southern most limits of distribution at Japan and Australia, respectively (Clark and Rowe, 1971) Like many other species of littoral sea urchins, (Appendix) *T. gratilla* covers its test with fragments of shell, rocks, algae, and other materials collected from its environment (Ogden et al., 1989).

Here we examined the covering responses of *T. gratilla* to exposure to various environmental conditions, both in the field and laboratory. The behavior was examined with the following questions in mind:

(1) Is covering behavior used for ballast? Furthermore, is there a direct

correlation between flow speed and the percent of the urchin's test covered? Or, the weight of cover worn?

1a.) Do the urchins also aggregate to cope with flow?
2.) Does coverage decrease as light intensity decreases from intense sunlight, to cloud filtered sunlight, to darkness? Is UVB the stimulus for covering behavior?
2a.) Does distribution also vary with light?
3.) Does the camouflage obtained by covering behavior protect the urchins from predators?
(3a.) Do urchins actively select materials from their environment to use as cover?

Materials and Methods

Study site:

Field studies were conducted during the months of October and November 1994 at the Temae "islet reef" on the North East coast of Moorea, French Polynesia (17 30' South, 149 50'). The site encompassed a 10000m^2 area extending 100 m east from the east corner of the lighthouse and 100 m north to the algal ridge (Appendix, map 1). The "islet reef" was characterized by 3 habitat types: (1) flagstone (0.5 to 0.6 m depth, extending 20 m from shore), which consisted of submerged conglomerate reef platform with sparse overlaying sand and occasional *Porites*; other dominant species: *Diadema savignyi*, *Halodeima atra*, gobis, wrasses. and goat fish; (2) rubble zone (1.1 to 1.3 m depth, 30-60 m from shore) characterized by consistently strong current, dense coral rubble and *Porites*; other dominant species: *D. savignyi*, Labridae, and Acanthuridae; (3) coral zone (0.3 to 0.45 m depth, 75-90 m from shore) characterized by crumbled reef flat with joined coral patches (vestiges of the barrier zone); it is in close proximity to the dominant algal species: *Turbinaria*, *Sargassum*, *Halimeda*, *Dictyota*. This area also has the highest echinoderm diversity.

Human disturbance in the "islet reef" appeared to be a major factor effecting the distribution and abundance of marine species. Since the barrier reef is directly connected to the coast and the water is relatively shallow, locals extensively utilize the islet reef for food resources. Due to gonad ripeness, peak harvesting of *Tripneustes gratilla* occurs during the days surrounding the full moon, most intensely in the flagstone habitat (personal observation). Since the study site is also heavily fished, the populations of Labridae, plate crushing fish, and puffer fish, the urchins' predators, were not large enough to strongly influence the urchins' population density.

The laboratory portion of this investigation was conducted at the University of California Gump Biological Field Station on Moorea, French Polynesia during the month of November 1994. Urchins captured at the study site were transported to the field station and housed on wet benches in 10 gallon aquaria (10 urchins per aquarium). The aquaria were connected to a circulating sea water system, whose intake was just offshore in Cook's Bay.

Flow Rates:

Flow rate measurements in the three zones were first attempted by releasing a neutrally buoyant vial and noting the time (to the nearest .1 sec) it took to travel a distance of 5 meters. This method proved unsuccessful because the vials motion was repeatedly blocked by craggy coral in the coral zone. To keep the measurements consistent so that speed comparisons could be made across the habitats the flow rates were instead measured by releasing a glass vial at the surface of the water. Because flow changed throughout the course of the day, six measurements were made in rapid succession before beginning the measurements in the next habitat. The flow rate was measured first in the flagstone, then the rubble zone, and finally in the coral zone. Using this procedure the time between the flagstones' first flow measurement and the coral zone's final flow measurement was approximately 20

minutes. This was repeated along the same 5 meters of habitat on three days, 11/8, 11/10, 11/14, between the hours of 0900 and 1200. On one day it was not possible to obtain measurements from the coral zone due to excessive turbulence.

A 2 way ANOVA was used to compare the flow rates in the three environments on day 1 and day 3. The data were then analyzed with a Bonferroni multiple comparisons test. A Mann Whitney U test was used to compare the means of the flow rates in the flagstone and rubble zone on day 2.

Flow Transplant experiment:

Transplantation experiments between the flagstone and rubble zone were performed to determine the effects of flow rate on the covering behavior of *T. gratilla*. These zones were chosen due to the large difference in flow rate (Table 1). Urchins were selected haphazardly from each habitat and carried to a central location. Half of the urchins were exchanged and transplanted to an alternate habitat. The remaining half were replanted in their original habitat. This ensured equal handling for control and experimental specimens. Control and experimental urchins were then spaced approximately 60 cm apart in order to avoid interactions. The urchins' behaviors were then recorded for ten minutes. The following categories of behavior were noted: burrowing or wedging, walking, number of rocks added and/or dropped, and percent of urchin's test covered at beginning and end of trial. The amount of test covered was divided into five categories: (0) 0%; (1) 1-25%; (2) 26-50%; (3) 51-75%; (4) 76-100%. Twenty-five replicates were conducted for the low to high transplant and twenty three were conducted for the high to low transplant. Experiments were carried out over a period of two days between the hours of 0700 and 1000.

A Chi-Squared test with 3 independent samples, (1) number of rocks added, (2) number of rocks dropped, and (3) no change, was conducted for each experiment to determine if urchin pebble collecting behavior was independent of final flow destination. Mann Whitney U tests were employed to compare adding and dropping behavior between the experimental and control specimens. Corrections were made for both ties and large sample size. A Z statistic was used to test the significance of the Mann Whitney results.

Spatial distribution of T. gratilla:

Clark and Evans (1954) nearest-neighbor (plotless) methods were employed to determine the spatial distribution of *Tripneustes gratilla* in the three selected zones of the "islet reef" environment. Three spatial scales, 4 m^2, 25 m^2 and 100 m^2 were examined in order to determine the optimal quadrat size for the study. The 4 m^2 plot was rejected because too many quadrats were found devoid of urchins. Since both the 25 m^2 and 100 m^2 squared quadrats always contained at least one individual, the 25 m^2 size was chosen because it was the most practical to use for our time constraints.

The urchin data were collected by randomly selecting three 25 m^2 plots per zone in the "islet reef." All urchins within the plot were numbered. To minimize urchin disturbance, rocks from the habitat were marked with numbered flagging tape and then placed alongside the urchins. Half the individuals in each plot were randomly selected and the distance to their nearest neighbor was measured and recorded (D in cm.). If the nearest neighbor fell outside the plot, the distance to that neighbor was measured. It was possible to have reciprocal nearest neighbors.

Clark and Evans (1954) nearest-neighbor method was used to analyze the data. A Z test was used to test the significance of a deviation from the ratio of expected average distance between urchins based on a Poisson distribution with the actual average distance.

The effects of naturally varying flow rates and sunlight conditions on the covering behavior of T. gratilla:

The following combinations of flow and sunlight were examined in each of the 3 habitats, cloudy/low flow, cloudy/high

flow, sunny/high flow, and nighttime/high flow. A sunny/low flow day was not observed during the duration of our research. Daytime experiments were conducted between the hours 0700 and 1000, with the evening experiment conducted at 2000. A 100 meter transect (to the east of the light house) was laid through the center of the selected habitat and at every ten meter point the nearest urchin to the north and south was selected. Data noted for each urchin included: (1) substrate occupied; (2) diameter and height (vernier calipers, nearest mm); (3) percent of test covered. The percent of test covered was divided into the same five categories as used for the flow transplant experiment. All the materials that the urchins carried were removed from their test and placed in plastic bags and then brought to the laboratory for analysis. The materials in the baggies were divided into five categories: (1) rock, (2) shell, (3) twig, (4) algae, and (5) miscellaneous. The wet weight of materials in each category was obtained for each urchin. These weights were summed to obtain the total weight of materials carried by the urchin.

Further samples of urchins (n=20) were brought to the laboratory where their wet weight and test diameter were noted. These data were used to create a regression line correlating the two variables. Urchin test diameter measurements taken in the field were then compared against the regression line in order to extrapolate wet weight.

Due to safety hazards, there were exceptions to the protocol. During the night experiment the flagstone was the only environment investigated. The rubble zone was too dangerous to study due to low visibility and high flow rates. The coral zone was inaccessible due to swarms of foraging *Diadema*. The sunny high flow experiment in the rubble zone was not feasible due to the strong current and depth of the habitat. Though we did attempt to conduct a similar experiment under cloudy, high flow conditions only forty meters of the transect was sampled with the standard protocol. The water condition then became too dangerous so a modified protocol was employed for the remainder of

the transect. Starting at the lighthouse we swam approximately ten meters upstream and collected the nearest two urchins to this point in separate ziploc gallon size plastic bags. After repeating this procedure at the next ten meter mark, we then delivered the urchins to shore. This was performed for 60 meters of the transect line. On shore we recorded all necessary data.

A 2 way ANOVA, with grouping of sun condition (cloudy/low flow and cloudy/high flow) and habitat (all three), was used to compare the differences in (1) urchins' percent cover, (2) weight of cover on urchins' test, and (3) weight of cover on urchins' test with urchin weight as a covariant. The first and second 2 way ANOVAs were analyzed with a Bonferroni multiple comparisons test. These tests were also performed with grouping of high flow (sunny and cloudy) and habitat (flagstone and coral). The 1 way ANOVA equivalent of these tests were performed with grouping of high flow (night, cloudy, and sunny), in the flagstone habitat.

Covering Behavior in Light/Dark/UVB Screened Conditions:

The covering behavior in various light conditions was examined through the 3 protocols below. Experiments were conducted in the order (1) LIGHT (2) DARK (3) UVB SCREENED
(n= 15) and in the reverse order (n=11) in case the experimental order influenced covering behavior. Water was changed after each trial to avoid overheating of the urchins.
LIGHT-Urchins were denuded of any previous cover and placed individually in 30 cm X 16 cm aquaria with enough coral rubble to completely cover the bottom. The aquaria were placed in direct sunlight and number of rocks collected as well as percent of test covered was noted at 1 minute intervals for a period of 10 minutes. The experiment was terminated prior to 10 minutes when the number of rocks collected surpassed 30 or at 100 percent cover.
UVB SCREENED-Experiments followed the light experiment protocol except for the presence of a UVB screen covering the top of the aquaria, blocking out 90 percent of UVB

light. Ambient light filtering in from the sides of the aquaria was disregarded.
DARK- At the termination of the light or UVB screened experiment, aquaria were removed from their respective light condition and covered with a black trash can, rendering total darkness to the urchins in their aquaria. Percent cover as well as position on the wall of the tank was noted at 5 minutes and 10 minutes of darkness. Experiments were terminated early if the urchin had removed all cover and ascended to the top of the water level after 5 minutes of darkness.

Since data were not normally distributed, a Friedman 2 way ANOVA was employed to compare urchin's percent cover in the three light conditions, light, dark, and UVB screened, (at five and ten minutes). A Wilcoxon matched-pairs signed-ranks test was utilized to compare urchins' percent cover under light and UVB screened conditions.

Diurnal/Nocturnal Distribution of Urchins:

Observations were conducted at night (1900 to 2100) and replicated during the day (0700 to 0900). Urchin distribution was examined in 3 circular plots within the flagstone habitat. A 4 m rope was used to circumscribe a plot at 3 selected points. The north-south coordinate of the point was chosen randomly within the boundaries of the flagstone habitat. The east-west coordinate was selected using a stratified random method every twenty meters along a one hundred meter transect. The furthest 40 meters from the light house were not sampled because there were no urchins due to locals collecting on previous days. Within the plots, number of peaks, percentage of peaks occupied by urchins, and number of urchins per peak was note. Peaks were designated as any protrusion in the substrate surpassing 10 cm in height. Live coral within the plot was excluded from peak estimates because urchins did not utilize it for foraging or refuge (personal observation). Underwater lights were used search for the individuals at night; direct illumination was minimized in order to avoid possible disturbance to their behavior.

A Mann Whitney U test was utilized to compare urchin peak occupation between night and day.

Predator Avoidance:

A modified version of McClanahan's (1988) procedure was utilized to assess the relationship between pebble cover and protection from predation. Sea urchin tests were pierced through the Aristotle's lantern and aboral surface with a large upholstery needle, threaded with monofilament line, and tied to a 20 m nylon transect line. This procedure has less than 1% mortality due to tagging. Three urchins were tied to each transect line, spaced approximately 4 m apart. Three experimental urchin types were used: (1) completely covered, original substrate; (2) completely covered, on flat slab of dead coral; (3) uncovered, on flat slab of dead coral. Two such transect lines were laid in the rubble zone. One was laid in front of a porcupine fish's dwelling, and the other in a haphazardly selected locale. Lines were monitored for 15 days, for evidence of predation. Visits were made at 24 hour intervals for 6 consecutive days, and then every 3 days thereafter. It was sometimes necessary to remove cover from type (3) urchins, because flow conditions occasionally allowed access to potential cover. At the termination of the experiment, specimens appeared healthy, and were set free.

Heterogeneity of Habitat:

Quadrats (0.5 m X 0.5 m, with 100 5 cm subdivisions) were laid using a stratified random method along 100 m transects in the 3 habitats. Diversity within each quadrat was assessed using the point intersect method. These data were used to assess percent cover of macroalgae and rubble in all three habitats. Habitats were ranked according to their mean percent cover of macroalgae and compared to habitats ranked by percent of urchins carrying macroalgae. This comparison was also performed for the rubble data

Results:

All ANOVAs and multiple comparison tests were done with BMDP

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statistical software (1990) . The remainder of the statistics unless otherwise stated were performed according to Siegel 1956.

Flow Rates:

Mean flow speeds differ significantly among the flagstone, rubble, and coral habitat zones in the approximate ratio of 1:6:2 (Figure 1). A 2 way ANOVA
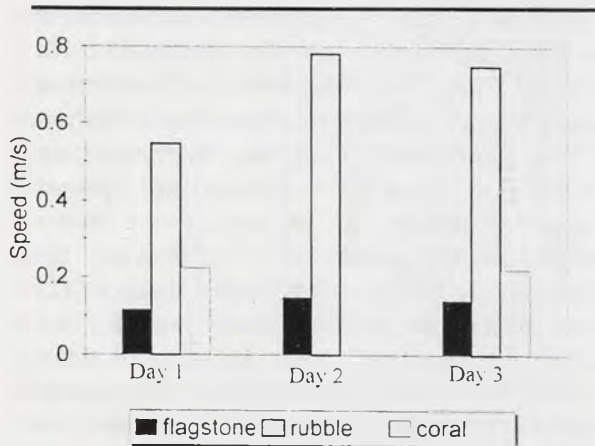
Figure 1. Mean Zone Flow Speeds

comparing mean flow speeds in the three habitats on day 1 and day 3 showed that the variables: day, habitat, and their interaction all had significant effects on flow speed (p<0.001; Table 1). A Bonferroni correction for multiple comparisons showed no significant differences between mean

flow speeds in the flagstone and in the coral zone for day 1 and day 3. All other multiple comparisons were significantly different. (p<0.01)

Flow Transplant experiment:

Urchin collecting behavior is not independent of transplantation destination. (p<0.001; Table 2 & 3). Individual urchins transplanted from the flagstone to the rubble zone added significantly more rocks than the control specimens (Mann-Whitney U Test with Z statistic for tie ranks and large sample size, U=766, P<.00003, Z=9.62). The rock dropping behavior of the experimental urchins was not significantly different than that of the control specimens. Urchins transplanted from the rubble to the flagstone zone dropped significantly more rocks than the controls (Mann-Whitney U Test with Z statistic for tie ranks and large sample size, U=633, P<.00003, Z=10.66. Their rock adding behavior was not significantly different than that observed in the control urchins.

Spatial distribution of T. gratilla::

The populations sampled tended towards an aggregate distribution, with seven of the nine R values at 0<R<1. One population from each habitat was significantly aggregated. (p<0.05; Table 4)

Table 1. Mean flow speeds were significantly different between the flagstone and rubble zone on day 2. (Mann-Whitney U Test, U=0, p<0.001). H_0= Flow speed is independent of both day and habitat.

SOURCE	SUM OF SQUARES	DF	MEAN SQUARE	F VALUE	TAIL PROBABILITY
Day	.0508	1	.0508	44.78	.000
Habitat	1.8409	2	.9204	811.5	.000
Interaction	.0752	2	.0376	33.14	.000
Error	.0340	30	.0011		

Table 2. <u>Collecting Behavior of Urchins' After Transplantation From the High Flow Rubble Zone.</u> *Key:* H_0: Urchin collecting behavior is independent of final transplantation destination. The observed frequency in each cell is shown, with the frequency expected if H_0 is true in parentheses. X^2 df=2(p< .001) = 27.9

<center>Urchin Collecting Behavior</center>

Final Zone Destination	No. of urchins that added rocks	No. of urchins that dropped rocks	No Change	Total
High Flow/Rubble	9 *(4.76)*	1 *(9.52)*	10 *(5.71)*	20
Low Flow/Flagstone	1 *(5.24)*	19 *(10.48)*	2 *(6.28)*	22
Total	10	20	12	42

Table 3. <u>Collecting Behavior of Urchins' After Transplantation From the Low Flow Flagstone Zone.</u> *Key:* H_0: Urchin collecting behavior is independent of final transplantation destination. The observed frequency in each cell is shown, with the frequency expected if H_0 is true in parentheses. X^2 df=2(p< .001) = 30.8

<center>Urchin Collecting Behavior</center>

Final Zone Destination	No. of urchins that added rocks	No. of urchins that dropped rocks	No Change	Total
High Flow/Rubble	24 *(15)*	1 *(0.5)*	0 *(9.5)*	25
Low Flow/Flagstone	6 *(15)*	0 *(0.5)*	19 *(9.5)*	25
Total	30	1	19	50

Table 4. <u>Urchin's Diurnal Spatial Distribution.</u>
Key: Asterisk indicates significance at alpha = 0.05 level. Clark and Evans' statistics: r = mean distance between an urchin and its nearest neighbor; E(r) = expected average distance between a randomly selected urchin and its nearest neighbor if the dispersion of individuals is at random; R = r/E(r) (if 0<R<1 the population is aggregated, if 1<R<2.15 the population has a regular dispersion pattern, and if R=1 the population is randomly distributed); Z tests for deviation from the expected value of R; N is the number of observations. H_0 = Urchins are randomly distributed in all three habitats.

<center>Clark and Evans' Nearest Neighbor Statistics</center>

Distance from Shore (m)		r	E(r)	R	Z	N
Flagstone	9	0.70	1.44	0.48	-1.396	2
	12	0.26	0.94	0.27	-2.80 *	4
	16	0.66	0.65	1.02	0.1215	8
Rubble	35	0.26	0.24	1.10	1.338	54
	36	0.27	0.29	0.92	-0.9454	36
	41	0.23	0.28	0.81	-2.24 *	40
Coral	81	0.17	0.20	0.84	-2.568 *	74
	90	0.36	0.47	0.75	-1.778	14
	93	0.69	0.94	0.74	-0.9911	4

The effects of naturally varying flow rates and sunlight conditions on the covering behavior of T. gratilla:

One and Two Way ANOVAs

In the three habitats, speed of flow between high and low flow days is not an important determinant for urchins' percent cover or for weight of cover carried by urchins (Table 5 & 6). However, the interaction of habitat and speed of flow significantly effect weight of cover carried by urchins but not urchins' percent cover (Table 5 & 6).

In the flagstone and coral zone, strength of sunlight between cloudy and sunny days is an important determinant for both urchins' percent cover and weight of cover carried (Table 8 & 9). The interaction of habitat and strength of sunlight significantly effects weight of cover carried by urchins but not urchins' percent cover (Table 8 & 9).

Habitat significantly influences both urchins' percent cover and weight of cover carried by urchins (in both two way ANOVAs) (Table 1, 2, 4 & 5). In the flagstone habitat, strength of light between sunny days, cloudy days and nights significantly influences urchins' percent cover but not weight of cover carried. (Table 11 & 12).

Urchin weight corresponds to diameter by the formula: $f(x) = 2.81\ E\text{-}3\ X\ (x^{2.53})$ and $R^2 = 9.65\ E\text{-}1$ (Figure 2). Weight of cover carried by urchins does not correlate to urchin weight (Table 7, 10, 12).
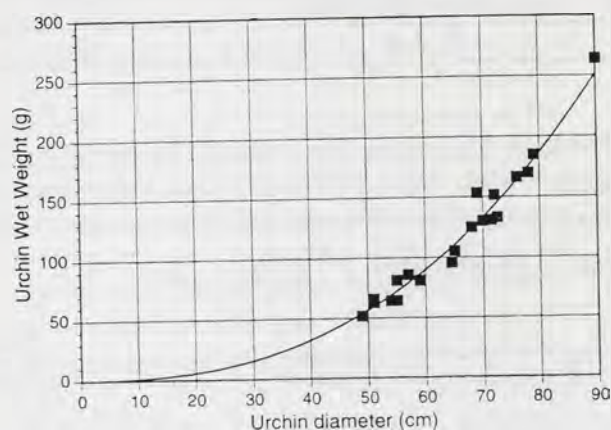
Figure 2. Correlation between urchin weight and diameter

Table 5. 2 Way ANOVA Comparing Urchins' Percent Cover Under Cloudy/ High Flow and Cloudy/Low Flow Conditions in the Three Zones: Flagstone, Rubble, & Coral. H_O= Urchins' percent cover is independent of both habitat and flow.

SOURCE	SUM OF SQUARES	DF	MEAN SQUARE	F VALUE	TAIL PROBABILITY
Flow	0.6750	1	0.6750	.087	0.3535
Habitat	5.4167	2	2.7083	3.48	0.0340
Interaction	0.3081	2	0.9250	1.19	0.3081
Error	88.650	114	0.7776		

Table 6. 2 Way ANOVA Comparing Weight of Cover Carried by Urchins Under Cloudy/ High Flow and Cloudy/Low Flow Conditions in the Three Zones: Flagstone, Rubble, & Coral. H_O= Weight of cover carried is independent of both habitat and flow.

SOURCE	SUM OF SQUARES	DF	MEAN SQUARE	F VALUE	TAIL PROBABILITY
Flow	43.79000	1	43.7900	0.14	0.7117
Habitat	3008.0588	2	1504.0294	4.71	0.0108
Interaction	4056.7460	2	2028.3730	6.36	0.0024
Error	36375.2309	114	319.0810		

Table 7. 2 Way ANOVA, with Covariates Urchin Weight and Volume. Comparing Weight of Cover Carried by Urchins Under Cloudy/ High Flow and Cloudy/Low Flow Conditions in the Three Zones: Flagstone, Rubble, & Coral. H_O= Weight of cover carried is independent of habitat, flow, urchin weight, and urchin volume .

SOURCE	SUM OF SQUARES	DF	MEAN SQUARE	F VALUE	TAIL PROBABILITY	Regression Coefficient
Flow	59.077414	1	59.07714	0.18	0.6690	
Habitat	1263.44540	2	631.72270	1.96	0.1450	
Interaction	3837.60708	2	1918.80357	5.97	0.0034	
Urchin Weight	36.2433	1	36.24733	0.11	0.73777	0.0226
Error	36338.98358	11	321.58393			

Table 8. 2 Way ANOVA Comparing Urchins' Percent Cover Under Sunny/ High Flow and Cloudy/High Flow Conditions in two Zones: Flagstone & Coral. H_O= Urchin's % cover is independent of both habitat and light conditions.

SOURCE	SUM OF SQUARES	DF	MEAN SQUARE	F VALUE	TAIL PROBABILITY
Type of Light	6.6125	1	6.6125	4.08	0.047
Habitat	10.5125	1	10.5125	6.48	0.0129
Interaction	2.1125	1	2.1125	1.30	0.2573
Error	123.25	76	1.6217		

Table 9. 2 Way ANOVA Comparing Weight of Cover Carried by Urchins Under Sunny/ High Flow and Cloudy/High Flow Conditions in two Zones: Flagstone & Coral. H_O= Weight of cover carried is independent of both habitat and light conditions.

SOURCE	SUM OF SQUARES	DF	MEAN SQUARE	F VALUE	TAIL PROBABILITY
Type of Light	12831.9250	1	12831.9250	13.19	0.0005
Habitat	10946.7550	1	10946.7550	11.25	0.0012
Interaction	7650.5032	1	7650.5032	7.86	0.0064
Error	73956.1606	76	973.1074		

Table 10. 2 Way ANOVA, with Covariate, Urchin Weight, Comparing Weight of Cover Carried by Urchins Under Sunny/ High Flow and Cloudy/High Flow Conditions in two Zones: Flagstone & Coral. H_O= Weight of cover carried is independent of habitat, flow, urchin weight, and urchin volume .

SOURCE	SUM OF SQUARES	DF	MEAN SQUARE	F VALUE	TAIL PROBABILITY	Regression Coefficient
Type of Flow	12966.4952	1	12966.49520	13.18	0.0005	
Habitat	3301.29661	1	3301.29661	3.36	0.0709	
Interaction	7637.61927	1	7637.61927	7.76	0.0067	
Urchin Weight	181.56840	1	181.56840	0.18	0.6687	0.0578
Error	73774.59223	75	983.66123			

Table 11. <u>1 Way ANOVA Comparing Urchins' Percent Cover Under Sunny/ High Flow, Cloudy/High Flow, and Night/High Flow Conditions in the Flagstone Zone</u>. H_O= Urchin's percent cover is independent of light condition.

SOURCE	SUM OF SQUARES	DF	MEAN SQUARE	F VALUE	TAIL PROBABILITY
Type of Light	8.6333	2	4.3167	4	0.0237
Error	61.55	57	1.0798		

Table 12. <u>1 Way ANOVA Weight of Urchin Cover Under Sunny/ High Flow, Cloudy/High Flow, and Night/High Flow Conditions in the Flagstone Zone</u>. H_O= Weight of cover carried is independent of light conditions.

SOURCE	SUM OF SQUARES	DF	MEAN SQUARE	F VALUE	TAIL PROBABILITY
Type of Light	1057.7697	2	528.8848	2.13	0.1284
Error	14165.3075	57	248.5142		

Table 13. <u>1 Way ANOVA, with Covariate, Urchin Weight, Comparing Weight of Cover Carried by Urchins Under Sunny/High Flow, Cloudy/ High Flow, and Night/High Flow in the Flagstone Zone</u>. H_O= Weight of cover carried is independent of light conditions, urchin weight, and urchin volume .

SOURCE	SUM OF SQUARES	DF	MEAN SQUARE	F VALUE	TAIL PROBABILITY	Regression Coefficient
Type of Flow	1057.70906	2	528.85453	2.09	0.1331	
Urchin Weight	4.40430	1	4.40430	0.02	0.8955	-0.0169
Error	14160.90324	56	252.87327			

Bonferroni Multiple Comparisons Test

Parameter 1: the three habitat zones
Parameter 2: high and low flow speeds (cloudy condition)

Urchins' percent cover does not significantly differ in either high or low flow conditions for any of the three habitats (Figure 3). Weight of cover carried by urchins in the flagstone environment on low flow days significantly differs from that carried in the coral zone on high flow days (p<0.01). On high flow days, weight of cover carried by urchins in the coral environment differs from that carried in both the flagstone (p<0.01) and rubble zones (p<0.05). All other pairwise comparisons for weight of cover carried by urchins were not significantly different (Figure 3).

Figure 3. Weight of cover carried

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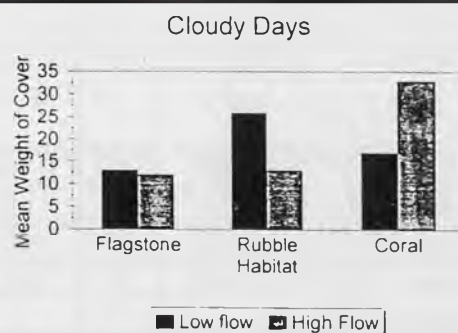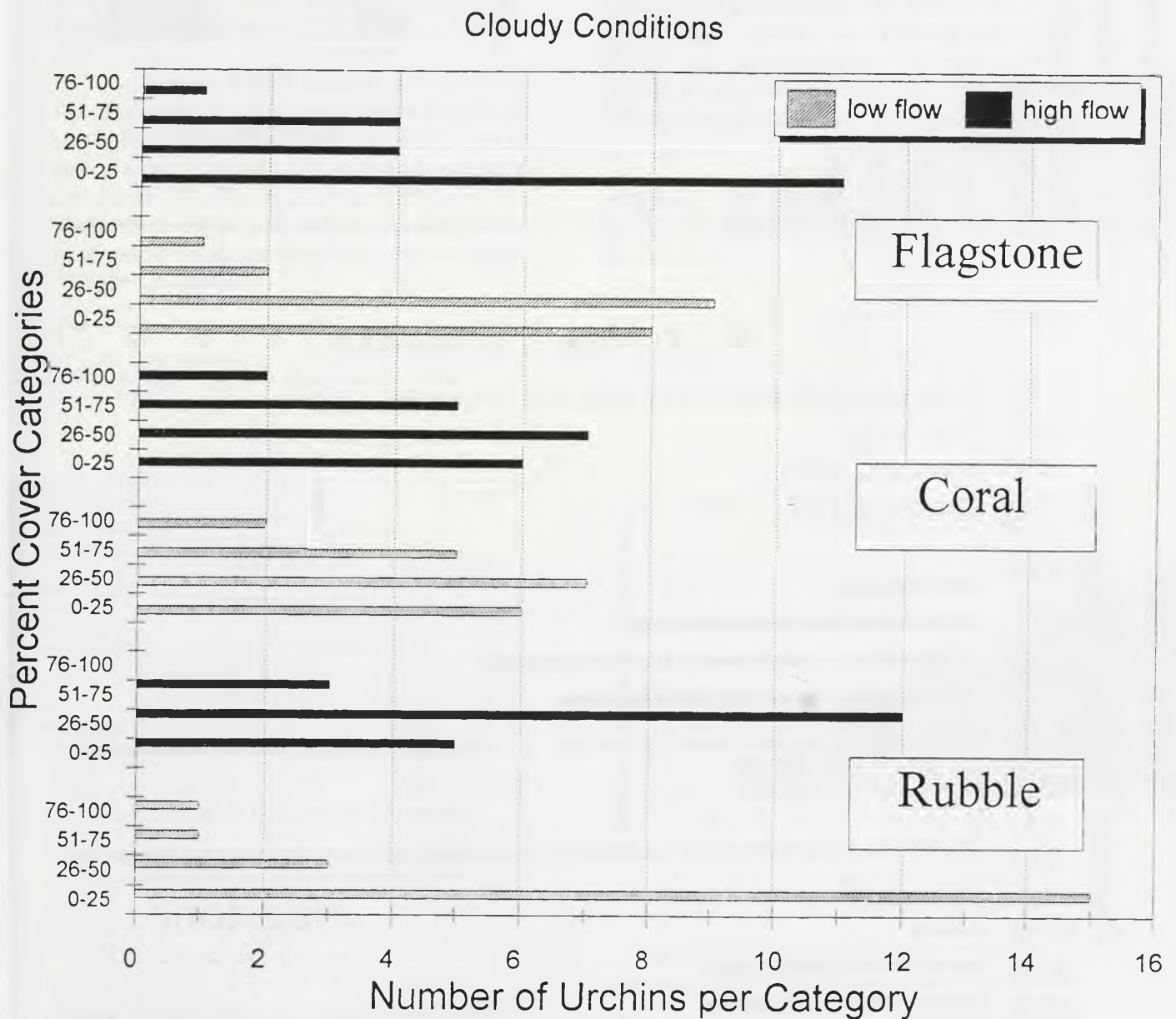
Cloudy Conditions

Figure 4. Distribution of Urchins' Percent Cover

Parameter 1: the flagstone and coral habitat zones
Parameter 2: sunny and cloudy days (high flow condition)

On cloudy days urchins' percent cover in the flagstone environment was significantly less than that observed in the coral zone under sunny conditions (p<0.05).

On sunny days, weight of cover carried by urchins in the coral zone was significantly higher than that carried in: (1) the flagstone environment ($p<0.01$) on sunny days; (2) in both the flagstone ($p<0.01$) and coral zone ($p<0.01$) on cloudy days. All other pairwise comparisons for both urchins' percent cover and weight of cover carried by urchins were not significantly different (Figures 5 & 6).
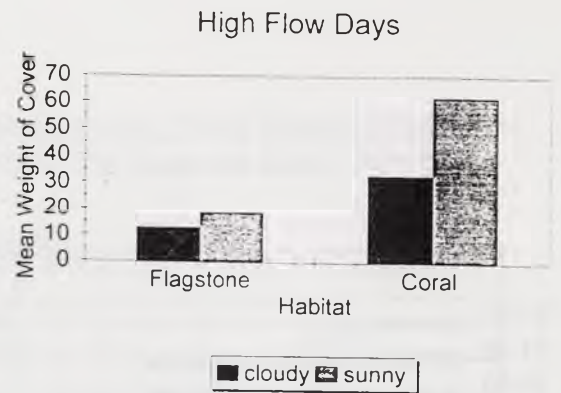
Figure 5. Weight of Cover Carried
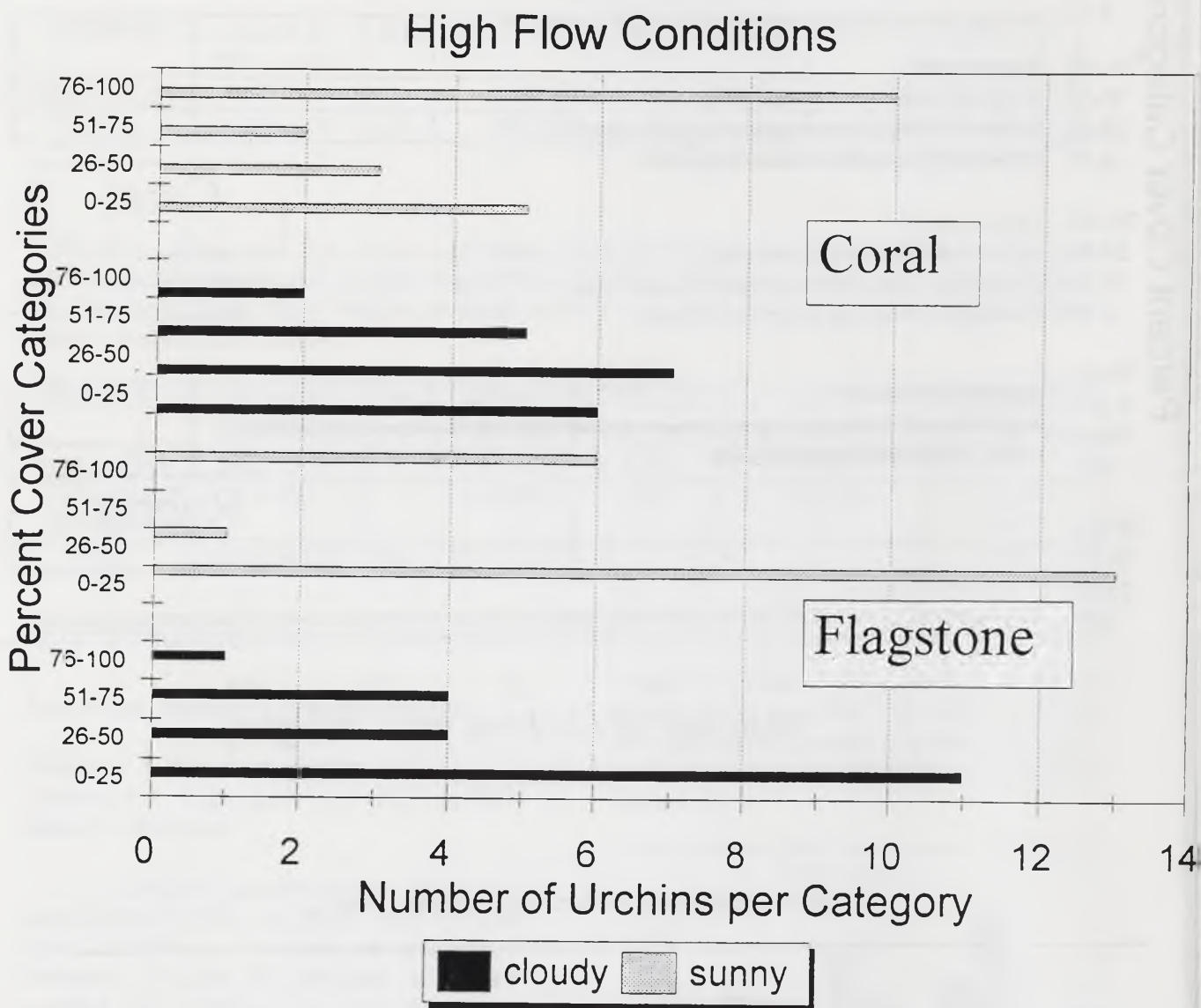
Figure 6. Distribution of Urchins' Percent Cover

Parameter 1: the conglomerate zone
Parameter 2: sunny, cloudy, nighttime (high flow conditions)

Percent cover during the night in the flagstone is significantly less than that observed during the day (p<0.05). But, percent cover on cloudy and sunny days is not statistically different (Figure 7). Weight of cover carried in the flagstone environment varies directly with strength of light (Figure 8).

Figure 9. Urchins' percent cover over time
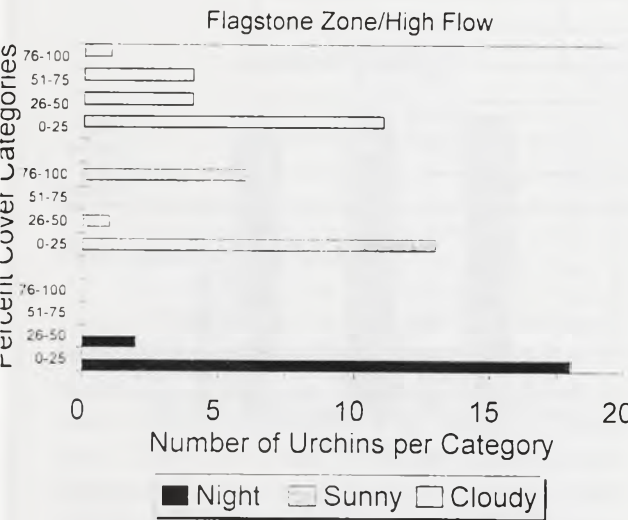
Figure 7. Distribution of urchins' percent cover
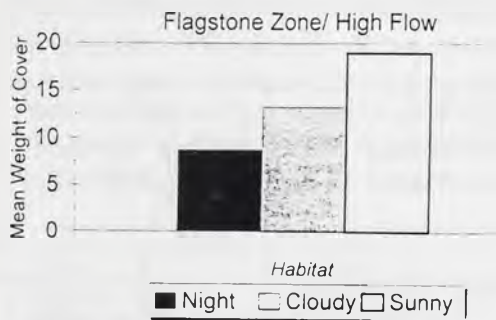
Figure 8. Weight of cover carried
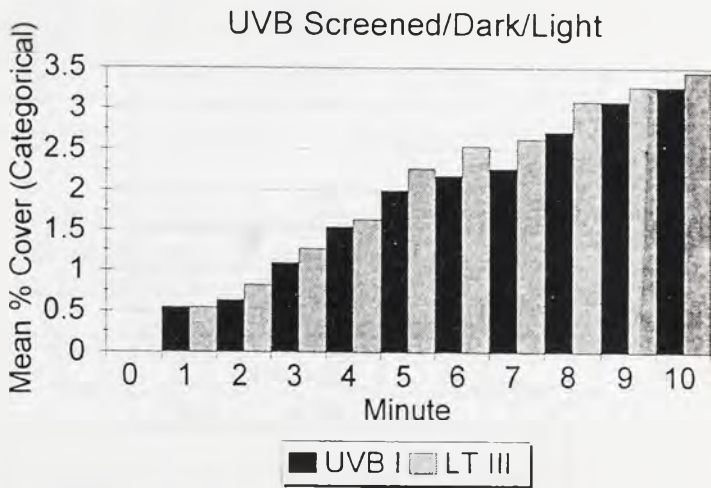
Figure 10. Urchins' percent cover over time

Covering Behavior in Light/Dark/UVB Screened Conditions:
For the experiment which ran in the sequence Light/Dark/UVB screened, there was a significant difference in urchin's percent cover during the Light and UVB screened treatments at each 1 minute interval. (Wilcoxin T test, all P<.001 (T stats are in Appendix); Figure 9) For the reverse order experiment, no significant differences were found (Wilcoxin T test - see Appendix, Tables 1 & 2) (Figure 10).

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The urchins' percent cover in the light/dark/UVB screened treatment at five (Friedman test statistic = 15.23, DF=2, p<0.0005) and ten minutes (Friedman test statistic = 22.30, DF=2, p=0.0000) differed significantly. The Friedman results for the reverse treatment, UVB screened/dark/light, were also significant at five (Friedman statistic = 15.95, DF=2, p<0.0003) and ten minutes (Friedman test statistic = 16.55, p<0.0003).

The multiple comparisons test for both minutes in both treatment directions suggest that urchins' percent cover in light and UVB screened treatments significantly differed from that obtained in the dark treatment (Figure 11) but, urchins' percent cover in light did not significantly differ from that observed in the UVB screened condition (Figure 12) (Table 14 & 15).

(Found On Peaks)

Figure 13. Peak climbing behavior

Light/Dark/UVB Screened Conditions

Figure 11. Urchin covering behavior

(Found Off of Peaks)
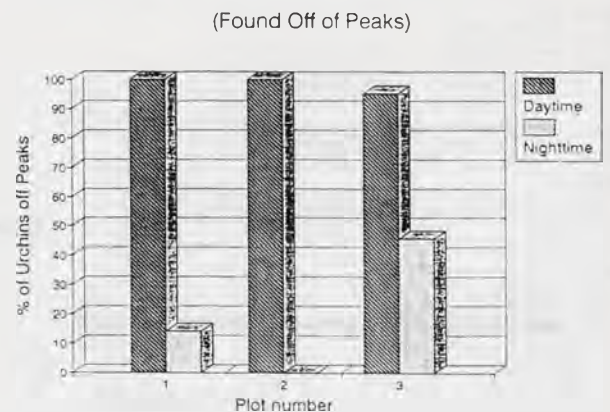
Figure 14. Peak climbing behavior

UVB Screened/Dark/Light Conditions

Figure 12. Urchin covering behavior

Diurnal/Nocturnal Distribution of Urchins

The percentage of urchins occupying peaks during the night hours is significantly higher than that observed on peaks during the day. (Mann-Whitney U Test, U=0, p<.05; Figure 13) Likewise, the percentage of urchins off of peaks during the day was significantly different from the percentage found during the night. (Mann-Whitney U Test, U=0, p<.05; Figure 14).

Predator Avoidance :

No predation was observed after 3 weeks of periodic observation of the predation lines.

Table 14. Multiple comparison tests for light/dark/UVB screened treatment. *Key:* ** = p<.05 H_0= there are no significant differences in urchins' percent cover for each of the pairwise comparisons.

	5 minutes		10 minutes	
Comparison	Z stat	Dif	Z stat	Dif
LT - DK	3.74**	20.50	4.66**	25.50
LT - UVB	0.91	5.00	1.64	9.00
DK - UVB	2.83**	-15.50	3.01**	-16.50

Table 15. Multiple comparison tests for UVB screened/dark/light treatment. *Key:* ** = p<.05 H_0= there are no significant differences in urchins' percent cover for each of the pairwise comparisons.

	5 minutes		10 minutes	
Comparison	Z stat	Dif	Z stat	Dif
LT - DK	2.88**	13.50	3.41**	16.00
LT - UVB	0.96	-4.50	0.21	-1.00
DK - UVB	3.84**	-18.00	3.62**	-17.00

Heterogeneity of Habitat

There is a rough correlation between the percent of a zone covered with macroalgae and the percent of urchins in that habitat covered with algae (Table 16). There is also a rough correlation between the percent of a zone covered with rubble and the percent of urchins in the zone using rubble as masking material (Table 17).

Table 16. Comparison Between Percent Algal Coverage in Habitat and Percent of Urchins with Algal Cover

Rank of Zones by Percent of Zone with Algal Cover		Rank of Zones by Percent of Urchins with Algal Cover	
Coral Zone	2.5%	Coral Zone	85%
Flagstone Zone	0%	Flagstone Zone	6%
Rubble Zone	0%	Rubble Zone	0%

Table 17. Comparison Between Percent Rubble Coverage in Habitat and Percent of Urchins with Rubble Cover

Rank of Zones by Percent of Zone with Rubble Cover		Rank of Zones by Percent of Urchins with Rubble Cover	
Rubble Zone	77.7%	Rubble Zone	100%
Coral Zone	18.8%	Flagstone Zone	95%
Flagstone Zone	1.6%	Coral Zone	87%

Discussion

Flow Rates:

The differences in flow rate are easily attributed to the varying substrate configurations in the "islet reef." Water entering the area flows in through the passes and over the algal ridge. The algal ridge is extremely craggy and thus inhibits laminar flow, making the speed of water

decrease as it flows over the coral zone. (Vogel, 1981). Urchins in this area felt varying degrees of turbulence and flow depending on their location. Some urchins were found in depressions up to 18 cm deep where flow is almost nil, while some were well exposed and felt much stronger fluid motion. Because we took the flow measurements at the surface of the water, the speeds calculated will only represent what urchins living in or close to this water layer experience. The flagstone area is partially protected by a flagstone shelf which acts as a wall along which the flow proceeds. This wall renders it the calmest of the three zones, hence the slow flow speed. The rubble zone is the deepest area and has few impediments to laminar flow. Though the substrate is rugose, being primarily composed of rubble, it causes comparatively little turbulence at the level of the urchins. (Koehl, 1977) Thus, urchins here probably experience the strongest impacts of flow.

Flow transplant:

The significant rock adding behavior after transplantation into high flow indicates that covering may confer some protection from flow. This behavior acts in conjunction with other behaviors such as wedging into the rubble, hiding in crevices, or moving behind *Diadema* patches to further increase protection. (personal observations). Apparently adding pebble cover not only increases weight, it also renders the urchin less susceptible to dislodgment; we observed some hapless urchins with very little or no cover get swept away by the current. It's possible that collecting is exclusively a thigmotaxic response stimulated by the greater amount of potential covering material afforded by the rubble zone. However, our data suggest that covering behavior is at least partially dependent on flow. We observed that urchin coverage directly corresponds to flow speed. Thus upon transfer from the high to low flow habitat, rocks that were no longer necessary for ballast were discarded.

Even though all urchins were handled equally only specimens transplanted from the high to low flow

habitat exhibited significant dropping behavior. Therefore, it is evident that handling does not cause dropping behavior. However, it is possible that handling disturbs the urchins and effects their adding behavior. Urchins may perceive motion during handling as a strong current, thus they add in order to weigh themselves down and prevent being tossed again.

Whether merely increasing cover is the best mechanism to deal with flow is uncertain. Adding pebbles creates a rough surface and hence causes turbulence in the water flowing above and along the test. Studies to determine whether a rough surface actually decreases or increases drag have been inconclusive. (Koehl, 1977) Most likely adding weight is advantageous to the urchin, and it's effects are probably compounded by other behaviors which cause less of the test to be subject to flow. It is difficult to draw conclusions because there is so little knowledge for covering in relation to ballast. Though it has been suggested that masking in the caddis fly larvae could be for ballast (Resh, personal communication), there is simply no literature which addresses the subject of flow in this or any other masking organism. Most of the literature focuses on covering as protection from light or camouflage from predators.

Because light has been shown as a trigger in covering, it's probable that fluid forces are acting in tandem with the factor of light. In order to deduce whether flow alone is a factor, it would be necessary to remove the light variable. This could be accomplished by one of two methods: (1) repeat the transplant experiments during night/high flow conditions or (2) place urchins in a heavily shaded flow tank to see if weight of materials selected for masking directly corresponds to flow velocity.

Spatial Distribution of T. gratilla:

T. gratilla's strong tendency toward an aggregate distribution confers with Cole 1946 who reported that clumping of varying degrees represents by far the commonest pattern in nature, almost the rule, when individuals are concerned. Clumping could be the effect of :

(1) *survival being better in some parts of the environment*

Resources may not have been evenly distributed throughout the plots during our study. Therefore, animals tended to aggregate in areas with the highest quality or abundance of food. It could also be possible that certain areas of the environments offer more protection from the negative effects of flow so organisms gravitate there for refuge.

(2) *the presence of one individual attracting other individuals to the same location*

Individuals in groups often experience a lower mortality during unfavorable periods or during attacks by other organisms than do isolated individuals, because the surface area exposed to the environment is less in proportion to the mass and because the group may be able to favorably modify microclimate or microhabitat. The aggregations of Diadema have been shown to hinder predation, increase fertilization success, and reduce flow speeds by creating velocity shadows. (Pearse 1969, Bernstein et al. 1981, & Levitan 1992). Since this distribution study was conducted while *T. gratilla* was spawning, during the days surrounding a full moon, their aggregations may be a function of reproduction. Similar aggregate distributions during reproductive periods have been described for *T. esculentes* (Lewis 1958, Moore 1963b). This hypothesis is highly likely because echinoderms have been shown to be attracted to chemical stimuli and gametes emanating from conspecifics (Reese 1966).

3) *the spatial scale used for study*

The distribution of organisms depends on the spatial scale used to study them. The distribution could appear aggregated because too large or small a frame of reference was used to study the species' distribution. However, this is highly unlikely because we conducted a pilot investigation to determine the appropriate plot size to use for our distribution study.

(4) *human predation upon urchins*

Patchy distributions of other *Tripneustes* species have been attributed to humans harvesting (Scheibling & Mladenov, 1988). When humans gather urchins they clear out complete areas, sometimes removing as many as 30 urchins at once (personal observation). The *T. gratilla* that are not collected then appear aggregated because they are surrounded by cleared areas.

***The effects of naturally varying flow rates and sunlight conditions on the covering behavior of* T. gratilla:**

The ANOVAs indicate whether there is a difference between the two selected groupings, but does not give an accurate significance level until a multiple comparisons correction is applied. Because the Bonferroni multiple comparison gives the difference between individual parameters, this is the data that is most relevant to our discussion. The high mean weight of cover seen in the coral zone on cloudy/high flow days accounts for the significant difference between the weight of cover in this zone and that of the flagstone zone (on both high and low flow days). Though no other comparisons were significant we know from our flow transplant experiments that an individual's covering behavior is effected by flow. Moreover, we observed that there were several other non-covering behaviors displayed which also minimized the negative effects of flow. For example, wedging into the substrate or hiding in a crevice both help withstand flow without additional cover or weight. Because we were looking only at percent cover and weight of cover carried without using these other behaviors as indices, the statistical tests were not sensitive to the individual variance which occurred. It is high variance in amount or weight of cover among individuals which causes trends in the population to be lost, hence making the comparisons appear non-significant.

The suspected variance in individuals was supported by the literature. (Millott, 1956). The reasons for such high individual variance in covering are unknown. One reason could be the age of

the organism; the gastropod *Xenophora*, cover themselves to highly varying degrees, and some who are poor collectors completely discontinue the behavior as they age (Portmann, 1959). Thus, it's possible that as an urchin ages and reaches a certain size it is not as susceptible to predation so it can discontinue the habit. Himmelson and Steele 1971 have shown that older urchins tend to escape predation by being too large to eat. We tried to examine this variable with urchin weight and found no correlation between weight carried and weight of urchin.

The results for Bonferroni multiple comparisons test suggest that urchins' weight of cover in the coral zone on a sunny day was the major factor causing the two way ANOVA to reveal that light condition, habitat, and their interaction are significant variables effecting masking behavior. Weight of cover carried in the coral zone may have been higher on the sunny high flow day because waves were crashing over the ridge and so the flow was coming in two directions at the urchin. On the cloudy day the flow was only along the coast so the urchins did not have to cope with the added stress of the wave surges. The flagstone zone on the sunny day probably did not show much difference in covering behavior from the other comparisons because the impacts of waves were significantly reduced by the time they contacted the flagstone environment. The weight of cover carried in the flagstone was greater but significantly difference.

The two way ANOVA for percent cover suggests that both strength of light and habitat effect covering behavior. However, after the Bonferonni test, differences between direct sunlight and cloud filtered light no longer appear to significantly effect covering behavior. The difference in these two light conditions probably do not significantly effect urchin behavior because the UV wavelengths which is one of the major stimuli in covering behavior can still penetrate clouds (Reese, 1966). The multiple comparisons test suggests that the only significant difference in covering behavior was between cloudy days in the flagstone and sunny days in the coral zone. It is most likely that the higher percent cover of urchins in the coral zone was not related to light strength but rather to avoid being dislodged by the wave surges.

After the Bonferroni correction on the 1 way ANOVA comparing urchin percent cover/weight of cover in the flagstone environment, we saw urchin percent cover was significantly different between night and day. This is likely due to light avoidance; however, previous results have shown that the trends across the population are not necessarily indicators of individual behavior, especially because weight of cover did not significantly differ between night and day, contradicting the previous results. It was obvious that a study of individual behavior was necessary to elucidate the trends completely. In order to deduce when the urchin is adding cover to increase its weight versus the percent of its test covered we would need to perform further experiments. A possible test to distinguish which of these variables is a better indicator of covering behavior in different environmental conditions would be to give urchins covering material that were the same size but varied in weight. This experiment could be performed in the laboratory with a flow tank and varying wattage tungsten lights.

Covering Behavior in Light/Dark/UVB Screened Conditions:

The covering behavior appeared to be very light sensitive, in accord with previous published works (Moore, 1966, Lewis, 1958). Since percent cover consistently increased as light exposure time increased, the data support the hypothesis that covering is a light avoidance mechanism. This behavior was observed under both natural sunlight and UVB filtered light conditions. Urchins perceive UVB filtered light to be a weaker light source than natural sunlight (Reese, 1966) so it is not surprising that under UVB screening, urchins masked to a lesser degree than under unfiltered light conditions. There is also the component of fatigue: after a period of five to ten minutes with exposure to strong light, urchins lessen both their speed and degree of covering (Millott

1956, Lewis 1958). This sensitivity to strength of light compounded by the fact that urchin's fatigue caused the order of experiments to significantly influence urchin covering behavior. For the experimental sequence light/dark/UVB screened, the additive effects of fatigue and UVB filtered light account for the significant difference in percent cover among the two light conditions. Though the urchins do not cease to cover themselves (as in complete fatigue), it is feasible that 20 minutes of covering and uncovering under the first two experiments might cause the onset of fatigue under the third. The presence of an interaction between light strength and fatigue is also supported by the data from the reverse experimental sequence UVB screened /dark/light. The stronger light source afforded by natural sunlight conditions caused the urchins to cover to a greater degree. This difference in mean percent cover between the light treatments would have probably been greater if fatigue was not a variable.

The urchins' rapid shedding of cover in the laboratory under complete darkness concur with Millott's 1956 results and give further evidence that light is a trigger for masking behavior. All urchins, even those who were completely burrowed, shed almost if not all of their pebble cover after 10 minutes. And, a great majority of these urchins ascended along the wall of the aquarium towards the surface of the water. In some cases their tests were partially out of the water. We believe that the urchins may shed their weight at night because carrying extra weight during their nocturnal foraging would necessitate that they expend extra energy.

Diurnal/Nocturnal distribution:

The nocturnal peak climbing behavior of *T. gratilla* is consistent with it's nocturnal climbing behavior observed in the laboratory and with the behavior of many other intertidal organisms. During the daylight few creatures can stand the strong sunlight at the water surface; thus, they tend to seek depths below the surface that are most appropriate for the functioning of their internal mechanisms. As dusk falls, many migrate upwards,

following the quality of light that suits them and they remain high in the water column until the stimulus of light again appears at dawn. (Stephenson & Stewart, 1955).

Their climbing behavior may also be linked to nocturnal foraging. The relationship between food and locomotive activity has been investigated by several authors. Dance 1987 has suggested that feeding behavior is a compromise between foraging to find food and remaining sedentary, thus conserving energy. Thus, urchins may climb to the tops of peaks where flow is faster. In this position they can remain immobile, conserving energy while catching drifting particles of food.

Predation:

It is very unusual that *T. gratilla* and its only known visual predator, *D. hystrix*, have overlapping nocturnal foraging patterns (Parker & Shulman, 1986). Generally echinoids are nocturnal because they are trying minimize temporal overlap with their predators, which are mostly diurnal fish (Dance 1987). Once predation pressure is lifted, urchins have been shown to reverse their activity pattern. For example, *Diadema setosum* exhibit a continuous feeding pattern in a habitat which lacks the urchin's diurnal predators (Fricke, 1974). Another example is the sea urchin *Paracentrotus lividus*, which exhibits an odd activity pattern. Here the urchin's foraging is strictly diurnal because its' predators are nocturnal (Ebeling et al. 1966). In our situation it appears that predation is probably not a major factor influencing the urchins' behavior *because T. gratilla* makes no apparent attempt to minimize temporal overlap in behavior with the porcupine fish.. Furthermore, throughout the study not many dead tests were found and those that were discovered appeared to be broken into almost perfect half spheres. This test condition is virtually identical to that created by the locals, who cut the test and remove the gonads. It is entirely possible that the tests we encountered were mostly attributable to human predation because locals dispose of the tests in the water after the gonads are removed. This idea is

further advanced because the number of dead tests always increased around the full moon.

The lack of predation of *T gratilla* on the experimental predation lines regardless of the amount of cover worn can be accounted for by the fact that there are so few predators of *T. gratilla* and such a high density of urchins. Only two *D. hystrix* were observed throughout the duration of the project. Densities of *T. gratilla* in some cases were as high as 30 individuals per square meter. Even though a transect line was strung in the vicinity of a *Diodon*'s residence it is entirely possible that the experimental specimens could have been overlooked, regardless of the amount of cover worn. The denuded urchin may not have appeared conspicuous. Under every environmental condition examined, there was a high variance in percent cover among the urchin population. Therefore, there would most likely be several urchins in the vicinity of the predation line who were also non-camouflaged and potentially equally as vulnerable to predation as the unmasked urchins on our predation lines. Furthermore, the limited power of our study would have been insufficient to detect small differences in survival. In order to determine if masking behavior minimizes predation a study with a sample size markedly larger would need to be conducted.

Heterogeneity of Habitat:

Because there is so little predation pressure, it is not clear whether the cover worn by urchins functions as camouflage from predators. One of the requirements of camouflage is that the disguise be a random sample of the background seen by predators (Endler 1978). The heterogeneity assessment shows that the masking materials found on the urchins are indeed a random sample of the habitat. The minimal selection for certain types of covering material, suggested by the disparity in the ranks of the data can be accounted for by other variables in the environment.

In all three zones, the percent of urchins wearing rubble greatly exceeds the percent of the environment composed of rubble. Results from our point intersect method of assessing habitat heterogeneity suggest that in both the flagstone and rubble zone the only suitable cover is rubble. Therefore the urchins wear the only material that is available to them. The percent of urchins wearing rubble in the flagstone area is probably higher than that observed in the coral zone because the urchins in the coral zone have two choices of covering materials, rubble and algae, available to them.

The high percentage of urchins wearing macroalgae in comparison to the low percent macroalgal composition of the both the coral and flagstone zones can also be explained by environmental conditions within the habitats. As the waves crash over the algal ridge, macroalgae is fragmented and carried to the coral zone, which has a relatively low flow. Here the algae can settle and be used as cover. The little algae that may be carried by the current (moving North west) to the flagstone area will also have a chance to settle and be utilized as cover. This explains why there were a higher percentage of urchins in the flagstone wearing algae than was anticipated by the point intersect method. The rubble zone urchins probably do not wear algae because the mean water speed is too high for algae to be able to settle and reach the urchins at this deeper depth.

Conclusion

Our studies lend support to the needs of hypothesis testing in ecology. The critical testing of the causes of masking behavior has been incomplete. Without sufficient evidence, many possible adaptive functions for the behavior have been accepted and repeatedly cited. In both field and laboratory settings (as facilities permitted), our study rigorously addressed hypotheses that had never been tested. Our study contributes to the ongoing exploration of the role masking behavior. It supports previous works that light causes masking behavior but it is novel in that our experimental manipulations provide evidence that covering behavior is also caused by varying intensities of flow. Our pilot predation study suggests that the masking materials are composed of a

random sample of the organisms environment but it was inconclusive in determining its effectiveness as a predator avoidance strategy. Even thought our study shows that these variables are important determinants in the masking behavior by no means can we conclude that the behavior is an adaptation to these environmental conditions. Steps from here that could be taken to determine whether this behavior is truly adaptive include: (1) provide further evidence that the pebble covering behavior is fit towards the environment, (2) conduct breeding studies to assess whether the covering behavior is a heritable trait (mate urchins who collect cover to different degrees) (3) assess whether fitness (survival) is improved by possessing this collecting trait, and (4) furthermore we would need to map a phylogeny, tracing when pebble collecting behavior first arose on the phylogenetic tree and if it has arisen many times separately. It would be especially important to see if the causal variable for adaptation was present when the adaptation arose. Fulfilling these requirements would not only provide definitive evidence that covering behavior is an adaptation, but would add a vast amount of knowledge to the biology of echinoderms.

Acknowledgments

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APPENDIX

Table 1. <u>Wilcoxin T table comparing percent cover of urchins between light and UVB screened treatments for the experimental sequence: light/dark/UVB screened treatment.</u> H_O= There is no difference in percent cover between urchins under both treatments.
Key: *= $T_{.05}(2)$ 15 p<.05)

Minute	T-statistic
1	0*
2	13.5*
3	14.5*
4	11.5*
5	18*
6	8.5*
7	0*
8	16*
9	7.5*
10	0*

Table 2. <u>Wilcoxin T table comparing percent cover of urchins between light and UVB screened treatments for the experimental sequence UVB screened/dark/light</u> H_O= There is no difference in percent cover between urchins under both treatments.
Key: *=$T_{.05}(2)$11 p<.05

Minute	T-statistic
1	25.5
2	32
3	32
4	28.5
5	20
6	18
7	26.5
8	26.5
9	32
10	25.5

Map 1. Temae Study Site

Lighthouse

Wall

Benchmark

0

3

50

X — Pemphis acidula

• — Porites boulders in conglomerate

47
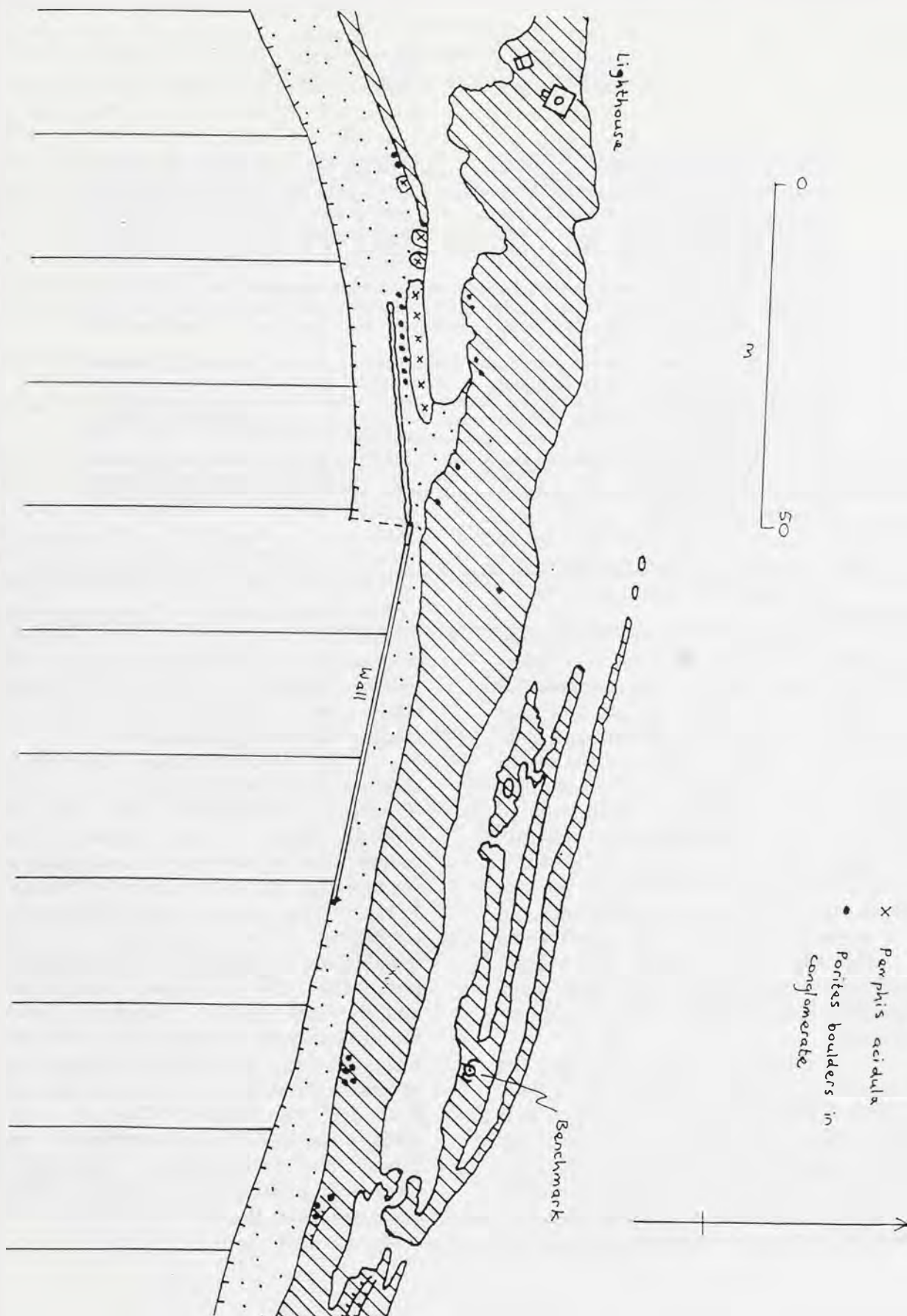
Differences in Population Structure of Three Wrasses in Relation to Habitat Variability

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ABSTRACT. The mechanisms behind social structure in wrasses, a family of coral reef fishes, has been studied for many factors, including age, size, hormonal control, local population size, and genetic control. Yet, social control is the only explanation proven as the determining factor of social structure in some species. This study argues that distribution of resources in the environment serve to determine the population structure of three wrasses, *Gomphosus varius*, *Halichoeres hortulanus*, and *Thalassoma hardwickii* in four different habitats.

Wrasses are protogynous hermaphrodites. Initial phase females undergo a sex reversal to become terminal phase males. Dichromatism occurs between the initial and terminal phase fishes, making the phases distinguishable. The reason behind the phase ratios has not been identified.

All species exhibited significant differences of percent terminal phase and abundance between separate habitats. *G. varius* and *T. hardwickii* had a significant relationship between abundance and percent algae, while *H. hortulanus* exhibited a significant relationship between abundance and chain length. Thus indicating that algae is a good indicator of food resources, and chain length of vertical complexity.

The environmental factors significant in influencing the percent terminal phase have not been identified. Further studies into the specific resources utilized by each species, may determine what resources in the habitat are important in determining the percent terminal phase.

Introduction

The principal factors influencing population structure in coral reef fishes have long been debated. Food resources and shelter are two important factors that dictate the structure of a population (Levin, 1993; Roede, 1990). Roede (1990) stated that "social systems control mating opportunities, yet spatial distribution of food and shelter determine social systems" in labrid fishes. Sale (1977) modified this view and argued that reef fish are not narrow niched in terms of food resource, but are selective in shelter. The selectiveness of shelter is defined for a broad habitat, but habitat partitioning may allow some species of fish to occupy different habitats of a reef.

A species of reef fish may be present in multiple habitats, but have higher fitness in habitats for which it is suited best. This fitness for a particular habitat may be related to distribution and structure of resources in different habitats. Alevizon and Landmeier (1984) found that parrotfish phase (male/female) ratios varied between habitats. The phase-ratio variability increased with larger environmental differences in separate reef habitats, although they did not determine what aspects of the habitat might be causing the distinct phase ratio's.

The wrasses (family Labridae), cichlids, embiotocids, and parrotfishes (family Scaridae) make up the order of labroid fishes. Most labroids are protogynous hermaphrodites, undergoing a sex inversion from female to male (Meyers, 1991). The adults are dichromatic, exhibiting distinct coloration for the female (initial phase) and male (terminal phase) fish. The females are usually drab and the males gaudy. Reinboth (1967) found two types of males, those born as males (primary) and those that undergo sex reversal (secondary). Primary males are drab, like the females. The sex of an initial-phase fish can be determined from dissection of gonadal tissue. Species that have both primary and secondary males are termed diandric.

This study examines the percent terminal-phase males and abundance of three wrasses, *Gomphosus varius*, *Halichoeres hortulanus,* and *Thalassoma hardwickii,* in separate habitats. A similar difference in phase ratios of parrotfish and wrasses is expected because of their similar sexual strategy. I assumed that percent terminal phase is a reflection of the male to female relationship. Significant differences in abundance were also predicted for different habitats. Correlations between the aspects of habitat and percent terminal phase and abundance should reflect their underlying distribution in a habitat.

Methods and Materials

Study Sites and Dates

This study was performed at four locations in the lagoon surrounding Moorea, French Polynesia. Moorea is located at 17°32' S and 149°50' W in the Society Islands. Data were taken at these sites October-November 1994. These sites were selected on the basis of their accessibility and on the presence of the three species of wrasses, *Gomphosus varius*, *Halichoeres hortulanus*, and *Thalassoma hardwickii*.

The four locations were designated as the West Back Reef, East Back Reef, Linareva, and Temae (Figure 1). All of these habitats were composed of similar coral species, indicating a source of stability between all habitats. Yet, because of differences in amount of live coral, algae, and vertical complexity, they can be viewed as different habitats.

The West Back Reef (WBR) site, located 50 m from the reef crest, west of the entrance to Cook's Bay, was composed of an opposite spur and groove pattern perpendicular to the reef crest. Strips of coral-head patches alternated with sand between coral heads 20-30 m wide, and strips of coral rubble 10-20 m wide.

The East Back Reef (EBR) site, located 50 m from the reef crest, east of the entrance to Cook's Bay, consisted of random coral-head patches. Coral rubble formed the substrate between coral heads. Patches were separated from each other by 15-30 m of a hard-pan, flat bottom substrate.
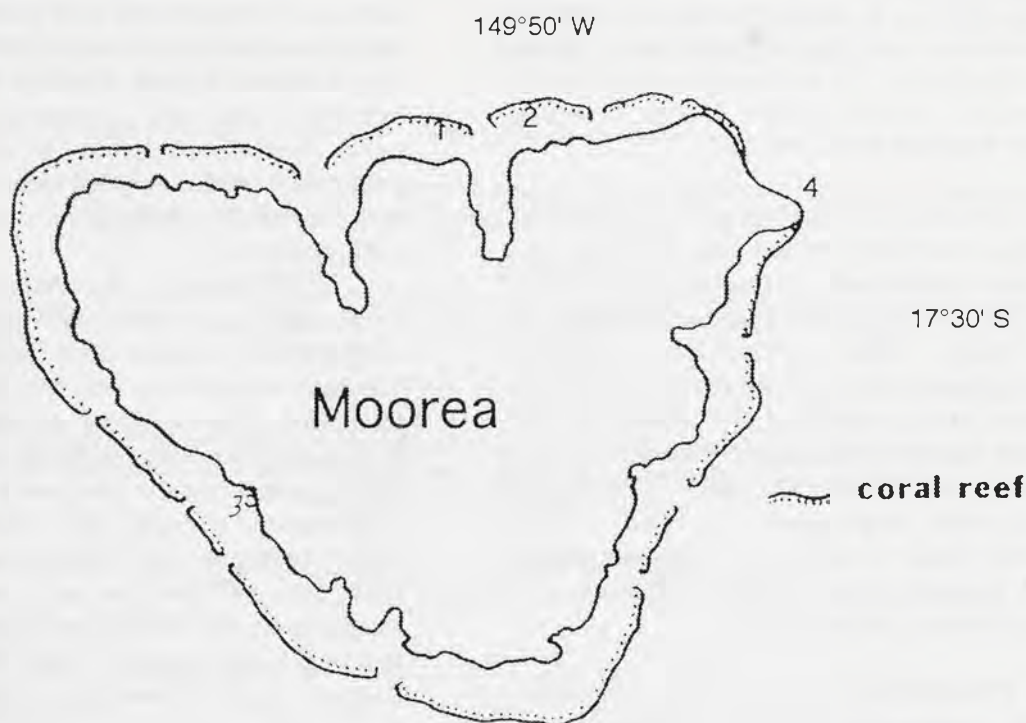
149°50' W

17°30' S

coral reef

Figure 1. Study sites on Moorea, French Polynesia.
1=WBR, 2=EBR, 3=Linareva, 4= Temae

The Linareva site was located at the fringing reef north of the restaurant Linareva, near Haapiti. This habitat consisted of a shallow sandy area bordered by large *Porites* coral heads on the edge of a steep drop off. The transects were taken on the border of the drop-off, not including the sandy area. *H. hortulanus* was not present in this habitat.

The Temae site was located at the patch reef west of Temae public beach. This patch reef is composed mainly of dead coral with areas of live coral growth. Sand forms the bottom substrate between coral heads, with very little coral rubble seen.

Study Animals

(1) *Gomphosus varius* (Lacepede, 1801), commonly called the bird wrasse, is found throughout Oceania and the western Pacific. It is named for its unusually long snout. *G. tricolor* (Quoy and Gaimard) is a synonym for the terminal-phase male. It can be found in coral-rich areas of lagoon and ocean-side reefs (Meyers, 1991). They are usually solitary, with terminal-phase males exhibiting territoriality (Colin and Bell, 1991). It feeds mainly on benthic crustaceans and less on brittle stars, fishes, and mollusks. It is closely related to *G. caeruleus* of the Indian Ocean (Meyers, 1991; Randall et al., 1990).

(2) *Halichoeres hortulanus* (Lacepede, 1801), commonly called the checkerboard wrasse, is found throughout the Indo-Pacific. It has a checkerboard pattern on its body. The females have a white background color and the males a distinctly green background color (Randall et al., 1990). They inhabit sand patches of clear lagoon and ocean-side reefs, with adults preferring large areas of sand. They mainly feed on sand dwelling gastropods and less on hermit crabs, bivalves, and polychaetes (Meyers, 1991).

(3) *Thalassoma hardwickii* (Bennett, 1828), commonly called the sixbar wrasse, is found throughout the Indo-Pacific. *T. schwanefeldii* (Bleeker) is a synonym (Randall et al., 1991). It is diandric

(Robertson and Choat, 1974), thus having both primary (initial) and secondary (terminal) males. Robertson and Choat (1974) found that only 3 out of 32 initial-phase were primary males. This gives us an error of 10-15% when estimating number of females from initial-phase numbers. The color pattern is similar for both phases, with the terminal-phase males becoming gaudier than the primary, initial-phase, males. It inhabits lagoon and ocean-side reefs, in clear-water areas of mixed coral, rubble, and sand. Its diet encompasses a wide variety of benthic and planktonic crustaceans, foraminiferans and small fishes (Meyers, 1990).

Transects

Visual fish censuses were taken to measure the percent of terminal-phase wrasses. Twelve, ten-minute timed transects were performed in each of the four habitats over a period of five weeks. Transects were limited to a defined habitat. Wrasses seen within a 180° arc and 2 m radius were recorded on an underwater slate, specifying species and phase. The transects were taken variously, between 7:30 a.m. and 5:00 p.m. Care was taken to swim at a constant speed, although the distance varied slightly due to the influence of current. As a result of the short time period, multiple transects were performed within a brief time span in the same habitat, resulting in data that lack independence.

To quantify the different habitats, coral and algal variability were measured as potential indicators of food resources. Vertical complexity of the habitat was measured as an indicator of shelter. A 100-m transect line was placed in each habitat. Every ten meters the line was marked with a permanent ink spot and within each ten meter segment a predetermined distance from the ink spot was selected using an integer from the random numbers table and marked with flagging tape. At the ten flagged spots, a one-meter quadrant was laid down to estimate visually the percent live coral and percent algae (macro and turf). As a measure of vertical complexity, a nine meter long piece of chain was placed

along the surface of the lagoon floor underneath the transect line, beginning at each of the ten flagged spots. The horizontal distance covered by the chain was measured by extending a measuring tape along the transect line, beginning at the flagging tape extending to the end of the chain. The smaller the value from the measuring tape, the greater the vertical complexity of the habitat.

Statistical Analysis

The percent terminal phase and total fish counted (abundance) were calculated for each species in a transect. These numbers were then used to look at the variation for each species of both percent terminal phase and abundance between habitats, using the Kruskal-Wallis test. A multicomparisons test for Kruskal-Wallis (Conover, 1980) was used to determine which pairs of habitats differed.

The variance within and between the habitats was determined by first computing the means for percent coral, percent algae, and chain lengths in each habitat. The variation within each habitat was calculated by the coefficient of variation. These data are graphed together to see the relationship.

The means of the percent terminal phase and abundance were calculated for the individual species in each habitat. Percent terminal phase and abundance were then compared within the individual species using the Ordinary Least Squares Regression test and correlations were calculated. Correlations were also calculated for the relationship of average values of percent live coral, percent algae, and chain length, to percent terminal phase and abundance. A t-statistic with 2 degrees of freedom was also calculated for each regression. A table of p-values (Bulmer, 1967) was used to determine if the t-statistic was significant for the 95% confidence interval. The p-values were not given if the t-statistic was not in the 95% confidence interval.

Results

Transects

The results of the statistical analysis for variation between habitats for each species was significant in all cases for both the percent terminal-phase and abundance (Table 1).

The multicomparisons test indicates that the largest difference in habitats pairs occurs between the East Back Reef and Linareva, followed by the East Back Reef and Temae (Table 2).

Table 1. p-values for the Kruskal-Wallis test performed on each species to determine if significant differences for the percent terminal phase and abundance occurred among habitats.

	G. varius	H. hortulanus	T. hardwickii
% Terminal Phase	.004	.000	.001
Abundance	.000	.000	.002

Table 2. The multicomparisons test for Kruskal-Wallis (Conover, 1980) specifies which habitats have the greatest differences. Significant difference between habitats is denoted by the * symbol.
1=WBR, 2=EBR, 3=Linareva, 4= Temae

	Habitat Pairs					
	1&2	1&3	1&4	2&3	2&4	3&4
G. varius						
% terminal phase				*		
abundance	*	*	*	*	*	
H. hortulanus						
% terminal phase		*	*	*	*	
abundance		*		*		*
T. hardwickii						
% terminal phase			*		*	*
abundance	*			*	*	

The averages and coefficients of variation for percent coral, percent algae, and chain length for each habitat are shown in Figure 2. Linareva had the highest average percent coral and algae, and lowest average chain length. On the other hand, EBR had the least average percent coral value, least average percent algae, and highest chain length. The values for the coefficients of variation decreased by habitat in the order of EBR, WBR, Temae, and Linareva.
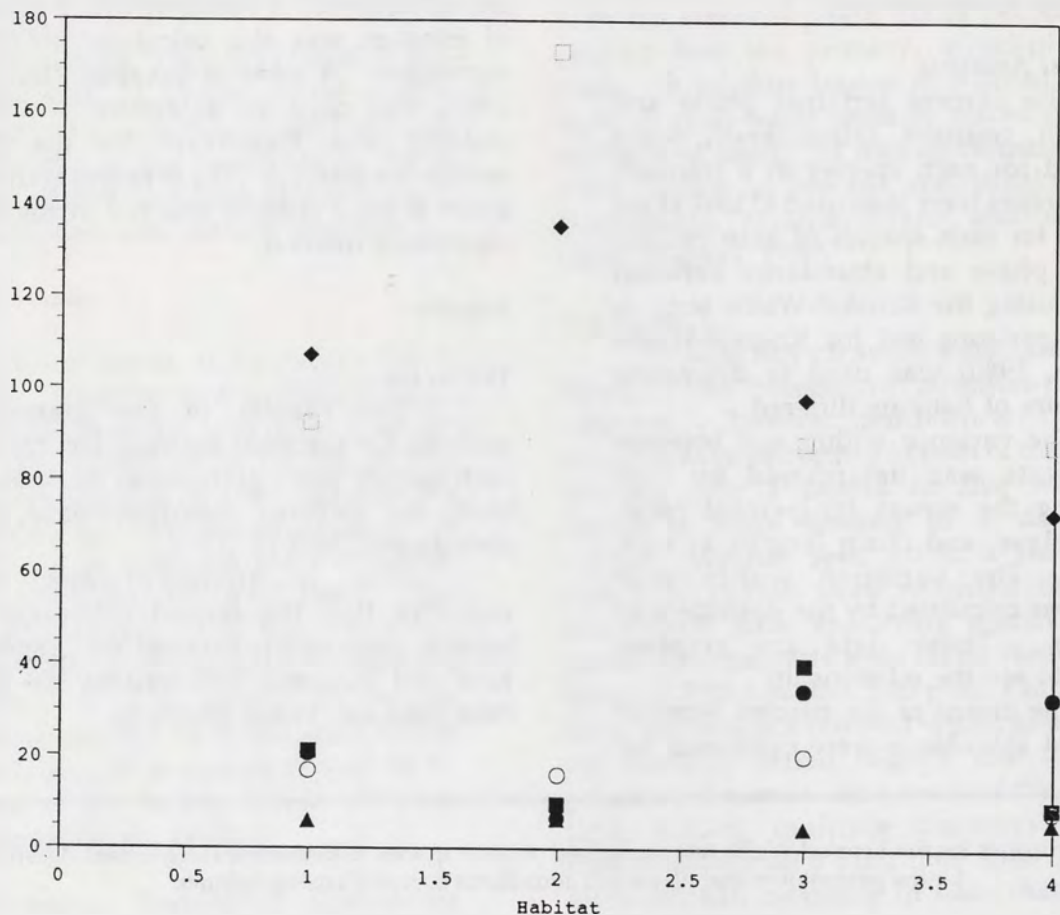
Figure 2. Means and Coefficients of Variation for Coral, Algae, and Chain Lengths

1=WBR, 2=EBR, 3=Linareva, 4=Temae

Figure 4

Average Percent Algae vs. Average Abundance

H. hortulanus abundance

T. hardwickii abundance
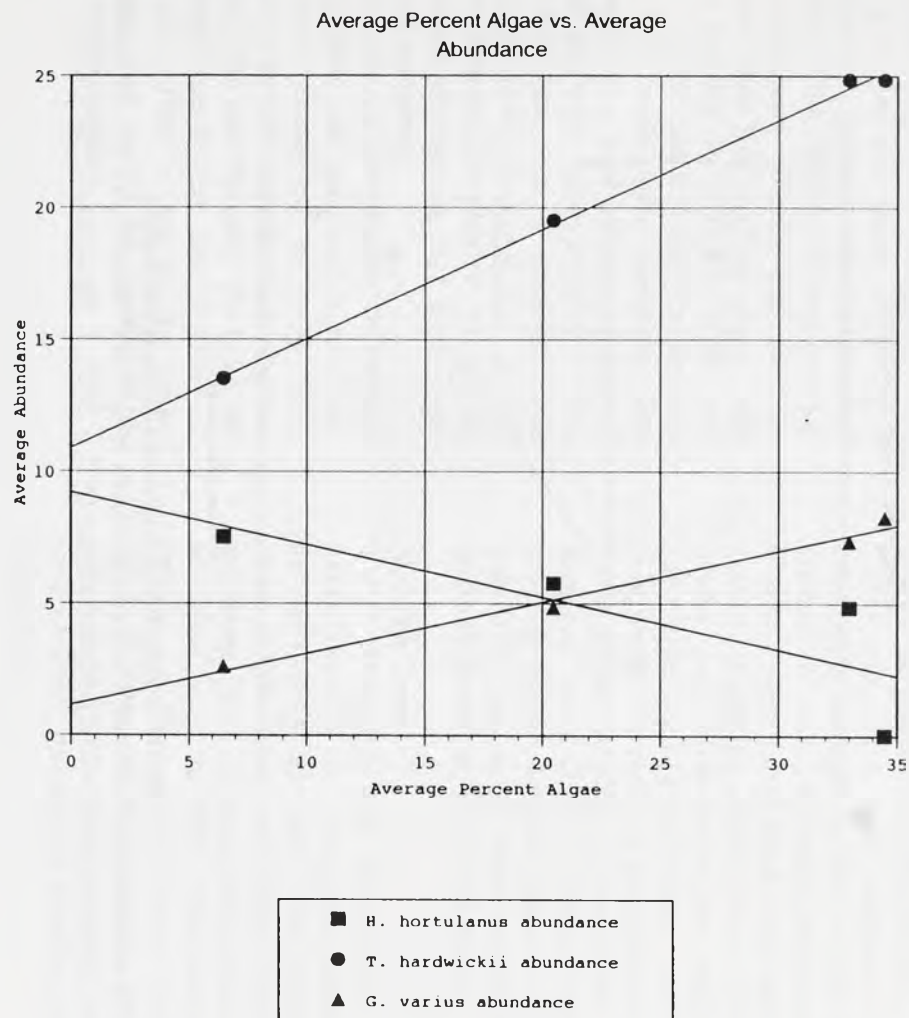
G. varius abundance

The correlation between % algae and abundance is presented for all three species. G. varius (r^2=.983), H. hortulanus (r^2=.649), T. hardwickii (r^2=.998).

Figure 3

Gomphosus varius
Average Abundance vs. Average Percent Terminal
Phase
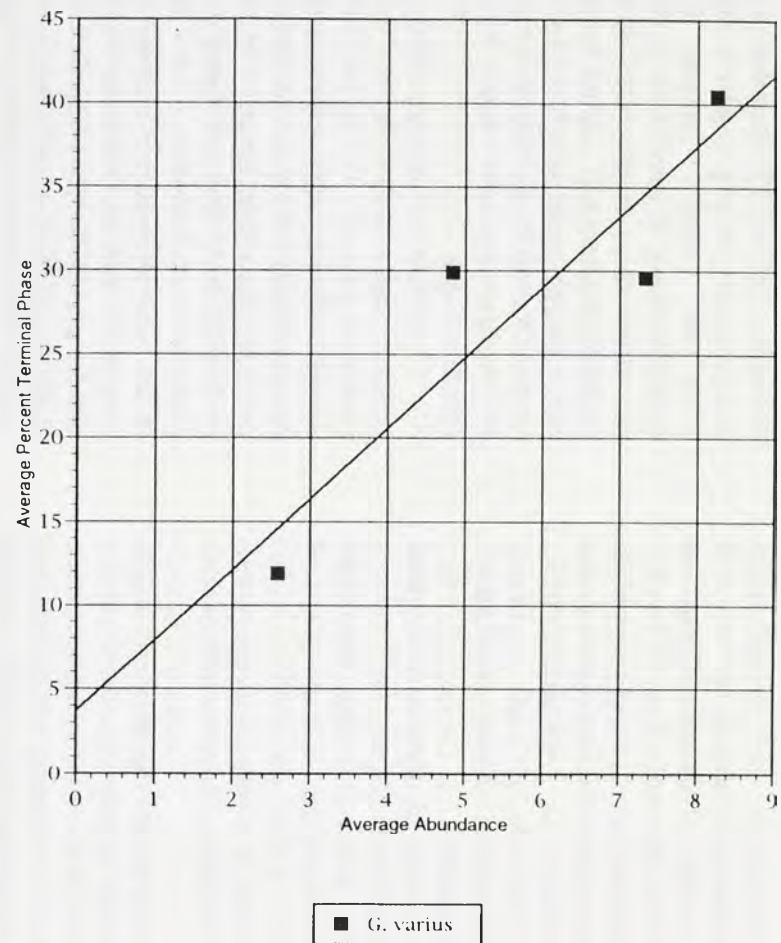
G. varius

G. varius. The relationship between abundance and % terminal phase.
(r^2=.833)

In comparing the relationship between percent terminal-phase and abundance with habitat, *G. varius* (.05>p>.025) was the only fish to have a significant positive relationship (Figure 3). A moderate positive correlation was found for *H. hortulanus* (r^2=.649), but *T. hardwickii* (r^2=.347) had a weak negative relationship. These correlations were not significant.

The strongest correlation found among all of the comparisons, occurs between the percent algae and the abundance for *G. varius* (.005>p>.001) and *T. hardwickii* (.001>p>.0005). *H. hortulanus* has a comparatively weak relationship (Figure 4), which was not significant.

In comparing the percent algae with the percent terminal-phase, *G. varius* (r^2=.824) exhibits a strong positive relationship, *H. hortulanus* (r^2=.599) has a moderate negative relationship, and *T. hardwickii* (r^2=.300) a weak correlation.

The data correlations with percent live coral do not show any significance. *H.* *hortulanus* (r^2=.785) abundance exhibited a moderately strong negative relationship with the coral, whereas *G. varius* (r^2=.339)and *T. hardwickii* (r^2=.225) do not show any correlation. A moderate positive relationship existed between coral and percent terminal-phase for *G. varius* (r^2=.610), but *H. hortulanus* (r^2=.219) and *T. hardwickii* (r^2.155) have weak relationships.

Unlike the previous comparisons of percent algae and coral to the percent terminal-phase, *G. varius* (r^2=.794) demonstrated a moderately strong negative relationship to the percent terminal-phase and average chain length. *H. hortulanus* (r^2=.582) only demonstrated a moderate positive relationship. *T. hardwickii* (r^2=.101) showed no correlation at all. Yet, *H. hortulanus* (.005>p>.001) had an almost perfect positive correlation between chain length and abundance, and *G. varius* and *T. hardwickii* had non-significant, moderately strong and moderate negative relationships respectively (Figure 5).

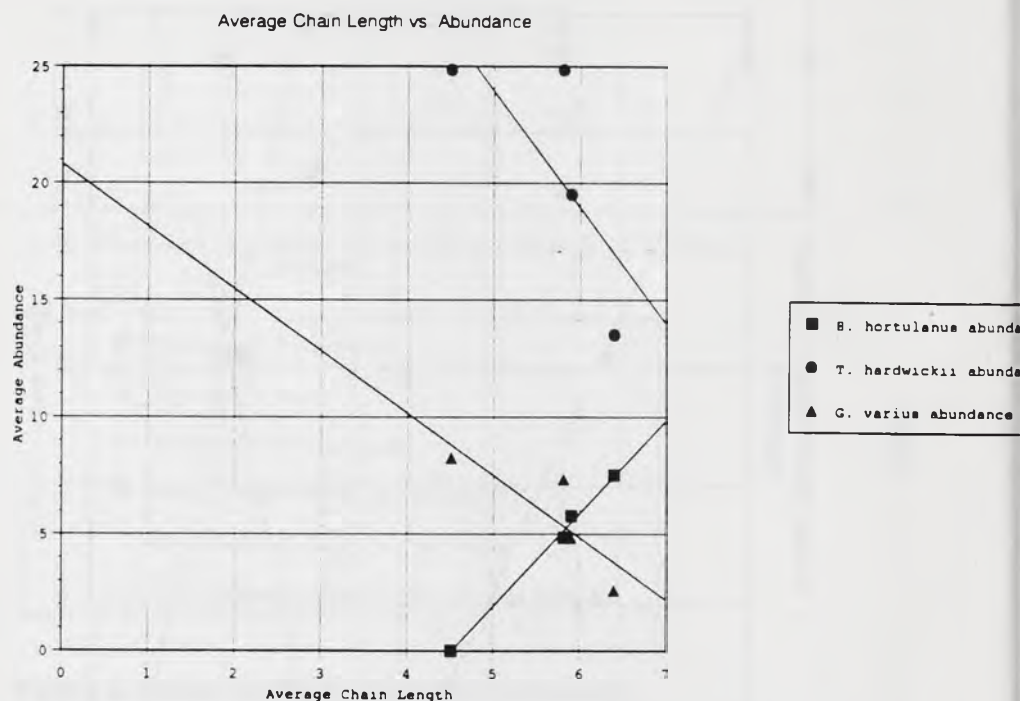Average Chain Length vs Abundance

Figure 5. <u>Average Chain Length vs. Abundance</u>.
The relationship between the average chain length and abundance for all species:
G. varius (r^2 = .704), *H. hortulanus* (r^2 = .995), *T. hardwickii* (r^2 = .555)

Discussion

The statistical analysis indicates that the population structure was affected by the environment. The percent terminal phase and abundance figures for each species were significantly different in each habitat. The largest differences occurred between the habitats that are the most different. EBR was the habitat with the least coral or algae, highest chain values, large coefficients of variation for coral and algae, and a small coefficient of variation for chain length. This translated into a habitat that had large expanses of hard pan and sand with few patches of coral and algae. Thus food resources were scarce and highly variable, as was shelter. WBR provided more resources in both algae and coral and less variation than did EBR. Shelter was also more available, with a slightly higher coefficient of variation.

Food resources and shelter were not limiting at Linareva and Temae. Linareva had the highest amounts of coral and algae, with moderately small variability. This suggests large food resources. The chain length was the least, reflecting a high degree of vertical complexity and thus shelter. This habitat did not provide limiting resources. Temae provided an environment that was high in algae, with variation similar to that of WBR and Linareva. Temae had just over the amount coral of EBR, with little variation. The amount of shelter was similar to that of WBR, though with less variation. This habitat was the least variable, thus making it the most homogenous. It had consistent vertical complexity, providing high amounts of shelter, and high algal related food resources.

The overall frequencies of percent terminal phase and abundance for each species were evaluated as were their relationships to the distribution of food and shelter. The confidence of the p-values is decreased due to the low degrees of freedom (2). This is due to the small sample size and could be resolved by sampling more habitats.

G. varius

The strong correlation between percent terminal phase and abundance in *G. varius* follows that hypothesis of Warner and Hoffman (1980b), that territorial mating success varies with local population to a certain density. As population size increases (and is not overloading the capacity of the environment), it becomes more beneficial for males to come to habitats with high densities of females.

The strong correlation between algae and abundance is a good indicator that algae is a good estimate of food resources for *G. varius*. Wrasses are carnivores, so *G. varius* is probably feeding on invertebrates and epifauna living on and around the algae.

A strong relationship between percent terminal-phase and abundance would also be expected for *G. varius*, because of the previous correlations. If female abundance increases with food resources (algae), the males should also have the highest density, because they are attracted to sites with more females.

Percent coral did not show any relation to population structure of *G. varius*. Coral was not a good indicator of food resources, because of the low correlation with abundance. Although the structure of live and dead coral heads may serve as a source of shelter. Both percent terminal-phase and abundance are negatively correlated with chain length. As habitat complexity increases, it may provide more living space for this territorial fish. This supports Sale's (1977) findings that living space is often a limited resource for coral reef fish. *G. varius* also establishes its territory in and around coral heads.

H. hortulanus

The strongest association of *H. hortulanus* is the negative correlation between abundance and chain length. As chain length increases, vertical complexity decreases. This increases the amount of flat substrate, as in the EBR. This matches the habitat description by Meyers (1991), of where *H. hortulanus* can be found. It is most camouflaged in this environment, and the sand dwelling gastropods it feeds on can be found here.

The correlations for all of the other comparisons were moderate, except for coral with percent terminal phase, which was weak. This indicates that the other factors measured were not important for their population structure. The abundance of algae might affect their food resources, but it is not a large enough factor to influence their population. The presence of sand seems to determine whether or not *H. hortulanus* is present. Linareva, a habitat with high vertical complexity, coral, algae, and no sand, was not suitable for it. In contrast, the bottom substrate at Temae was composed of sand in addition to having a high percent algae; this allowed *H. hortulanus* to inhabit this habitat. Examining the distribution of sand dwelling gastropods might give a better indication of food resources.

T. hardwickii

T. hardwickii demonstrated the strongest relationship between abundance and percent algae. This can be viewed as a good indicator of food resources. On numerous occasions, I observed groups of initial phase sixbar wrasses attacking patches of turf algae on dead coral heads. They are probably feeding on the invertebrates and epifauna on and in the algae. This feeding behavior also supports Hoffman's (1983) assertion that females primarily food-foragers.

The other relationships did not demonstrate any strong correlations, except for a moderate negative relationship between abundance and chain length. The increased vertical complexity indicated increased capacity for fish. The low number of correlations is probably due to *T. hardwickii's* loose social structure (Robertson and Choat, 1977).

Environmental features drive the population structure within a habitat. My ultimate goal would be to estimate the percent terminal phase and abundance from features of the habitat. In the species studied, food resources, shelter, and camouflage are the factors most strongly associated with abundance. The abundance reflects the population size that the habitat can support. In *G. varius*, the abundance gives us an estimate of the percent terminal phase for *G. varius*, but not *H. hortulanus* and *T. hardwickii*. This information supports the hypothesis of Warner and Hoffman (1980) regarding local population size and territorial defense, although a decrease in the percent terminal phase at a high abundance was not observed. *G. varius* might not have reached their carrying capacity in the habitat. Yet, there is still the question of what features of the environment determines the percent terminal phase in a population for *H. hortulanus* and *T. hardwickii*? What environmental factors influence non-territorial social systems?

It is interesting that species of the same family and sexual type use different social strategies within the same habitat. They all have evolved specializations for a social system which provides them the highest fitness for a habitat. This supports Sale's (1977) argument that coral reef fishes high specialization for resources may allow them to occupy multiple habitat. More in depth habitat analysis, targeting specific resources of each species, might provide new information of what environmental factors are controlling the percent terminal phase within a habitat. This raises some questions for further research. How does the partitioning of resources with other animals affect population structure? Is resource partitioning the same for all species? And what features of the habitat determine which percent terminal phase will make the population most reproductively successful?

Acknowledgments

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Abundance and Diversity of *Conus* gastropods
in Subtidal Reef Habitats

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ABSTRACT. Percent cover of particular types of substratum have proven to be important factors influencing abundance and diversity of predatory invertebrates on coral reef platforms. The most favorable portions of reefs for the gastropod *Conus* tend to be areas that are made up of predominately sand, dead coral, and algae. Areas with high densities of live coral harbor few *Conus* individuals. On Moorea, an island in French Polynesia, nine transects placed in three different habitats on coral reef platforms showed that microhabitats with high percentages of algae and dead coral are strongly favored by *Conus* as reflected by high population density and high species richness in this specific habitat.

Introduction

Conus gastropods contain approximately 500 species and a geologic history that extends back 55 million years. *Conus* has evolved rapidly to become the largest genus in its order and is most likely the largest of marine invertebrates (Kohn, 1994). About half of these species inhabit the Indo-Pacific region that spans the central tropical Pacific and Indian Ocean to the Red Sea. Almost all are found in areas associated with coral reefs including subtidal reef platforms, moats and lagoons, and intertidal benches.

Conus species diversity and population density are significantly correlated with substrate topographic diversity (Leviten and Kohn, 1980). In intertidal benches associated with tropical coral reefs, habitat heterogeneity is an important determinate of abundance and *Conus* species richness (Kohn, 1983). Low species richness and high population density characterize *Conus* assemblages on intertidal benches throughout the tropical Indo-West pacific region. On subtidal reefs, which have more heterogeneous habitats, gastropod population densities are lower than on intertidal benches (Kohn, 1971; 1983). However, maximum *Conus* diversity occurs on subtidal coral reef platforms, where 12-27 species may occur in the same square kilometer (Kohn, 1994). Topographically simpler, physically harsher intertidal bench habitats favor lower species diversity, smaller body size and higher population density while a topographically more complex subtidal coral reef habitat favors higher species diversity, larger size, and lower population density (Kohn, 1968; 1971; Kohn and Nybakken, 1975). Ideal conditions for *Conus* are those areas of the reef platform that have >20% cover of algal-bound sand and <20% cover of living coral.

This study tests Kohn's (1983) generalizations regarding habitat heterogeneity and its correlation with *Conus* species richness and population density. The study was conducted in Moorea, French Polynesia at three separate study sites that represented different kinds of subtidal reef habitats. Because of the lack of accessible intertidal benches in Moorea, bench habitats could not be examined. Therefore this paper focuses on whether there is a significant relation between subtidal reef habitats and *Conus* species diversity and abundance.

Materials and Methods

Study Site

This study was conducted in Moorea, French Polynesia which is located

at 17°32′ S and 149°50′ W. Data was collected from October to November 1994. Study sites were chosen according to their accessibility and by whether they contained areas with natural gradients in important habitats related to *Conus* populations. Because *Conus* population density can be low in some areas of coral reef platforms, random placement of transects would have provided limited data. (Kohn, 1971; 1983). Therefore an area was first selected where a moderate *Conus* population had been observed. From this site successive transects were placed in adjacent areas with a relatively different habitat composition. Areas of selected habitat had to be large enough to allow for replicate sampling at three transects each placed 10 m apart. Microhabitat types were assessed according to the classification scheme listed by Reichelt (1982) and Kohn (1983). These microhabitat categories were slightly modified to reflect substratum observed at the selected study sites (Table 1).

Table 1. Summary of microhabitat categories. Modified table from Kohn (1983).

A. Sand	1) level surface 2) in depression
B. Coral rubble, with or without sand	1) level limestone surface 2) in depression 3) under coral rock 4) with algae
C. Very thin layer of sand	1) level limestone surface 2) in depression
D. Reef limestone	
E. Thin layer of algal-bound sand	
F. Dead coral head or boulder	
G. Living Coral	
H. Sand under rocks	
I. Algae	1) foliose 2) crustose

Figure 1. Location of Study Site in Cook's Bay

All three study sites were located in or near Cook's Bay on the north side of the island. The first site was located on the fringing reef in the lagoon directly outside of the Richard Gump Biological Station (Figure 1). The transects were set perpendicular to the shore, 106 m from the Station's property line. The second site was located just north of site 1 at 196 m from the Station's property line. These transects were placed parallel to the shore to ensure they remained within similar habitat type. The third site was located just west of the pass into Cook's Bay on the reef crest. These transects were placed perpendicular to the algal ridge.

Methods of Collection

Data on *Conus* abundance, diversity and microhabitat use was collected from a total of nine transects located in three different habitats on a subtidal reef platform. In each habitat three transects 10 meters long, were each placed 10 meters apart. At the first study site three transects were placed in a habitat that consisted mostly of sand and coral rubble. The second site contained a habitat that was predominantly dead coral, and that had a relatively high percentage of algae. The third and final site lay directly on the lagoon side of the reef crest and consisted of sand, rubble and some algae. Three replicate samples were taken from each transect. Each 10 m transect was divided into twenty 1 m^2 quadrats, ten on each side. For the first daytime sample all *Conus* snails were collected from the quadrats on one side of the transect. For each gastropod collected, species, length, width (to the nearest 0.5 mm), and microhabitat type occupied were recorded. In the second daytime collection the other side of each transect was sampled. Finally, one nighttime sample was completed for each transect. Activity increases at night for many gastropod molluscs and nocturnal foraging is common for *Conus* species on coral reefs ((Reichelt, 1982). Therefore a night sample was thought to be necessary in order to document microhabitat occupied at night and to collect active snails. Due to increased risk

from diving at night, all twenty quadrats of each transect were collected from at once, instead of in two replicate samples as with the day collections.

To determine composition of the substratum, the link-transect method was used (Reichelt, 1982; Kohn, 1983). This method assesses coral reef diversity by documenting all types of substratum occupying a habitat. A 10-m chain, labeled at every meter was stretched over each transect. The chain contained approximately 70 links per meter. Microhabitat type under every 7th link was recorded on an underwater slate. It was easy to lose track while counting links, so to minimize this problem a clothes pin was used to mark the link from which the habitat was being recorded from. There were ten samples of microhabitat recorded per meter , providing a total of 100 microhabitat samples for each transect. Percentage of cover was determined by summing the total number of each specific habitat out of the 100 samples taken.

Results

A total of 341 *Conus* were collected of 11 species. Site 1 had a mean of 24 individuals and 5 species. Site 2 had a mean of 60 individuals and 7 species. This site had the highest abundance and the highest diversity of *Conus* of the three different sites (Table 2). On transect 5 of this habitat, during a night collection, forty-four *C. coronatus* were discovered in one quadrat clumped together under one branch of algae. In none of the other transects were any *Conus* seen to be physically touching each other. This was a very unusual occurrence. The abundance of *Conus* at site 3 was similar to the abundance at site 1 with a mean of 28 individuals. However site 3 had the lowest *Conus* diversity with a mean of 3 species per transect.

Microhabitat for the transects varied at the different sites. Site 1 consisted of 50% sand, 22.3% rubble, and 18.6% dead coral (Figure 2). Site 2 had almost equal parts algae, sand and rubble making up 60% of the habitat. There was almost no live coral, although there was more dead coral

				Transects 1-9						
Species	1	2	3	4	5	6	7	8	9	Total
C. coronatus	5	2	4	20	56	19	0	0	12	118
C. ebraeus	0	0	0	1	1	2	0	0	0	4
C. eburneus	1	1	0	0	0	0	0	3	4	9
C. flavidus	0	0	0	3	0	2	0	0	0	5
C. leopardus	2	1	0	1	0	0	0	0	0	4
C. lividus	1	0	6	12	4	14	9	9	3	58
C. miliaris	0	0	0	2	1	1	0	0	0	4
C. pulicarius	13	20	13	3	8	8	11	17	15	108
C. sponsalis	0	0	0	16	6	1	0	0	0	23
C. striatus	1	1	3	0	0	0	0	0	0	5
C. vitulinus	0	0	0	0	0	1	2	0	0	3
Total	6	5	4	8	6	8	3	3	4	341

than any other type of substrate (Figure 3). At site 3 the habitat closely resembled that of site 1. The substratum consisted predominantly of sand, rubble, and dead coral (Figure 4). There was very little algae in sites 1 and 3, relative to site 2.

A Kruskal-Wallis test (Conover 1980) was used to examine the variation between the habitats. The mean for abundance and diversity was computed for each transect and was then calculated by the coefficient of variation. This test showed that there was no significant correlation between abundance and habitat($p=0.061$). However there was a correlation between diversity and habitat ($p=0.03$).
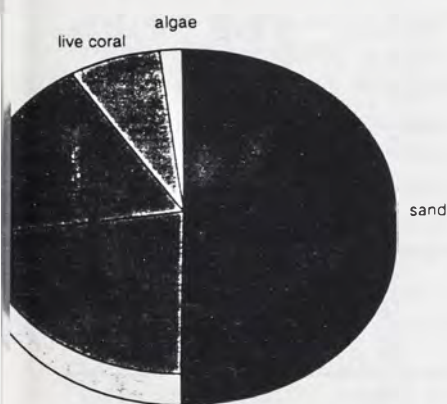

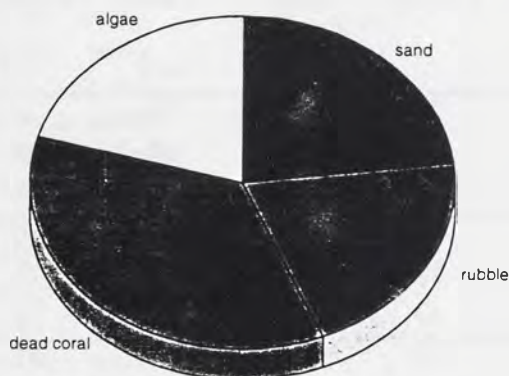Figure 2. Habitat 1 microhabitats

Figure 3. Habitat 2 microhabitats
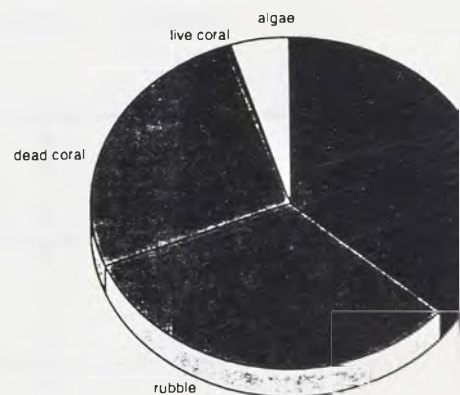
Figure 4. Habitat 3 microhabitats

The microhabitat occupied at time of collection was recorded for every snail. All *Conus* were discovered in one of the following five habitats: sand, coral rubble, dead coral, sand under rocks, and coral rubble with algae (Table 3). Ninety-six percent of the individuals found were discovered in either sand or in rubble. Less than 10 individuals were found in each of the other three habitats. Almost no active snails were collected from the night dives. All that were collected at night were burrowed in the same types of habitat as they were seen to occupy in the daytime.

Table 3. Numbers of individuals found in specific microhabitats. Capital letters refer to the microhabitats listed in Table 1.

		Microhabitat Type					
Species	A	B	B4	H	F	Total
C. coronatus	89	25	4	0	0	118
C. eburneus	9	0	0	0	0	9
C. ebraeus	2	1	1	0	0	4
C. flavidus	2	2	1	0	0	5
C. leopardus	4	0	0	0	0	4
C. lividus	10	46	1	0	1	58
C. miliaris	1	3	0	0	0	4
C. pulicarius	104	3	0	1	0	108
C. sponsalis	6	17	0	0	0	23
C. striatus	1	0	0	4	0	5
C. vitulinus	0	3	0	0	0	3
Total	228	100	7	5	1	341

Table 4. A list of the number of species and number of individuals found per transect. Population density is the number of individuals per m^2. Also a list of the percentage of substratum for each transect.

Site	Transect	# species	# indiv.	pop. density	% sand (A)	% rubble (B)	% dead coral (F)	% live coral (G)	% algae (I)
	1	6	23	1.15	53	30	3	12	2
1	2	5	25	1.25	65	22	13	0	0
	3	4	26	1.3	33	15	40	9	3
	4	8	58	2.9	13	10	60	0	17
2	5	6	76	3.8	42	26	16	0	16
	6	8	48	2.4	14	26	31	0	29
	7	3	22	1.1	42	21	35	0	1
3	8	3	29	1.45	30	52	10	0	8
	9	4	33	1.65	38	24	33	0	5

Discussion

Statistical analysis showed that there was no significant correlation between abundance and habitat. This probably stemmed from the similar mean densities of *Conus* provided by site 1 and site 3, and from the extremely high density provided by site 2. By examining the data on substrate composition for site 1 and for site 3, the similarity between these two habitats can be seen (Table 4). It is most likely that these two sites consisted of almost the same number of individuals due to their similar habitats. In site 2 there was a large percentage of dead coral and moderate amounts of algae, rubble and sand. The large amount of dead coral and the evenly distributed substrate most likely allows for many refuges or crevices that offer protection and attract gastropods. This would explain the relatively high population discovered at site 2.

However, from data collected it was revealed that there was a correlation between diversity and habitat. Although site 1 and site 3 were similar in substrate composition, they did have a significant difference in species richness. Site 3 had a mean of 3 species per transect which is relatively low. Site 3 was also in a physically harsher environment which could explain the lower mean number of species as compared to sites 1 and 2.

The transects in site 3 were originally placed on the reef crest itself, but due to the thick algae covering the ridge, the breaking waves and the many small cracks and crevices filled with pinching crabs, collection of gastropods proved to be difficult. The transects were then moved into the lagoon just south of the reef crest where *Conus* could be located and collected more easily. The transects were still close to the crest making them susceptible to strong currents and rapidly changing conditions. Most of the gastropods (70%) found at this site were species that burrow deep in the sand. Because these species burrow deep in the sand they are less vulnerable than those that burrow partially in the sand or those that simply rest on top of rubble or dead coral. At site 1 where the conditions are calmer, species that would be normally vulnerable at site 3 could live comfortably at site 1. Site 3 also had boulders that species such as *C. striatus* could burrow beneath for protection.

Conclusion

Although it appears that there is no correlation between abundance and habitat, there are many other habitats in Moorea where *Conus* could be explored and studied. While only 11 species were found in the transects of this study, a total of 22 species were observed around the island. On the north side of the reef crest the habitat is extremely different, containing little sand. It is made up of a limestone bench that inhabitants many different species of *Conus* not seen in the lagoons or on the fringing reefs. They are very prevalent in this bench environment. It would therefore be interesting to see if a correlation between abundance and habitat would appear from studying the *Conus* in this region.

Acknowledgments

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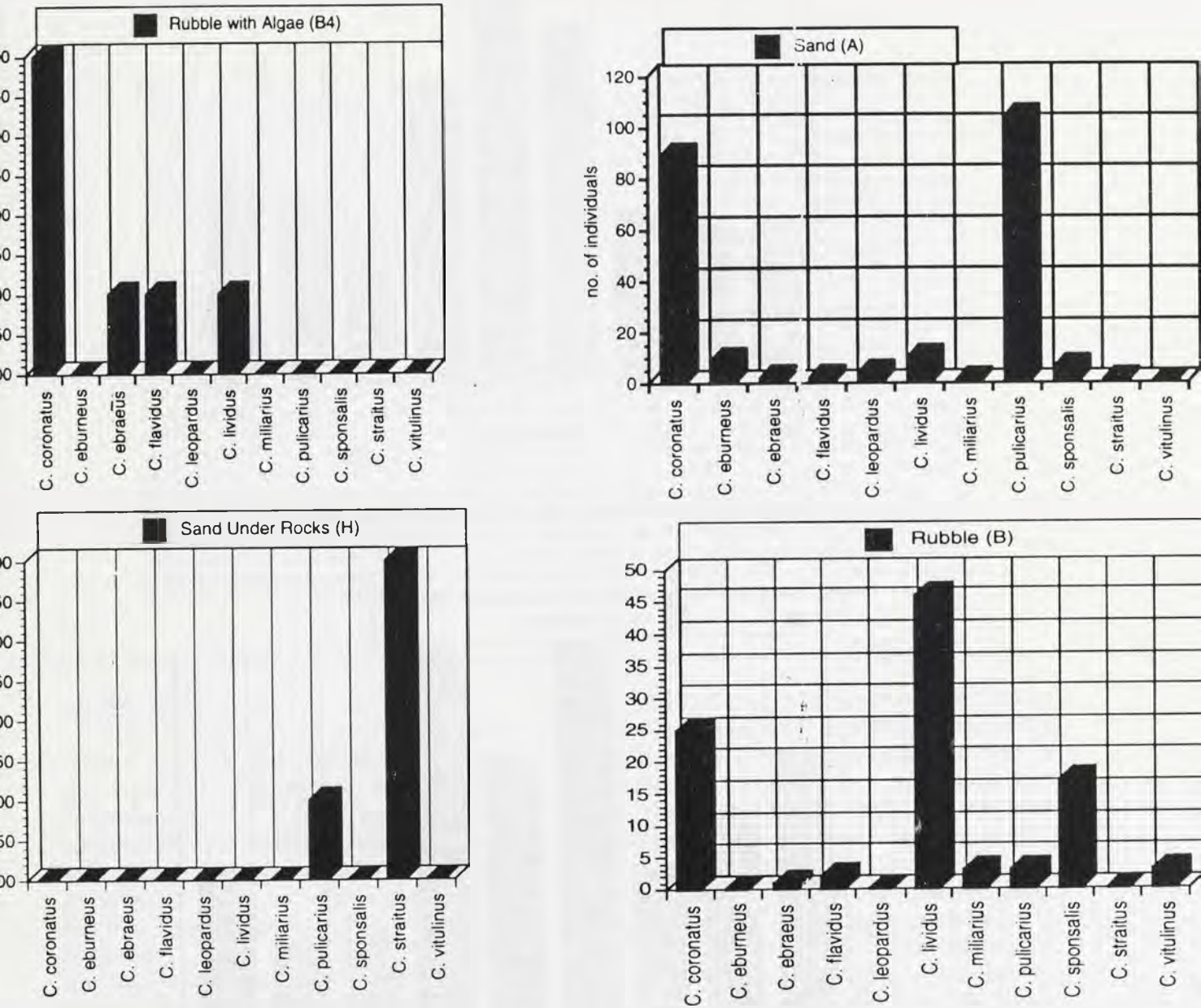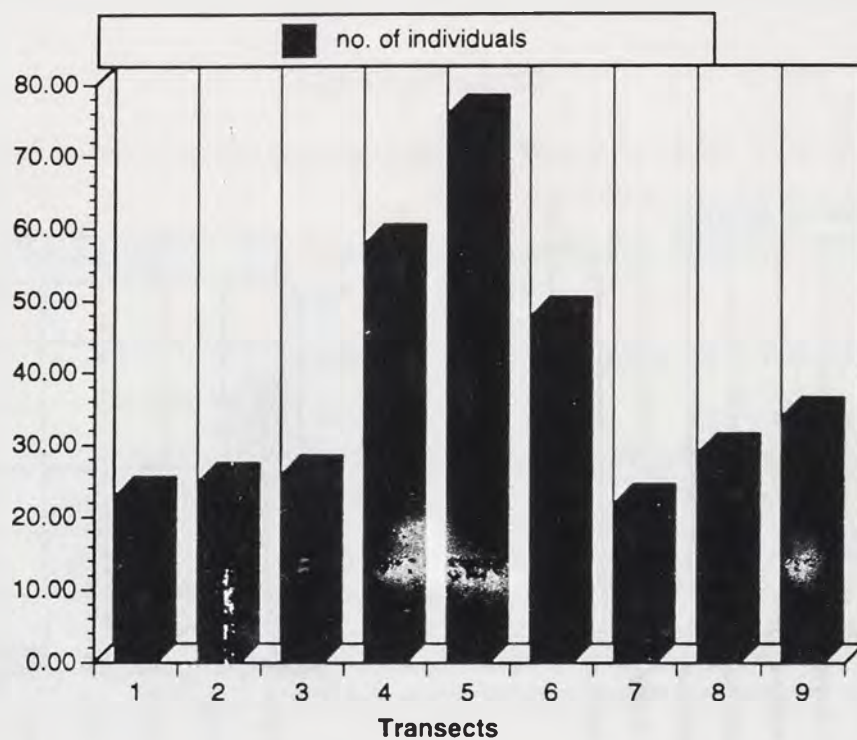**Figure 1.** Number of Individual of Species in Different Microhabitats
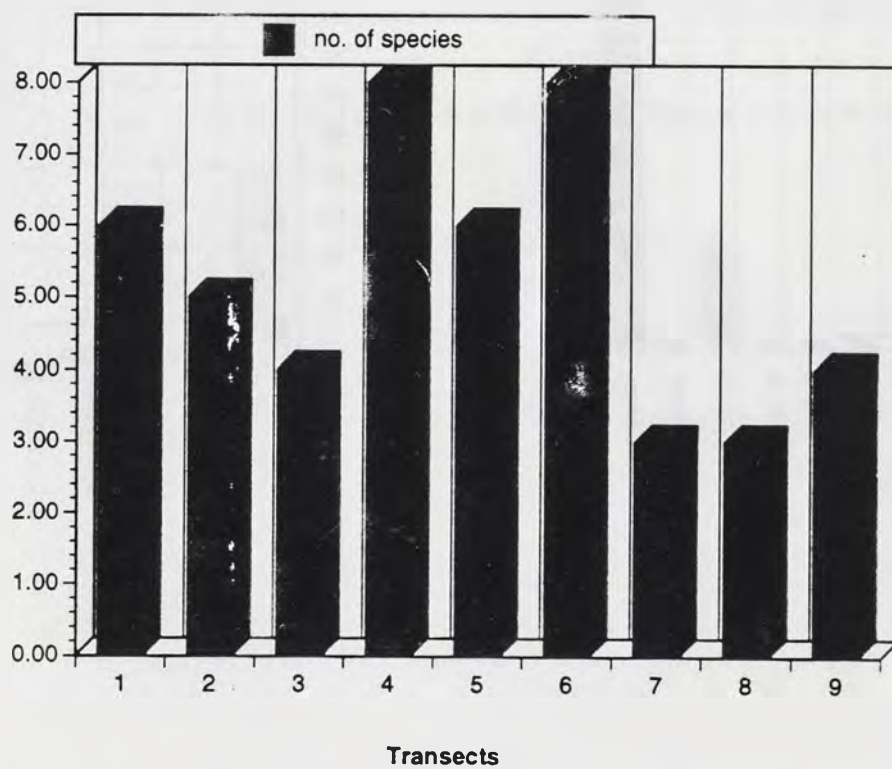
Figure 2. Abundance in Different Transects

Figure 3. Richness in Different Transects

Relative abundance, depth, and linear distribution of six species of sea urchin along continuous reef to shore profiles at two differing sites in the lagoon on Moorea, French Polynesia

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ABSTRACT. Echinoid populations can be a major factor contributing to algal grazing and bioerosion in Indo-Pacific coral reef habitats. It is important to thoroughly describe the distribution of this class of animals in order to properly understand their role within the coral reef ecosystem. Previous investigations have not described the relative abundance and distribution of sea urchins with respect to depth and the relative density variation along continuous complete lagoon profiles. This preliminary biogeographic study examines two contrasting lagoon profiles along meter wide transect sites on Moorea (Society Islands). The first transect, in the lagoon off Papetoai, was 1 km long and remarkable for two channels, the landward of which was dredged. It contained six different species of echinoid, a total of 1614 individuals. Their relative abundances, from most to least populous were: *Echinometra mathaei, Echinostrephus molaris, Echinothrix calamaris, Echinothrix diadema, Diadema savigni, Tripneustes gratilla.* Distinct horizontal and vertical ranges emerged for most species. *E. mathaei* had the most extensive range across horizontal and vertical oceanographic zonation, while *T. gratilla* and *E. molaris* were most limited horizontally, and *gratilla* alone vertically. At the second site, northwest of the public beach off the land spanned motu of Temae, two short parallel transects were mapped at the edge of a narrow, high flow channel. These channels both had remarkably shallow profiles with a maximum depth of only 1.2 meters. Strikingly different species abundances were found here, with *D. savigni* and *E. mathaei* of comparably high abundance in relation to the other species present, followed by *E. molaris* , *E. diadema*, *T. gratilla* and *E. calamaris* respectively. Distribution was clumped along both transects at Temae, and generally increased in abundance towards the algal ridge. Graphical depth distribution trends were obtained despite shallow and somewhat homogenous substrate characteristics and low abundance of some species. This study will serve as a useful preliminary baseline survey to facilitate future investigations of the interrelationships between echinoid populations and bioerosional, environmental and geographic changes.

Introduction

The distribution of sea urchin with respect to depth and position within coral reef lagoons is a potentially vital factor in determining their role in ecological and bioerosional phenomena. Echinoids are a major component of the benthic community in specific areas throughout the Indo-Pacific continental shelf regions (Birkeland, 1989). They are abundant in the lagoon at many sites around Moorea where they have been shown to be significant contributors to the processes of coral substrate bioerosion (Bak, 1990). Many areas around Moorea appear to have highly variable levels of coral health and coverage. Recent bleaching events in the region underscore the importance of thoroughly understanding all factors which may play a role in coral colonization (Dart, 1972) and sediment generation.

Previous qualitative investigations have been carried out in this area (Galzin, 1985) in the context of a general survey of the reef on Moorea. Prior research outside of the Indo-Pacific has shown that echinoid densities in coral lagoons tend to increase towards the algal ridge. This was demonstrated in Mauritius where echinoid densities near the algal ridge were found to be tenfold those observed immediately off the beach (Langer et al., unpublished). Qualitative data is available on the linear zonation (presence/absence) of three species of sea urchin in the Tiahura lagoon within zones determined from measurements of coral cover (Nithart, 1990).   Echinoid population density was studied along multiple short transects with the purpose of contrasting population levels in Moorea's two large bays (Iwanchuk, 1993), but did not examine complete profiles from beach to

fore reef, depth or distribution. A qualitative inventory of Moorea echinoids was completed (Pearse, 1989) which described some depth related distribution while including all species observed in this study.

This report presents the results of a quantitative biogeographic survey recording depth and species specific echinoid density along contrasting reef to shore profile transects in the lagoon off Papetoai, and Temae, just inside a narrow, high flow channel. The intent of this study is to graphically elucidate species specific ranges of horizontal and vertical distribution, and the relative total and ranged abundances of these animals. These results and accompanying analysis are briefly discussed in the contexts of bioerosional, environmental and ecological phenomena. Potential studies are suggested which might employ these results.

Study Sites

The island of Moorea is located at 149°50' W 17°30' S in the Pacific Ocean. The two study sites were chosen for their contrasting profile characteristics and differing locations with respect to wind and waves, as well as for logistical reasons such as daily accessibility and maximum depths. (Figure 1) They were studied during a period between Oct. 16 and Nov. 22, 1994. The Papetoai transect was located on the western edge of the town of Papetoai, 1.2 km from the south east edge of the barrier reef west of Tareu Pass. The abutting terrestrial area known as Miria was cultivated for coconuts and vegetables, and contained numerous dwellings. A green dwelling with a gray roof was located directly in front of the shoreward end of the transect, about 15 meters from the beach. To the west of the house was a large coconut grove and to the east, about 150 meters away, was a stream outflow originating in the northern drainage basin of Mt. Tautuapae.
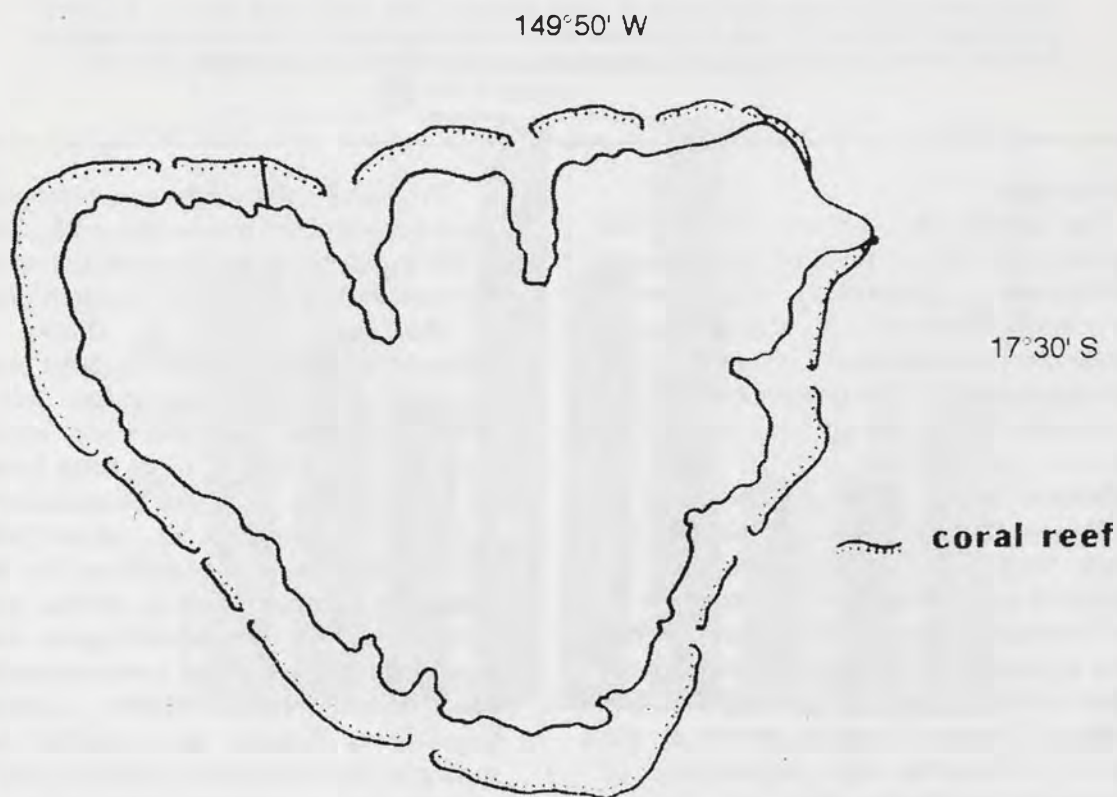

149°50' W

17°30' S

coral reef

Figure 1. Map of Study Sites on Moorea

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The transect itself followed a 350° bearing from the shore across the lagoon to the barrier reef crest, cutting across two channels and diverse microhabitats. The seaward channel is a natural extension of Opunohu Bay, and is centered 385 meters from the reef crest on the transect, where it reaches a maximum depth of 18 meters. The shoreward channel is a maximum 5 meters deep 860 meters from the reef crest. It was most recently dredged by the town of Papetoai in 1987, according to the reports of locals. At this time an old dock was removed from the port located east of the transect site, and a new one, which at the time of this study remained unbuilt, was planned. The total transect length was 1000 meters, with an extra 4 meters before the end of the tidal zone beyond the studied area

Moving shoreward, the seaward side of the transect began at the algal ridge, where shallow depths and low lying, encrusting and massive corals, *Halimeda*, *Turbinaria* and other calcareous algae and encrusting organisms were abundant. Wave action was predictably high at the ridge, particularly during high tides. Massive corals, dominated by *Porites*, began to appear as depths increased, and calcareous algae thinned out as coral heads became larger, and the spacing between them, greater. Particle size in these inter-coral head channels progressed from large pieces of coral rubble to coralline sand and small rubble near the seaward channel. The seaward channel dropped off quickly from the 3.5 meters of depth at 330 meters from the ridge crest, with the down slope covered by small rubble with occasional heavily eroded chunks of dead coral and some small, live fragments. The bottom of the channel was sandy and virtually flat for about 30 meters. The seaward slope was covered with a mix of large live and dead coral outcrops from 15 meters depth. The region between the two channels began with diverse corals, dominated by *Porites*, with decreased size and increased spacing towards shore. There followed a shallow zone of heavily eroded, sediment and short seagrass covered coral heads, and into an area of highly spaced, small, barrel type

Porites heads near the dredged channel. The dredged channel dropped off almost vertically and lacked any abundance of live coral on its walls, which were composed primarily of an amalgam of loose silty sand and chunks of loosely bound dead coral. Some patches carpet-like brown algae were on the sandy bottom, and the landward slope was as devoid of coral as the seaward. The final eighty meters near shore were covered with silty coral sand finishing at a manmade retaining wall.

Three regions of the Papetoai transect were chosen to be run along thirty meter sections parallel to and ten meters west of the main transect for the purpose of roughly verifying the homogeneity of the region. These were chosen for three distinctive, spaced apart from one another, centered at 255, 405, and 975 meters from the reef crest. The 255 section was in the zone of large, widely spaced coral heads on the backreef, the 405 down the shoreward slope of the natural channel, and the 975 on the shoreward side of the dredged channel.

Temae site is a large reef island located off and terrestrially linked to the east side of Moorea (Figure 1). The transect abuts the beach 120 m from the northern edge of the public beach, where the lagoon becomes a narrow, high flow channel. The site is marked by a 25 cm diameter bleached tree stump on the grassy rise above the beach which is visible from the conglomerate by the water's edge and from the reef crest.

Two transects were delineated at this site, both extending from the beach to meet the algal ridge perpendicular to the reef crest. The stump marked the southern-most transect, while the other was parallel and located ten meters north northwest of the first. The narrow nature of the channel allowed the time for two parallel transects at the Temae site, for the purpose of verifying the homogeneity of profiles in the location. The second transect stopped in shallow water short of the reef crest at Temae due to the dangerous surf on this more exposed side of Moorea at the time of study, and the narrow nature of the ridge crest here.

At this site the channel had three notable zones along its width profile. The

seaward side of the channel began with the algal ridge and diverse taxa of encrusting corals and calcareous algae. Moving shoreward, this quickly progressed to a zone of low lying corals interlaced with channels of small sized coral rubble which became dominant towards the center of the channel. The particle size increased while the particle density decreased until eventually giving way to the reef flat which was interspersed with heavily eroded dead coral heads abutted the conglomerate platform.

Study animals

There were six species of echinoids found within the boundaries of the transects studied. A seventh species was also observed outside the transects during the course of this research, but two other species recently identified on Moorea (Pearse, 1989) were not found. These seven species are briefly described below. Range, identification and characteristics information was synthesized primarily from information contained in Guille et al.. (1986) and George (1979).

(1) *Diadema savigni* is a member of the family Diadematidae, and can be found on hard bottoms throughout the Indo-Pacific. It is sometimes solitary and cryptic, and sometimes aggregating, but seldom exposed on all sides during the day. It has a diameter of up to 30 cm and can be recognized by its long, thin spines and blue-black coloration, with banding in juveniles. It is notable for an iridescent blue star pattern on the top of the test.

(2) *Echinothrix calamaris* is a member of the family Diadematidae, and is found generally solitary and cryptic under coral heads and outcrops during the day, while emerging to graze at night. It has large white, often banded primary spines and smaller brown secondary spines, with a aquamarine pentagonal pattern on the test, and a diameter of up to 20 cm.

(3) *Echinothrix diadema* is a close relative of *E. calamaris*, and has similar habits and morphology, with darker coloration, lacking also the pentagonal pattern on the test. There appear to be some individuals who share the characteristics of both species, having dark coloration, banding and a blue test epithelium.

(4) *Echinometra mathaei* is a member of the family Echinometridae, and can be found wedged and burrowed into coral and rock crevices throughout the Indo-Pacific. This species has short, strong spines, variable coloration, and a maximum diameter of 10 cm. There are four known subspecies of this animal.

(5) *Echinostrephus molaris* is also in the family Echinometridae , and is found burrowed deeply into rock and eroded, dead coral throughout the Indo-Pacific. It has a diameter of up to 5 cm, fine spines and dark brown-black coloration. Individuals of this species use their spines and Aristotle's lanterns to bore into the carbonate, and are known to be capable of boring into steel (Irwin, 1953).

(6) *Tripneustes gratilla* is a member of the family Toxopneustidae, and has short spines and variable coloration, with a diameter of up to 15 cm. It is often seen in open, flat rocky areas, and occasionally covered with bits of debris held by in place by the tube feet.

Different species of sea urchins use variable strategies to feed on a variety of algae, detritus, foraminifera, and other food sources accessible on the substrate. Some species are able to glean particles from their spines, tests and the water column with their pedicillariae, but most primarily graze the algal lawn which grows quickly on areas not covered by healthy, live coral.

Data Collection

Depending on the current depth, observations were made snorkeling or on SCUBA. Each transect was divided into 10 m long segments delineated by a straight, stretched 30 meter surveyor's tape. Depth was measured at the midpoint of each 10 m segment using a depth meter. All echinoids were counted and categorized in a one meter wide strip along the entire length of each transect and recorded on an underwater slate within the 10 m segment corresponding to their location. Variation in relief and cryptic specimen locations

made continuous direct measurement of transect width impractical, and initial measurements were compared to the length of the data collectors' forearms, allowing two researchers working side by side to work independently from one another in two, half meter strips on each side of the tape. Large coral heads were examined on all sides, underneath, on top and in any cracks or crevices present. Small coral heads and any rubble larger than fist sized were overturned and examined thoroughly for any urchin present. These methods were designed to detect all echinoids of the subclass Regularia.

Observations were undertaken during the day, between the hours of 1000 and 1600 for logistical reasons. Tidal fluctuation during the period of observation was between 1.5 and 4.5 above M.L.S.T., resulting in an error bar range of +/- <30 centimeters for any given depth observation. The transect at Papetoai was observed from ridge to shoreward, at Temae, from shore to ridge due to differing accessabilities of the two transects depending on wave action.

Significant qualitative notes on the characteristics of the regions studied were taken. These were recorded in an effort to complement the quantitative data herein, and were transferred to the appropriate sections of this report.

Results and analysis

PAPETOAI

Depth measurements taken along the length of the Papetoai transect resulted in a profile map (Figure 2; Figure 3, bottom) which spans it's entire length. The vertical scale of all profiles presented herein are exaggerated to facilitate presentation. Six species of sea urchin were observed along the length of this transect. The total specific abundances were calculated (table 1). *E. mathaei* was by far the most abundant, while *T. gratilla* was the least common. Specific densities (urchins/m^2) within 50 meter ranged zones can be determined by dividing 50 into each specimen count total for the zone. These count totals can be gleaned from the species specific graphs of the number of

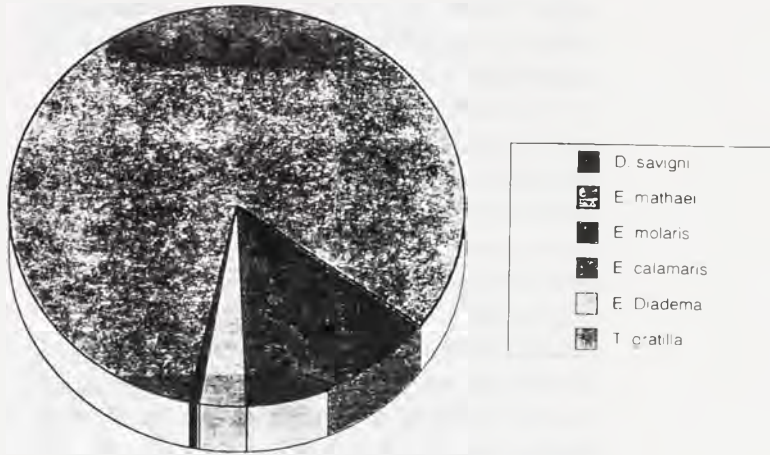**Figure 1.** Relative total abundance, Papetoai

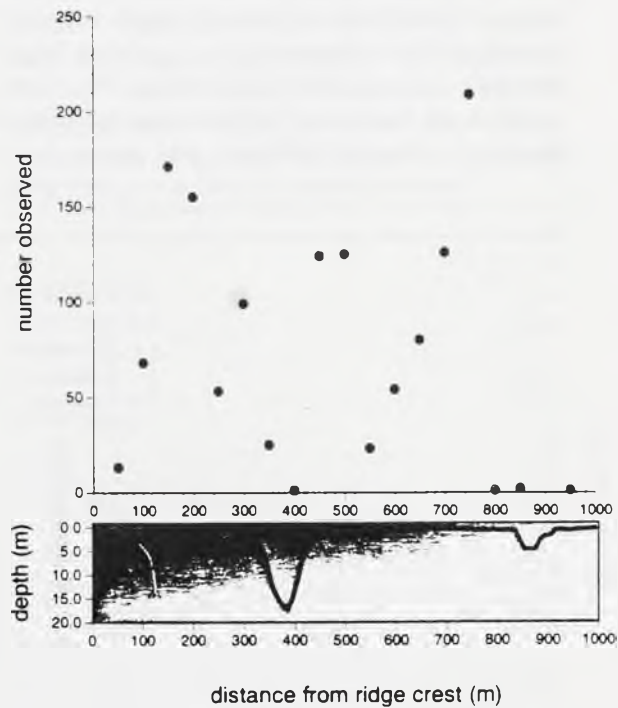**Figure 2.** Ranged *E. mathaei* distribution along Papetoai profile

Table 1. Relative abundance, Papetoai

Species	Number
D. savigni	8
E. mathaei	1330
E. molaris	136
E. calamaris	84
E. diadema	53
T. gratilla	2

individuals observed vs. distance from ridge crest (Figs. 2 & 3), and visually mapped directly to the profile which is presented below them.

The ranged distribution of *E. mathaei* was relatively low near the algal ridge and increased to a peak centered around the 125 meter mark. (The points on the graph correspond to the end of each 50 meter section, and the actual peak of the number of specimens observed over each range is 25 meters seaward of each point.) The density decreased again towards the natural channel, where it tapered off to virtually nothing, and quickly rose to another peak in the region of mid-sized coral heads shoreward of the channel. It quickly dropped off within a sandy region starting at the 500 meter mark and steadily increased as the presence of highly eroded, low lying coral skeletons increased. The highest densities were recorded within this zone. The level dropped again to near absence as the zone of small *Porites* "barrel" corals was reached before the dredged channel, and remained low up to the shore.

D. savigni had a low abundance along this transect, and its range was limited to the region bordering both the zone of diverse, relatively large coral shoreward of the natural channel, and the adjacent zone of low-lying eroded coral and short seagrasses.

E. molaris showed high densities near the algal ridge, peaking at the 75 meter mark and decreasing steadily towards the natural channel. This species was not present shoreward of the channel along this transect.

The two species of the *Echinothrix* genus showed a marked distributional peak in areas of large to mid-sized coral heads on both the backreef and fringing reef. They were also present in the nearly vertical walls at the edges of the dredged channel, and *E. diadema* was found within one of the more structurally substantial eroded coral areas of the central fringing reef.

T. gratilla was limited to the areas relatively barren of other species, nestled up against dead and live coral in the regions of eroded low lying and live Porites dominated corals on the fringing reef.

The species specific depth distributions of these species (Figure 4) show higher overall total abundances at shallow depths. These figures mean little in terms of actual depth distributions, because the

Figure 3. Ranged distribution along Papetoai profile
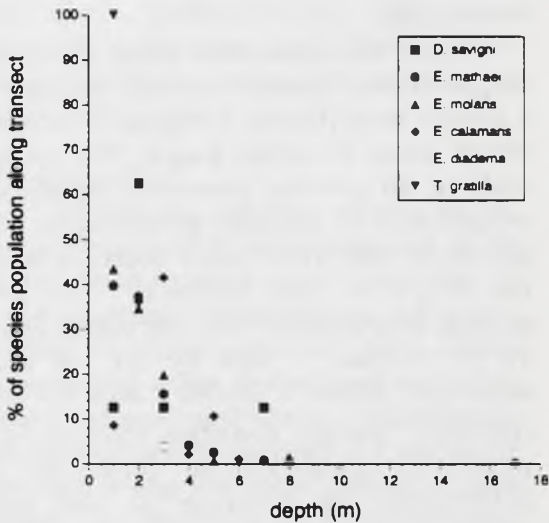
Figure 4. Depth distribution, Papetoai

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percentages must be rendered independent of the frequency of particular depth levels. This was done by weighting the percentages of each species' total populations against the frequency of a particular one meter depth range. The percentages were divided the number of times that range occurred, and the resulting numbers were extrapolated back to a total of 100 % to yield relevant data (Figure 5). It should again be noted that the horizontal position of the points on this graph are displaced from their true position because they define the deeper boundary of each depth range.
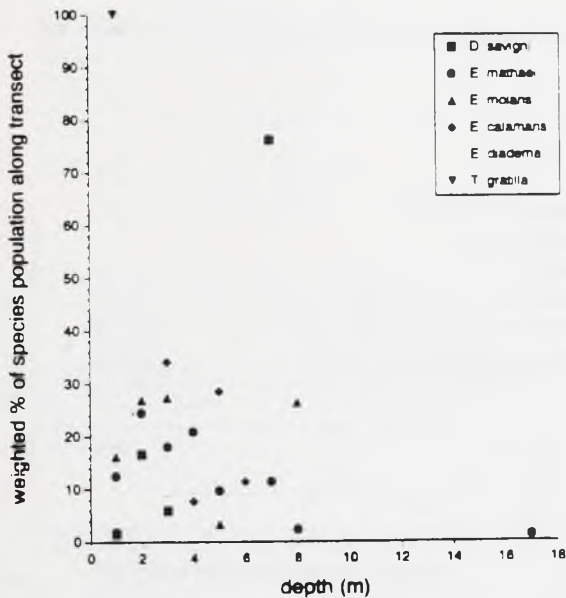
Figure 5. Weighted depth distribution, Papetoai

The weighted data revealed initially low *E. mathaei* densities at the most shallow depths, quickly peaking at the 1.5 meter mark, and gradually fading out towards the deeper depths. A few individuals occurred below a depth of seven meters, but their densities were conspicuously sparse.

E. molaris densities were highest in midrange depths, but were artificially depressed by this method of weighting, since they did occur almost exclusively in the most shallow depths of the backreef, but were drowned out by all the identical depth sections in the fringing reef, where they were not found.

D. savigni and *T. gratilla* had marked preferences for 6.5 and 1.5 meter range midpoints, while *T. gratilla* was limited to the most shallow range. The two species of *Echinothrix* showed highs at 2.5 m for *E. diadema* and 1.5 m for *E. calamaris*.

The parallel transect regions run at Papetoai showed generally similar species presence in corresponding linear regions (Figure 6). (The legend in Figure 6 denotes data points from the parallel transect by species name, and the corresponding main transect region symbol is shown below and listed as *Main*) One exception to this trend is the presence of an individual *E. molaris* in the natural channel. Another interesting find along the parallel seaward section were two juvenile individuals whose
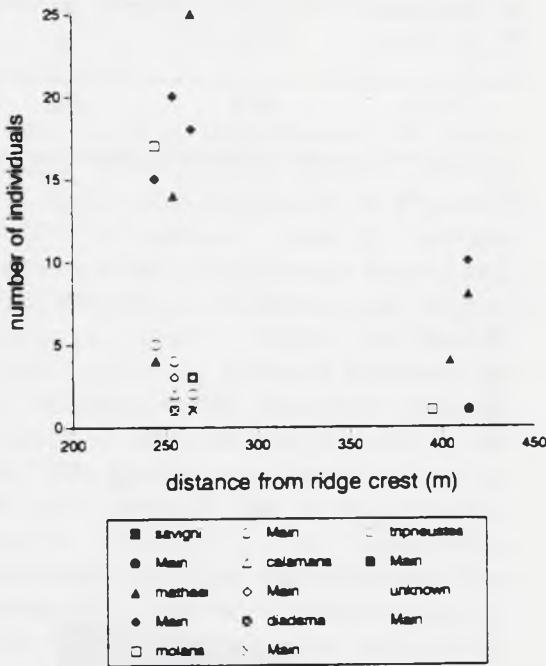
Figure 6. Contrast of parallel transect regions, Papetoai

identity is still uncertain. The general outward morphology in these individuals resembled *D. savigni* but whose their microscopic details suggested a young *E. molaris*: verticillate spines and crenulated tubercules.

TEMAE

The total and relative specific abundances of urchin along the transects at Temae are shown in table 2. *D. savigni* was predominant in transect 2, and *E. mathaei* most abundant along transect 1. Both of these species were among the top two in total abundance along both transects. These two were followed by *E. molaris*, *E. diadema*, *T. gratilla* and *E. calamaris* respectively along both transects.

Table 2. <u>Relative Abundance. Temae</u>

Species	Transect 1	Transect 2
D. savigni	166	369
E. mathaei	216	206
E. molaris	68	88
E. calamaris	0	1
E. diadema	5	4
T. gratilla	4	0
Total	459	668
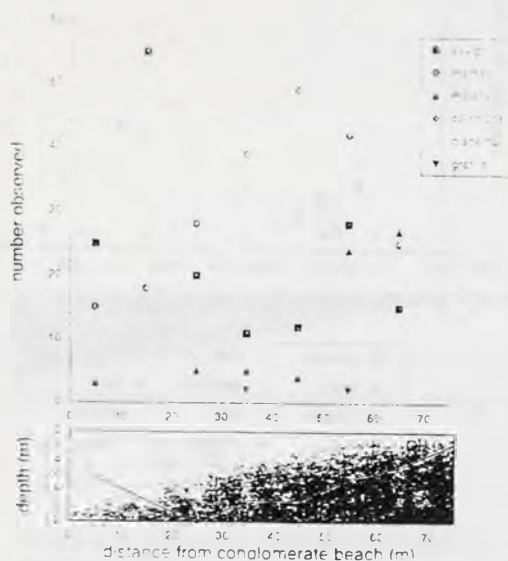
Figure 7. Distribution along Temae Profile, Transect 1

The horizontal distribution of species along both Temae transects showed some similar large scale trends, although relative population levels at any one position along the profile were often radically different in each transect (Figs. 7 & 8). *E. mathaei* density went from low to high on both transects, peaking on the upslope of the algal ridge, and in the case of the longer transect 1, dropping off again right at the ridge, where there were shallower depths and high wave action made accurate specimen counts dangerous and nearly impossible on the day of study for transect 2.
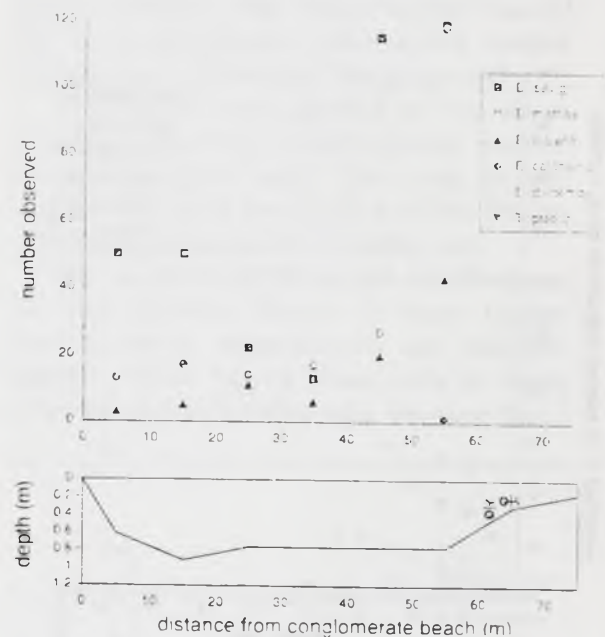
Figure 8. Distribution along Temae Profile, Transect 2

Two peaks can be seen in the distribution of *D. savigni* in both transects. Initial highs first occur just off the conglomerate platform on the reef flat, and densities drop towards the middle of the channel before rising again towards the ridge, and finally dropping on the ridge upslope. This species showed predominant clumping behavior throughout this entire region.

E molaris showed a clear pattern of distribution, with large numbers of

individuals found near the algal ridge, tapering off to low levels towards the conglomerate. From brief inspection of the uncounted high wave action area of transect 2, this trend would have likely continued before dropping off again at the ridge crest itself.

E. calamaris, E. diadema and *T. gratilla* had poorly resolved horizontal distribution trends along this transect due to their extremely low numbers. The only *calamaris* found in either transect was near the ridge in the zone of interwoven channels where live coral protection was greatest. *E. diadema* showed different pattern, although it was generally observed in isolated patches of live coral, even though it was primarily found on the rubble stretch and on the reef flat. *T. gratilla* was observed in the rubble stretch and live coral zone.

Figure 10. Weighted depth distribution, Temae, Transect 2

Figure 9. Weighted depth distribution, Temae, Transect 1

The vertical distribution on these transects showed some definite patterns which can be seen graphically in Figures 9 and 10. *E. mathaei* and *D. savigni* densities peaked in midrange depths and fell off slightly in shallower and deeper regions. *E. molaris* depth distribution showed conflicting patterns between the two transects, with densities peaking midrange in one and peripherally in the other. This species was observed only in dead and eroded flat coral surfaces, perhaps explaining its apparently inconsistent vertical distribution. The numbers of *E. diadema*, *E. calamaris* and *T. gratilla* were so low that again, trends were difficult to establish, although *T. gratilla* did occur in exclusively shallow depths, and *E. calamaris* was limited to a single mid-depth location. These results are

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replicated as contrasting histograms in Figures 11 and 12 (analogous to Figures 9 and 10), where depth is the horizontal axis of each comparative mini-graph, and weighted % is the vertical axis. The purpose of this representation in to facilitate the visualization of inter-species differences in depth distribution.

Discussion

In summary, well defined abundances and horizontal and vertical distribution patterns were observed in both sites for most species (See results and analysis and figures). These distributions mapped onto profile diagrams gleaned from the data, providing a clear graphical representation of the inter-specific differences. The site descriptions provide additional data which confirm the substrate dependent survival strategies indicated in previous research (Nithart, 1990; Pearse, 1989; Bak, 1990). These sites will provide specific, quantitatively described regions for future studies of distribution and abundance with a variety of potential contexts, such as coral diversity, erosional state, algal environment and interspecific competition.

The nearshore channel environment had a variety of human impact variables which would make interesting topics for research. The beach at the Papetoai site region was littered with scattered trash and debris, and the stream east of the study site was filled with considerable quantities of objects such as rusty cans, bottles, automobile batteries and other waste products of modern living. On one occasion in the final days of the study, numerous young, dead trigger fishes were observed washed up along the shore at Papetoai. A comparison of this site to similar, more pristine areas could potentially reveal a variety of environmental concerns affecting echinoid densities such as eutrophication (perhaps accounting for the high *E. mathaei* counts found in the nearshore environments) and chemical toxicity to competitors such as herbivorous and scavenging fish.
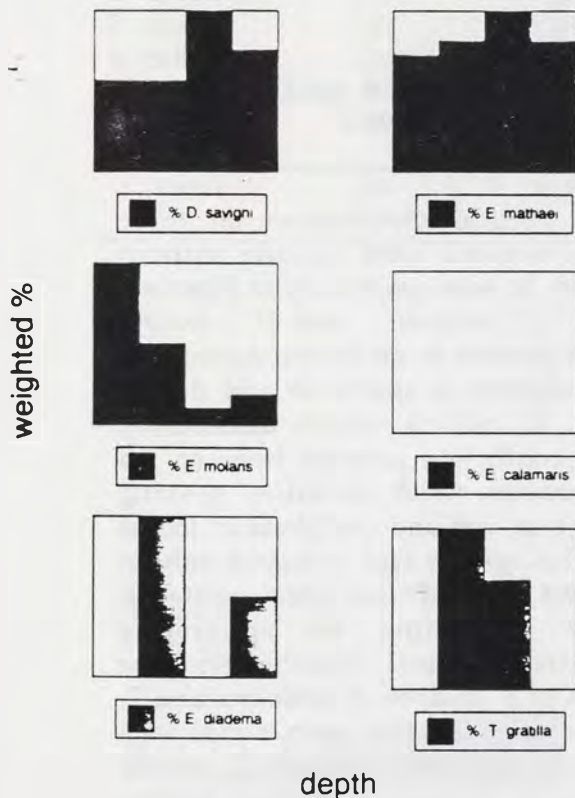
Figure 11. Comparative weighted depth distribution Transect 1- Temae
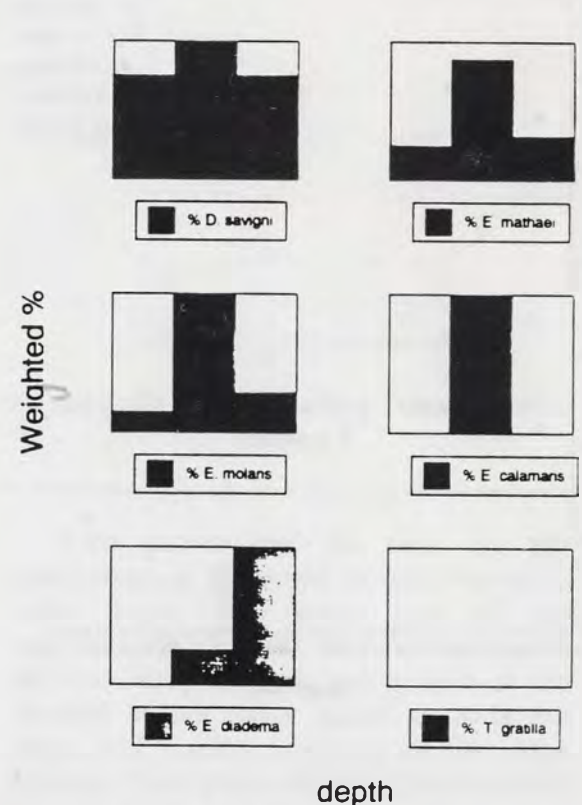
Figure 12. Comparative weighted depth distribution Transect 2 - Temae

The wide variety of different substrate zones within these two sites make interesting succession and bioerosion studies possible, particularly over time. Previous investigations have indicated that relative echinoid species population levels in a region undergo cycles within a region as erosional processes change the nature of the habitat to better suit particular species' survival strategies.

Echinoids are closely linked to the ecological, environmental (Hughes, 1994) and geographical characteristics of the areas where they are found. More research is needed to properly synthesize our understanding of these diverse interactions, and thoroughly reveal the importance of this class of animals in assessing the impacts of human activities and natural phenomena.

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Long Term Trends in Coral Bleaching:
a study in Moorea, French Polynesia

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ABSTRACT. Recently coral bleaching has become a crucial issue of study due to the frequency and intensity of the events, and the world-wide mortality and local extinctions of coral genera associated with them. Bleaching events are defined as world-wide or local incidents where much of the coral community whiten resulting from the loss of symbiotic zooxanthellae and/ or a reduction in photosynthetic pigment concentrates in the zooxanthellae

Bleaching events occurred in Moorea, French Polynesia in 1973, 1982-1983, 1986, 1991, and 1994. The two most recent events were studied during and after the events in order to analyze the coral and coral community for the relative susceptibility of the common genera and changes in community composition. Four common genera *Pocillopora, Acropora, Montipora*, and *Montastrea* were chosen to use in comparisons of changes in coral health over time because of their relative susceptibility to bleaching. I compared the data from four months after the '91 bleaching event, during the 94 bleaching event, and six months after '94 event expecting to see a decline in not only the health of each genus, but also in the coral community. Using a Spearman Rank and t-tests, I found that there was no significant differences in the health of any genus or in the coral community from the 91 event to the 94 event. Even so, coral bleaching needs to continue being monitored on a long-term scale using a standard method, in order to understand the causes or potential effects of frequent world-wide bleaching events.

Introduction

In the last decade bleaching of tropical scleractinian (hard) corals has been a subject of concern because of the mortality and local extinctions associated with the large scale bleaching episodes. (Glynn, 1991) Because of the widespread belief that bleaching episodes have increased dramatically in frequency, geography and intensity within the last ten years, there has been much speculation about the cause of the events and the eventual resulting destruction of worldwide reefs (D'Elia et al., 1991). Coral reef bleaching can be defined as the whitening of diverse coral taxa resulting from the loss of symbiotic zooxanthellae and/or a reduction in photosynthetic pigment concentrations in zooxanthellae residing within the gastrodermal tissues of host animals (Glynn, 1992). Until recently most incidents of bleaching were confined by location and time, and could be explained by local change in temperature, salinity, light, sedimentation, aerial exposure, or pollutants (Hoegh-Guldberg and Smith,

1989; Goreau, 1964; Jokiel and Coles, 1977; Marszllalek, 1982). However because of the scale of the frequent world-wide bleaching events, they have not been explained so convincingly. There is much concern recently that these bleaching events are directly correlated with ENSO (El Niño/ Southern Oscillation) or global warming, but the ecological consequences, and correlation with global climate change remain uncertain (Glynn, 1992; Williams and Bunkley-Williams, 1990). Further attempts to relate the severity and extent of large scale bleaching events to particular causes have been hampered by lack a of standardized methods to assess bleaching, and continuous, long-term data bases of environmental conditions over the periods of interest (Glynn, 1992). Until recently in much of the world accounts of coral condition, bleaching intensity, and bleaching consequences are here-say passed on from natives (Brown and Ogden, 1993).

The short-term ecological consequences of bleaching events include widespread reef mortality with resultant

decreases in coral cover (Brown and Suharsono, 1990). In addition to the immediate decline in zooxanthellae density, loss of chlorophyll pigments, and declines in coral protein, lipid and carbohydrate (Hoegh-Guldberg and Smith, 1989; Goreau and Macfarlane, 1990; Jokiel and Coles, 1990); bleaching may also cause important long-term effects including diminished rates of coral growth and calcification, impairment of reproduction, and tissue necrosis (Glynn, 1992). This reduced growth could decrease the capacity of corals to compete favorably for space with other reef benthos, such as sponges, algae and tunicates (Cortes et al., 1984). If the coral's capacity to reproduce is impaired it could have an extremely negative impact on coral recruitment, and this would be critical in an annually reproducing species, because an entire reproductive system would be missed (Jokiel and Coles, 1990). It is also possible that diseased corals may be more prone to bleaching or that corals stressed by bleaching become more susceptible to various diseases. Regardless, diseased corals lose live tissue and when this results in colony fragmentation (partial mortality) remnant patches become more susceptible to continuing mortality (Hughes and Jackson, 1975).

Little is known about the potential long-term changes in species composition as a result of coral bleaching. Since different genera have differential susceptibility to bleaching and different rates of recolonization (Williams and Bunkley-Williams, 1990), this may determine the community consequences of bleaching events. In many instances fast growing, branching coral species are the first to bleach and die(Brown and Suharsono, 1990). Some massive coral species do not bleach, bleach just partially, or bleach only toward the end of an event (Glynn, 1990). While this pattern holds true for all studies that took place in the Pacific, the opposite conclusions were made for genus susceptibility to bleaching in the Caribbean and the Atlantic (Williams and Bunkley-Williams, 1990).

Bleaching events in French Polynesia have until recently received little attention, though there are records of events in 1973, 1982-1983, and 1986-1987 (Williams and Bunkley-Williams, 1990: Gleason, 1992). Mary Gleason conducted a study during a bleaching event in the Society Islands that began mid-March, and continued through late September, 1991. She described and quantified the 1991 bleaching event in Moorea in terms of the relative susceptibility of the common genera, differential bleaching and studied her sites four months later to look at changes in community composition and recovery (Gleason, 1991). In March of 1994 during a local bleaching event, Michelle Perez worked in Moorea looking at the effect on different coral species, as well as the community as a whole.

The role of disturbance in a community depends in part on the frequency of disturbance events (Sousa, 1984). And in view of the dynamic nature of coral communities long-term and regular monitoring is a necessity, to estimate the future community consequences (Glynn 1991). On Moorea in the fall of 1994, I continued Gleason's and Perez's work in an attempt to assess the changes in coral health, changes in community structure, live coral coverage, and changes in genus susceptibility and recovery in this time of frequent bleaching events.

Methodology

This study took place on the leeward side of Moorea island, which is situated 17° 32' South and 149° 50' west, and 25 km from Tahiti in the Society archipelago in French Polynesia. In the summer of 1991 after a mass coral bleaching event, Mary Gleason measured the significant differences in the effect of bleaching on Moorea's common coral genera: *Acropora*, *Montastrea*, *Montipora*, *Pocillopora*, *Porites*, *Pavona*, *Leptastrea*, and *Millepora*. She did surveys of bleaching status in 3 parallel transects along the back reef. Each coral colony was described by the degree of bleaching (percentage of colony bleached) and the degree of tissue

loss (i.e. percent of colony dead) (Gleason, 1993) (Table 1). In June 1994, after a less widespread bleaching event Michelle Perez did bleaching surveys on 12 transects in approximately the same areas as Gleason's transects.

Table 1. Categories of bleaching and intensity level used in analyses and graphs

Bleaching Level	Score Description
% colony affected	1 = none, healthy
	2 = <10%
	3 = 10-50%
	4 = >50%
	5 = 100%
	6 = dead
Intensity of Bleached Section	1 = healthy
	2 = slightly pale
	3 = medium
	4 = stark white
	5 = covered with predator algae
	6 = dead

In order to understand the long term effects these frequent bleaching events have on local coral species, I did bleaching surveys in the fall of 1994, approximately 6 months after the most recent bleaching event. Three 15m by 3m transects were established in the same location as Gleason's, parallel to the backreef and 50m in front of the back reef at 10 ft. in depth. Two of the transects were located just east of Opunohu bay, while the other was just west of Cook's Bay. In each of these transects one 15m by 1m quadrant was selected at random to survey for coral percent coverage and bleaching status.

Each colony over 5 cm in size was categorized by genus, percent bleached, intensity of bleaching or algae cover, and by size. Using Gleason's table (Table 1) for percent bleached each colony was given a number 1-6 with 1 meaning colony healthy, 2=<10% bleached, 3=10-50% affected, 4=>50% affected, 5=whole colony, and 6=dead.

Each colony was also scored for intensity of bleaching status or health 1= healthy, 2=slightly pale, 3=medium, 4=stark white, 5= covered with predator alga, and 6=dead. Each colony was put into 3 size classes(<10cm, 10-20cm, and >20cm) (Perez, 1994). with this information each colony was given an individual identity code. Each quadrant was surveyed twice to insure accuracy.

Since studies of bleaching events have recorded that fast growing branching species are more susceptible in the Pacific than massive species (Williams and Bunkley-Williams, 1990) and Gleason found in her 1991 study that *Acropora, Montastrea, Montipora, and Pocillopora* were most affected by the bleaching event. Therefore, these are the genera used for the long term comparisons. Each genus was graphed so a direct comparison could be made in the percent of colonies of each genus affected by bleaching over time (Figure 1). The graphs show what percent of colonies of each genus are healthy, affected by bleaching and by how much, or dead. From these graphs a Spearman's rank was done, to test for absolute changes in the health of each genus over time. For each genus, t-tests were done between the three time periods for each bleaching level. This test was used to examine whether the change in each bleach level over time was significant, and whether it can be said with 95% confidence that the difference between the time periods is due to chance, or there is another cause.

Results

For the fall of 1991, I found that the live coral coverage for the backreef of Moorea is 20%. Unfortunately neither Gleason nor Perez found the live coral coverage in the same way, so I did so I can not compare this data.
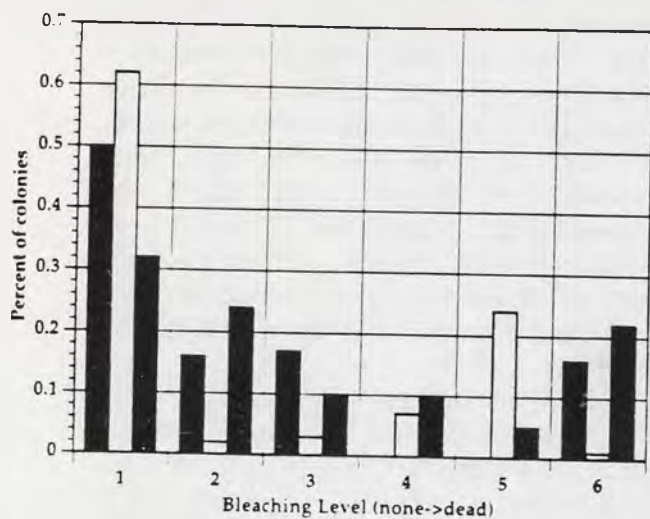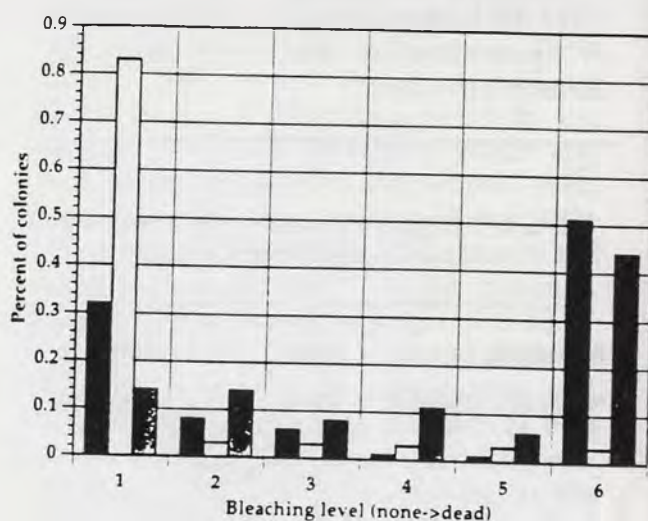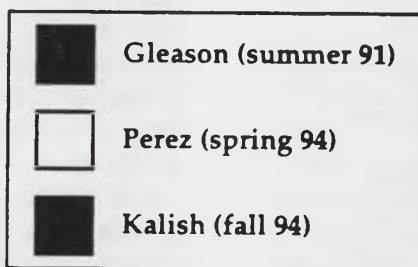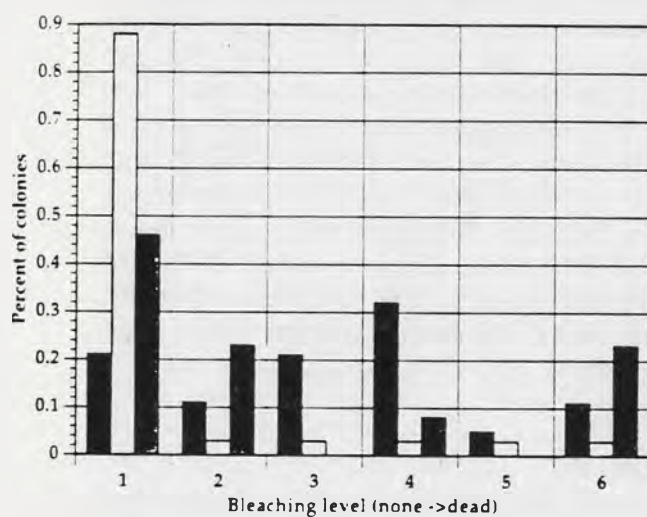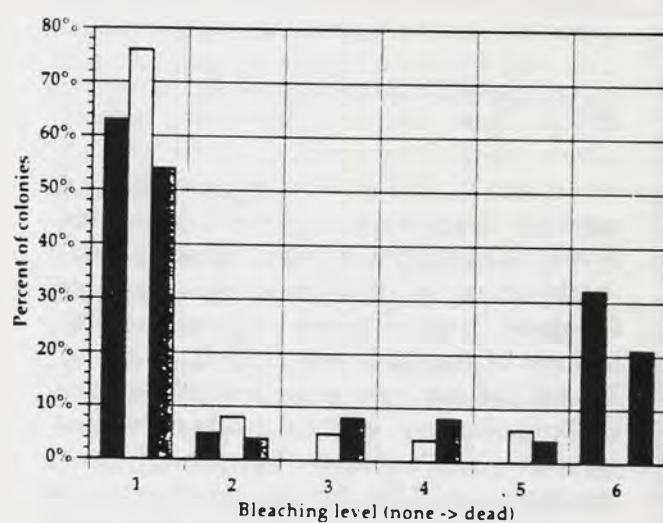
Figure 1. Bleaching Levels in Coral Species over a three year span:

A. Pocillopora, B. Acropora, C. Montastrea, D. Montipora

Table 2. Multiple year comparison of coral health and bleaching susceptibility

Pocillopora

	% affected by bleaching	% unaffected	% dead
Gleason (summer 91)	35%	50.20%	14.80%
Perez (spring 94)	36.6	62.3	1.1
Kalish (fall 94)	46	32	22

Acropora

	% affected by bleaching	% unaffected	% dead
Gleason (summer 91)	43	23	33
Perez (spring 94)	13.3	86.6	3.3
Kalish (fall 94)	39	32	22

Montipora

	% affected by bleaching	% unaffected	% dead
Gleason (summer 91)	28	48	24
Perez (spring 94)	24.4	75.5	0
Kalish (fall 94)	24	54	21

Montastrea

	% affected by bleaching	% unaffected	% dead
Gleason (summer 91)	71	19	10
Perez (spring 94)	11.4	88.6	0
Kalish (fall 94)	31	46	23

Table 2 shows the percentage of each genus bleached, healthy and dead during the three time periods studied. The unaffected are the same as 1 on the bleach level chart, affected by bleaching is the same as 2-5, and dead is equal to a 6. By comparing the scores, the resiliency and susceptibility of the corals to bleaching is clear. For example in the summer of '91, 14.8% of *Pocillopora* was dead, but during the bleaching event of spring '94 only 1.1% were dead. Then by spring of '94 , 22% were dead. Table 2 shows a wide variation between the scores, but does not necessarily show any directionality to them. Thus there do not seem to necessarily be more affected, or dead after the bleaching event in '94, than in '91. There are also more similarities between Gleason's (summer '91) data and my spring '94 data, then either of our data with Perez's.

Table 3. Spearman Rank Test

	Pocillopora	Acropora	Montastrea	Montipora
Gleason '91 and Perez '94	0.64	0.40	0.47	0.55
Gleason '91 and Kalish '94	0.77	0.74	0.44	0.36
Perez '94 and Kalish '94	0.82	0.49	0.28	0.45

Pocillopora- t-test

Bleaching level	1	2	3	4	5	6
Gleason(summer 91) and Perez(spring 94)	<.01	<.01	<.01	<.01	<.01	<.01
Gleason(summer 91) and Kalish (fall 94)	>.05	>.05	<.01	>.05	<.01	>.05
Perez(spring 94) and Kalish (fall 94)	<.01	<.01	>.05	<.01	<.01	>.05

Acropora- t-test

Bleaching level	1	2	3	4	5	6
Gleason(summer 91) and Perez(spring 94)	<.01	<.01	<.05	<.01	<.05	<.01
Gleason(summer 91) and Kalish (fall 94)	<.01	<.01	>.05	<.01	<.05	<.01
Perez(spring 94) and Kalish(fall 94)	<.01	<.01	>.05	<.01	<.05	>.05

Montastrea- t-test

Bleaching level	1	2	3	4	5	6
Gleason(summer 91) and Perez(spring 94)	<.01	<.05	<.01	<.01	<.05	<.01
Gleason (summer 91) And Kalish(fall 94)	<.01	<.05	<.01	<.05	>.05	>.05
Perez(spring 94) and Kalish(fall 94)	<.01	<.05	<.01	<.05	<.05	<.01

Montipora- t-test

Bleaching level	1	2	3	4	5	6
Gleason(summer 91) and Perez(spring 94)	>.05	>.05	<.01	<.01	<.01	<.01
Gleason(summer 91) and Kalish (fall 94)	>.05	>.05	<.01	<.01	<.01	>.05
Perez(spring 94) and Kalish (fall 94)	>.05	>.05	>.05	>05	>05	<.01

Table 4. T-tests for Bleaching Level Differences

The Spearman rank test compares the overall health of each genus between years. (Table 3) On the chart the closer the values are to 1, the greater the correlation between the two years. Thus the correlation between Gleason and this study for *Pocillopora* and *Acropora* are .77 and .74, which are both very high. *Pocillopora* seems to be the most consistent genus since the correlation between the data found for all three researchers is high. Although the Spearman test can compare the general health of a genus between two years, it says nothing about exactly what the difference in health is between the years.

I used a t-test to look for significant differences between years for each bleaching level and every genus (Table 4). If the p value was >.05, then there is a 95% confidence level that the two sets of data are not significantly different and could not be caused by random chance. On the Pocillopora test Gleason and I had 4 different levels at >.05. While Perez and I had 5 values >.05 on the Montipora test.

Discussion

I did not find a drastic change in the amount of deaths caused by the bleaching events from the 91 bleaching event to the 94 event. Instead there was little variance between Gleason's and my data, for over all coral health as well as within each genus. Since both of our studies were done about 4-6 months after each event, this study showed that frequent bleaching events did not increase the percent of corals effected or killed in each following event. The Spearman rank test along with the t- tests seem to support these observations. Gleason and I showed a strong correlation between our data for *Pocillopora* and *Acropora*. in the Spearman Rank After examining the graphs the low correlation for the *Montipora* seems due more to the Spearman Rank's weakness, rather than a significant difference between the coral health in the summer of '91 and the fall of '94. Based on the results of the t-tests this theory seems correct. The results of the t-tests show that for 3 out of the 6 bleaching levels examined for *Montipora* there is a 95% confidence level

that the correlation between the summer 91 data and the fall 94 data is not only not significantly different, but could not have taken place by chance alone.

The data reiterates the literature about *Pocillopora* and *Acropora*'s susceptibility to not only bleaching, but also death as a result of the bleaching. Both Gleason and I found percent of *Acropora* dead was higher than all of the *Acropora* that Perez found affected by bleaching together.

It is surprising to me that such a high percent of the *Acropora* that Perez found was healthy, but this may be explained by her low number of *Acropora* studied. Although Perez had 12 transects, while Gleason and I only had 3, her number of *Acropora* was 30 while Gleason's was 75 and mine was 46.

The results of the t-test suggest that *Montipora* has a low susceptibility to bleaching or change in coral health due to bleaching. The t-tests showed a value of >.05 for 5 out of the 6 bleaching levels for *Montipora* between the spring of 94 and fall of 94. This means that there was a 95% confidence level almost all the way across the board that there was no significant difference between the 94 bleaching event and 6 months later.

Even though my hypothesis was nullified in this study, further long term studies should be continued to look for changes in coral composition, species richness, density, and diversity as well as coral health by genus during and after bleaching events. In view of the dynamic nature of coral reef communities: long term-monitoring becomes a necessity: the inherent variance of any system must be estimated before the significance of future changes can be evaluated (Glynn, 1993). A protocol to standardize the degree of severity of coral bleaching and methods to evaluate the causes should be developed as soon as possible. Whatever the cause, or consequences, bleaching could have potentially important implications for the community structure, growth and accretion of coral reefs. Coral bleaching is not only a potential threat to the coral community itself, but also to developing countries who

are particularly dependent on coral reefs for food resources and have made heavy investments in reef related tourism (Brown and Ogden, 1993).

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An Analysis of Zooxanthellae in Hermatypic Corals Sampled from Shallow Depths

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ABSTRACT. This study examines zooxanthellae densities in corals at shallow depths. Two bleach sensitive (*Acropora*, *Pocillopora*) genera and one bleach resistant (*Porites*) genus were analyzed from three shallow depth regions in Moorea, French Polynesia. All three genera were observed to suffer a loss of zooxanthellae as they approached the surface. Densities from corals collected within 0 - 1.5 m were significantly lower than those collected from 1.5 - 2.3 m below the surface. The results indicate the presence of a shallow-depth related environmental stress. Significantly higher zooxanthellae densities were detected in *Porites* than in the *Acropora* or *Pocillopora*. It is suggested that this elevated level of zooxanthellae contributes to the resiliency *Porites* demonstrates towards bleaching.

Introduction

Hermatypic (reef building) corals are dependent on a symbiotic relationship with photosynthetic algae known as zooxanthellae. These dinoflagellate algae live within the tissues of coral hosts. The photosynthetic algae provide the animal host with fixed carbon and in turn absorb nutrients from the coral (Davies, 1984). The coral chemically alters the permeability of the unicellular algae membrane, promoting the release of photosynthetically fixed carbon (Falkowski et al., 1993). The macromolecules exuded by zooxanthellae have recently been found to contain all of the essential amino acids (Markell and Trench, 1993). Zooxanthellae fix 90-99% more carbon than they need to sustain themselves; this surplus is transferred to the host coral. Most of the transferred carbon is respired by the coral and used as a source of energy (Goreau et al., 1990; Falkowski et al., 1993). The transferred photosynthetic products provide the main energy source for the coral host (Streamer et al., 1993). Zooxanthellae are also an intricate part of coral calcification (Barnes and Chalker, 1990).

During bleaching events corals loose their zooxanthellae and/or photosynthetic pigment of remaining zooxanthellae (Glynn, 1993). The frequency of coral bleaching episodes has dramatically increased over the past decade (Glynn, 1993). The severity and extent of the events have also increased. The causative factors of coral bleaching have not been clearly determined although several factors have been associated with this phenomena (Suharsono and Brown, 1992). Temperature, nutrient levels, salinity and light are the primary factors associated with coral bleaching (Hoeksema, 1991; Glynn, 1990; Williams and Bunkley-Williams, 1990). Recent reports have shown a correlation between UVb radiation and coral bleaching (Gleason and Wellington, 1993; Kinzie, 1993; Lesser et al., 1990). Several studies have suggested that bleaching is a synergistic result of multiple factors (Coles, 1978; Williams and Bunkley-Williams, 1990).

Bleaching events can result in widespread mortality with a loss in coral cover and changes in species composition (Glynn, 1993; Brown and Suharsono, 1990). Bleaching has also been shown to reduce growth rates as well as reproductive fitness of corals (Goreau and Macfarlane, 1990; Szmant and Gassman, 1990). Single events can cause extensive mortality as in the 1982-83 El Niño related event in which 50-98% of the corals on eastern Pacific reefs died and three species were lost (Glynn, 1990). Recovery occurs by the gradual increase in zooxanthellae densities and/or by the increase in pigmentation in existing

zooxanthellae cells (Williams and Bunkley-Williams 1990). Tolerance to bleaching is dependent on the coral species. (Glynn, 1990; Gleason, 1993).

The effects of bleaching reach beyond the coral and their zooxanthellae. Coral reefs are among the worlds most diverse and productive ecosystems (Williams and Bunkley-Williams, 1990), many organisms find shelter in or under coral. During and after bleaching the surrounding community can experience loss of coral cover, loss of species diversity, and increased algal growth with subsequent overabundance of grazers (Glynn, 1993). On an evolutionary scale, corals are important land builders in tropical areas (Goreau et al., 1990) They excrete a hard skeleton of calcium carbonate which eventually becomes consolidated into the reef framework (Mather, 1993). Without the corals, the reef itself would not exist. Uncovering the mechanisms of coral bleaching will involve elucidation of coral-zooxanthellae symbiosis as well as coral and zooxanthellae species-dependent stress tolerances.

The risks of bleaching induced by temperature and UV radiation increase upon approaching the surface. The ocean's surface layer retains heat, and temperature often decreases over a "thermocline" through near surface depths. Similarly, calm water with the absence of suspended particles in the water column permits an abnormally high level of UV radiation to penetrate the photic zone (Gleason and Wellington, 1993). Turbulence in weather conditions such as high winds or strong currents can effectively mix the thermocline resulting in isothermal temperatures and high turbidity from sediment mixing. In the lack of adequate mixing, these two stress factors may be creating a synergistic effect on near surface coral communities.

This study sought to determine if there are changes in zooxanthellae as corals approach the surface, which would indicate the presence of depth related environmental stress. Since coral species have been determined to show different bleaching rates (Gleason, 1993; Harriot, 1985; Williams and Bunkley-Williams,

1990), it is interesting to compare bleach sensitive and bleach resistant coral. This study examines the density and growth rate of zooxanthellae in two bleach sensitive coral genera (*Pocillopora, Acropora*) and one bleach resistant coral (*Porites*) at varying depths. The depth range was near surface (0 - 3 m), the main factors correlated to this range are temperature and UVb radiation (280-320 nm) (Lesser et al., 1990; Gleason and Wellington, 1993; Cook et al., 1990).

Materials and Methods

The collection area was located on the island side of the barrier reef on the north coast of Moorea, French Polynesia (approx. 17°30´ S, 149°50´ W). Samples were taken west of Cooks Bay within approximately 50 m of the reef crest (Figure 1). Samples were taken via snorkeling from three depth transects (0-.75, .76-1.50, 1.51-2.30 m). Three samples per genera (*Pocillopora, Acropora, Porites*) were taken at each depth transect (n=27). Only healthy corals were sampled. A small sample piece was removed from the coral, placed in a plastic ziplock bag, and then in a large covered cooler. The samples were transported to the lab and stripped of their tissue using filtered seawater in a high powered water jet (WaterPic™). All of the resulting slurry was contained and measured. The transportation sample water for each sample was analyzed for expelled zooxanthellae as an indicator of sampling stress. The skeleton on the sample was saved for determination of surface area.
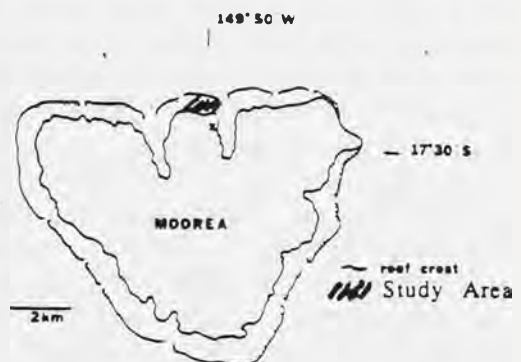
Figure 1. Study Area on Moorea

The tissue slurry was vigorously homogenized using a whisk for 5-7 minutes. A biomass sample was separated from the slurry. A 200-250 ml zooxanthellae density/growth rate sample was separated and fixed in 5% formalin.

Biomass was measured for each sample. Three aliquots (200-250 ml each) of the tissue slurry were dried in the Gump Station Oven at approximately 70-80°C (Setting of 1 1/2 on the oven would heat 250 ml of water to 70°C in twenty minutes). To adjust for the dissolved salt in the filtered seawater, an average weight was established (p > .95) and subtracted from the sample dry weights.

The surface area of each sample was determined by entering the weight of aluminum foil it took to cover the piece into a weight vs. area curve of aluminum foil (correlation coefficient = .999).

Zooxanthellae density was determined through microscopic examination (400x) on a hemacytometer. The hemacytometer had two equal counting platforms. Only one platform of the hemacytometer was counted since early counts showed the two platforms to produce equal results (p > .95). Six counts were taken from each sample. The number of algae cells per hemacytometer were extrapolated to the number of cells per cm^2 coral using the hemacytometer volume, the slurry volume, and the surface area of the sample.

The growth rate of zooxanthellae was determined through measuring the mitotic index. A makeshift centrifuge was fashioned out of a bicycle. The wheel and peddling gears were secured horizontally on a table and a post, they were then balanced with tied ropes. Four sample vials were secured inside the wheel at an angle with the end of the vials facing the bottom of the rim and the top of the vials facing the interior of the wheel. The "centrifuge" was turned using the pedals and gears of the bicycle. Samples were spun at approximately 2500 RPM for 5-7 minutes. The zooxanthellae dropped out of solution and the supernatant was discarded. The zooxanthellae were mounted on the hemacytometer and viewed at 450x. The

mitotic index is the number of cells with a clear division furrow (including cells appearing as doublets) divided by the total number of cells viewed. Six counts were made for each sample. In each count 100-200 cells were viewed. The growth rate of zooxanthellae was calculated using the formula:

$$\mu = 1 / t_\partial \ln (1+ f)$$

where μ is the growth rate, t_∂ is the duration of cytokinesis (approximately 11 hours for zooxanthellae) and f is the Mitotic Index (Falkowski et al., 1993).

Results

Biomass was linearly related to density in *Acropora* spp. (r = .84), however there were no other correlations to biomass. Growth rates did not correlate to depth, density, or biomass for any of the species. Depth was linearly related to density in all three genera (*Acropora* r = .86, *Pocillopora* r = .84, *Porites* r = .83). An ANOVA analysis showed each of these correlations to be significant. In each genera of coral, zooxanthellae density decreased significantly at the deep-medium transect interface (approximately 1.5 m). *Acropora* showed a steady decrease in zooxanthellae from 2.3 to 1.5 meters (p< .001) and a significant decrease between the 0.76-1.5 m medium zone and the 0-0.75 m shallow zone (p=.0016) (Figure 3). *Pocillopora* revealed a steady decrease in zooxanthellae from 2.3 to 1.5 meters (p< .001) and then fluctuated over the top 1.5 meters (Figure 2). *Porites* did not show a steady decrease in density at 2.3 to 1.5 meters but demonstrated a significant loss of zooxanthellae throughout the top 1.5 meters (p< .001) (Figure 4).

The three corals differed in the range of zooxanthellae they hosted. *Porites* had the highest densities of zooxanthellae as well as the widest range (1.1 x 10 ^{6} -3.2 x 10 ^{6} cells/cm²), *Acropora* filled the middle range (1 x 10⁶- 2.3 x 10⁶ cells/cm²), and *Pocillopora* hosted the lowest range (4 x 10⁵ - 1.5 x 10⁶ cells/cm²) (Figure 5).

Pocillopora Zooxanthellae Density vs. Depth

Depth (m)
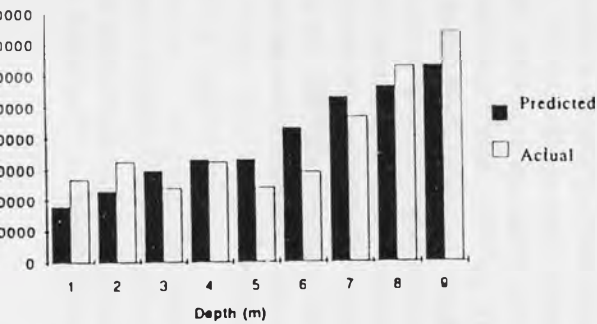
■ Predicted
□ Actual

Figure 2a Regression for *Pocillopora* Zooxanthellae vs Depth R= .84
bar indicates the zooxanthellae predicted for a perfect
relation between depth and density Second bar is the actual
sured zooxanthellae density The differences between the two
indicate the residuals for the regression, which are fairly low

Acropora Zooxanthellae Density vs. Depth

Zooxanthellae Density

0.38 0.38 0.76 0.91 1.22 1.3 1.68 1.75 2.13
Depth (meter)
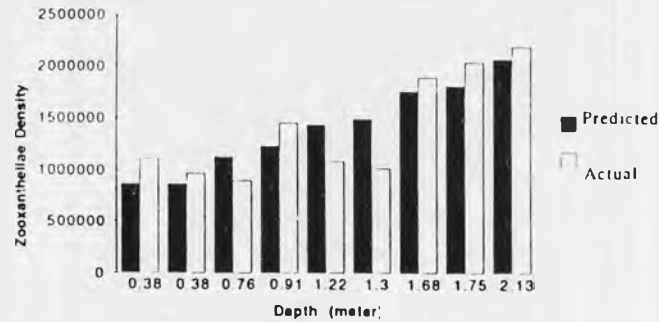
■ Predicted
□ Actual

Figure 3a Regression for *Acropora* Zooxanthellae vs Depth R= 84
First bar indicates the zooxanthellae predicted for a perfect
correlation between depth and density Second bar is the actual
measured zooxanthellae density The differences between the two
bars indicate the residuals for the regression, which are fairly low

Porites Zooxanthellae Density vs. Depth

Zooxanthellae Density

0.3 0.3 0.46 0.91 0.91 1.22 1.83 1.98 2.29
Depth (meter)
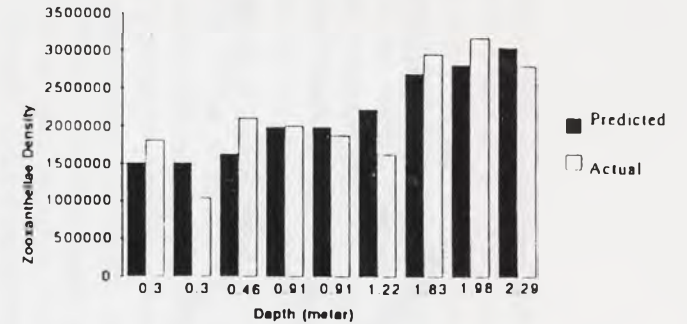
■ Predicted
□ Actual

Figure 4a Regression for *Porites* Zooxanthellae vs Depth R= 84
First bar indicates the zooxanthellae predicted for a perfect
correlation between depth and density Second bar is the actual
measured zooxanthellae density The differences between the two

Pocillopora Zooxanthellae Density Ranking

Sample Percentile for Zooxanthellae Density

S: shallow
M: medium
D: deep

Figure 2b Ranking of *Pocillopora* Zooxanthellae This indi: the
highest to lowest order of the densities sampled for P
depth of each sample is indicated

Acropora Zooxanthellae Ranking

Density One

Sample Percentile for Zooxanthellae Density

s: shallow
m: medium
d: deep
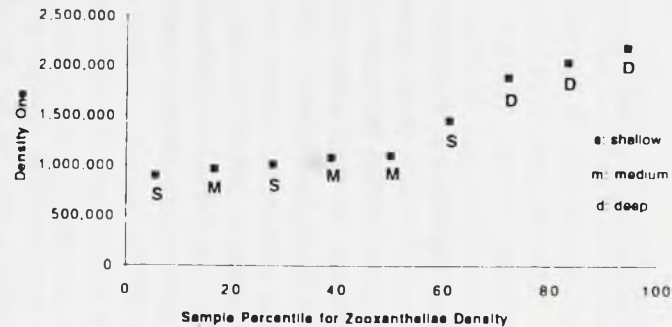
Figure 3b Ranking of *Acropora* Zooxanthellae This indicates the
highest to lowest order of the densities sampled for *Acropora* The
depth of each sample is indicated

Porites Zooxanthellae Density Ranking

Zooxanthellae Density

Sample Percentile for Zooxanthellae Density

s: shallow
m: medium
d: deep
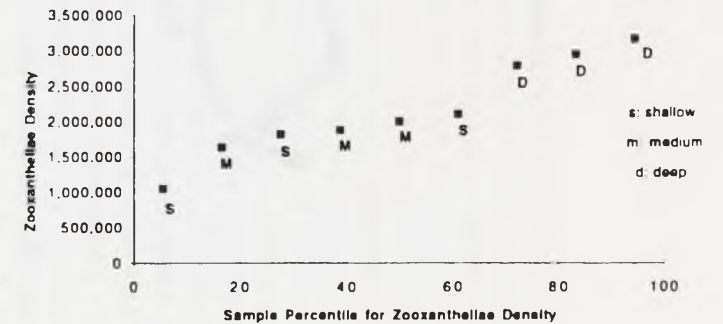
Figure 4b Ranking of *Porites* Zooxanthellae This indicates the
highest to lowest order of the densities sampled for *Porites* The
depth of each sample is indicated

Zooxanthellae Densities

3500000

3000000

2500000

2000000

1500000

1000000

500000

Porites Zooxanthellae Density

Acropora Zooxanthellae Density

Pocillopora Zooxanthellae Density

[Shallow and Medium transects][Deep transects]
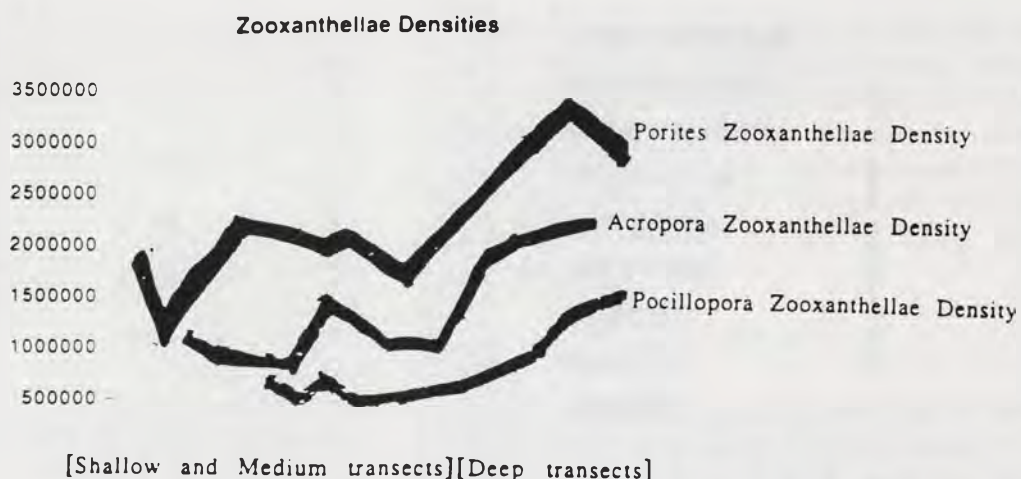
Figure 5: Compares zooxanthellae densities of the coral

Discussion

Biomass

Since tissue generation is a delayed effect of fixed carbon deficiency, it is reasonable that consistent correlations were not found. Also the depressed level of zooxanthellae in shallow and medium transects may not transcended below the basal photosynthetic requirements of the coral. However, due to the limitation of the facilities, the measurement of biomass left much room for error.

Growth rate

Growth rate is a valuable tool to indicate the zooxanthella's ability to re-inhabit the affected host. It is noted that the method of mitotic index determination used in this study has been shown to produces misleading results.

Suharsono and Brown (1992) found that zooxanthellae released into the coelenteron from the endoderm during temperature increase, divide at a faster rate than those remaining in the tissues (although temperature is sited here, it is assumed that zooxanthellae released due to any general stress would still divide faster). They suggest that current methods to measure mitotic indices in tissue homogenates are not indicative of the division rate of zooxanthellae embedded in

the tissue due to the inclusion of released and dividing algae in the polyp coelenteron (they use serial section assays of intracellular algae, which only examine zooxanthellae embedded in tissue).

A number of factors may regulate the division rate of zooxanthellae in coral tissues (Suharsono and Brown, 1992). These include limited space availability in the tissues and nutrient limitation of zooxanthellae which is controlled by the coral. Suharsono and Brown (1992) suggest that once zooxanthellae are released into the coeleteron, they are free to divide without host restriction. They suggest an alternative theory that the host selectively expels dividing zooxanthellae rather than nondividing which would result in higher division rates of algae found in the coelenteron.

This alternative theory suggests that growth rate may be an important trigger in coral bleaching. Temperature increase can stimulate zooxanthellae cell division (Suharsono and Brown, 1992). If corals selectively expel rapidly dividing cells, growth rate may be an intricate part of the temperature induced bleaching mechanism.

Density

The consistent decrease in zooxanthellae of three coral genera along the same depth zone suggests a "threshold depth" at which

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an environmental stress or combination of stresses induce the loss of symbiotic alga. The signified loss of zooxanthellae in corals as they approach the surface suggest the presence of an environmental stress associated with extreme shallow depths. The two main stress factors associated with shallow depths are temperature and UV radiation (Lesser et al., 1990; Gleason and Wellington, 1993; Cook et al., 1990). The surface layer accumulates heat, and UV radiation can penetrate shallow waters with little refraction (Gleason and Wellington, 1993). These effects are greatly amplified in calm weather. It has been widely thought that temperature stress expel zooxanthellae while overexposure to UV pales pigments (but does not expel zooxanthellae). However, Gleason and Wellington (1993) reported zooxanthellae expulsion with increased UV exposure. This demonstrates that both temperature and UV radiation stress can induce zooxanthellae expulsion. Together they may create a synergistic effect.

Lesser and Shick (1989), suggested oxygen toxicity as a possible mechanism of UV radiation-induced bleaching. Their study detected increased production of active oxygen in zooxanthellae exposed to UV radiation. Through the reduction of oxygen, respiring cells produce superoxide radicals (O_2^-), which can be further reduced to hydrogen peroxide (H_2O_2) and then to hydroxyl radicals $(HO\cdot)$ (Lesser and Shick, 1989; Streitwieser and Heathcock, 1985). Hydroxyl radicals can cause severe cellular damage (Streitwieser and Heathcock, 1985). Enzymes are present in respiring cells which "neutralize" active oxygen (Lesser and Shick, 1989). An increased presence of active oxygen demands the increased production of neutralizing enzymes. This demand may inflict a significant energy drain on the coral. Lesser et al. (1990) suggested that corals may expel zooxanthellae in response to UV induced oxygen toxicity or the energy strain of defending against it.

Temperature increase has been shown to decrease the photosynthetic ability of zooxanthellae which would cause a reduction in the transfer of photosynthetic products to the coral (Iglesias-Preito et al., 1992). This could create an energy drain on the coral, promoting it to expel the zooxanthellae. Through photoinhibition, elevated temperature also promotes active oxygen which adds to the oxygen toxicity effect previously described (Lesser et al., 1990). Iglesias-Preito et al. (1992), suggested that some of the photosynthetic products transferred from the zooxanthellae act as chemical recognition signals for the coral. In the reduction or absence of recognition signals, the corals may interpret the zooxanthellae as a foreign organism, prompting expulsion (Iglesias-Preito et al., 1992).

Thus, in the presence of elevated temperature and UV radiation, the energy requirement to fight against oxygen toxicity coupled with the decrease of the corals main energy source (photosynthetically fixed carbon) may very well synergistically combine to cause a mass expulsion of the symbiotic alga.

Several alternative explanations for the decrease in zooxanthellae are possible. Coles and Jokiel (1978) suggested that temperature, salinity and light could synergistically stress corals. They report that low salinity reduces coral tolerance to elevated temperature. They found the temperature induced tissue damage sustained by the coral to be aggravated by high intensities of natural light. Also, salinity alone is accepted as a viable environmental stress (Glynn, 1993). Salinity may be depressed by heavy rains and subsequent freshwater lens mixing or conversely elevated by calm still waters and increased evaporation. Turbidity as well as nutrient imbalance are additional established factors in bleaching (Glynn, 1993; Cook et al., 1994). However, in past studies and literature, turbidity and nutrient imbalance are rarely correlated with variations in shallow depth.

Although this study indicates that coral are experiencing some sort of environmental stress correlated to shallow depths, the determination of the exact stress would require further investigation. It would be interesting to analyze temperature, UV absorbency, weather

patterns (to indicate the frequency of calm water), and salinity and nutrient levels throughout a one year period to include seasonal variation. If zooxanthellae densities were also metered throughout the period, reactions to individual stresses may be detected.

The second significant result from this report is the differences between the densities of zooxanthellae found in the different species. *Porites* was found to have significantly elevated zooxanthellae densities compared to *Pocillopora* and *Acropora*. This could be a central contributing factor to the resiliency of *Porites*. Although *Porites* is rarely bleached in Moorea, this study showed the species to react to an environmental stress in the same manor and to the same extent as the bleach sensitive *Pocillopora* and *Acropora* corals. The only difference between the corals was the elevated zooxanthellae densities of *Porites*. If the amount of zooxanthellae present in *Porites* exceeds the amount necessary to provide the photosynthetic requirement of the coral, *Porites* could be affected by stress (loose zooxanthellae) without being damaged (maintain photosynthetic requirements).

Assuming that this were true, the elevated population of zooxanthellae would produce excess photosynthetic products. Coral responds to excess fixed carbon by exuding it as mucus (Davies, 1984; Drollet et al., 1993). It is interesting to note that *Porites* were observed to have exorbitant amounts of mucus. Although the amounts were not quantified, *Acropora* and *Pocillopora* would sometimes exhibit a slick film of mucus while *Porites* consistently showed an abundant viscous mucus. Mucus creates a medium to hold UV screening compounds and acts as a physical shield in protection against turbidity (Drollet et al., 1993).

The elevated zooxanthellae density of *Porites* could begin a cyclical process promoting resilience toward bleaching. The overabundance of zooxanthellae may "buffer" stress induced zooxanthellae expulsion. The mucus resulting from the overproduction of photosynthetic products provides

protection for the coral. Protection against perturbation, especially tissue damage, enhances the corals ability to maintain its elevated density.

An additional support to this theory is that the calcification rate of *Porites*. Photosynthesis of zooxanthellae is a driving force in coral growth (Muscatine, 1981; Barnes and Chalker, 1990). Campion-Alsumard et al. (1993), reports a general increase in calcification rates of *P. lobata* in Moorea from 1981 to 1988. The rates were determined by chemical measurements and were confirmed by field observations of numerous small colonies of *Porites spp.*, which Campion-Alsumard et al. (1993) sites as an indication of increased calcification.

Through calcification, carbonate (HCO_3) taken from the seawater goes through a series of reactions using photosynthetically fixed carbon dioxide (CO_2) resulting in an increased concentration of carbonate ions (CO_3^{-2}) and subsequent raised pH of the coral tissues. By releasing its excess CO_3^{-2} in the form of insoluble calcium carbonate ($CaCO_3$), the coral polyp is able to restore its pH to the normal level (Goreau et al., 1990).

Fang et al. (1989) found that rapid coral metabolism (consumption of photosynthetic products) generates more ATP (adenosine triphosphate) which supplies energy for the active transport of calcium ions to the site of the carbonate ions where they are deposited as $CaCO_3$. ATP releases energy through its conversion to ADP (adenosine diphosphate) and phosphate via the Krebs cycle (Campbell, 1993) and is commonly used to transfer energy in living cells. Increased photosynthetic activity results in the increase of carbon dioxide and ATP which will subsequently increase the rate of calcification.

Higher densities of zooxanthellae have the potential to increase photosynthetic rates within the coral. The higher density of zooxanthellae in *Porites* (assuming the cells contain average chlorophyll pigmentation) may create an abundance of photosynthetic products adequate to increase calcification. The

observed increase in the calcification of *Porites* in Moorea may be another indication that the coral is producing more than adequate amounts of photosynthetic products.

This study indicates that corals in Moorea are experiencing some sort of environmental stress at shallow depths. The high zooxanthellae densities of *Porites* may be a central factor in this corals resiliency to bleaching. Coral reefs are among the worlds most diverse and productive ecosystems. Coral bleaching is a serious ecological threat, uncovering the mechanisms of coral bleaching will involve elucidation of coral-zooxanthellae symbiosis as well as the coral and zooxanthellae species-dependent stress tolerances.

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A Phylogeny of Moorean Nudibranchs
with a test of nudibranch palatability

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ABSTRACT. A phylogeny for Moorean opisthobranchs is presented including twenty-one taxa and twenty-seven characters. The relationships between different taxa are explored and the value of characters discussed. Distastefulness and conspicuous coloration are traced on a tree to show the evolution of aposematic coloration. Possible evidence for aposematic coloration is also demonstrated in two species of nudibranchs. Fish predators are shown to avoid conspicuous nudibranchs when they are encountered in a natural setting. Fish also rejected disguised bits of the same nudibranchs as possible food. It is concluded that these nudibranchs are avoided because of their toxicity. Their conspicuous coloration may warn potential predators of this noxiousness. Both unpalitability and conspicuousness may be artifacts of the nudibranchs prey items. It may be biologically impossible for a nudibranch **not** to be aposematic. Aposematism in nudibranchs may reflect an allocation of different resources in a shared environment. Different species may have similar ways of handling the toxic and color rendering byproducts of their different prey items. Further tests need to examine nudibranch digestion and toxin sequestering. Selection toward conspicuousness paired with distastefulness may be the end result of these biological processes in conjunction with predator learning.

Introduction

Opisthobranchs or sea slugs are the most diverse of the three subclasses of Gastropoda (Gosliner and Ghiselin, 1984). They range from tiny sacoglossans less than 2mm long to anaspideans that weigh more than 2kg (Thompson, 1976). Due to the huge amount of variability within this subclass many questions have been raised about its evolutionary history (Gosliner, 1981; Faulkner and Ghiselin, 1983; Gosliner and Ghiselin, 1984; Brunkhorst, 1993). It has been very difficult to answer some of these questions. The fossil record is not useful because most of the phylogenetically important information is contained within the soft bodied organisms (Gosliner and Ghiselin, 1984). There is also a high incidence of parallelism in the subclass Opisthobranchia. Many characters have evolved similarly over separate lineages and this leads to confusion (Gosliner, 1981). This paper addresses some of the very basic questions about the evolution of opisthobranchs on Moorea, French Polynesia and opisthobranchs in general.

Very little is known about the sea slug fauna in the South Pacific (Willan and Coleman, 1983; Coleman, 1989). Inventory was taken in 1985 for the Fifth International Coral Reef Congress (Richard, 1985), and a few pictures appear in Shells of French Polynesia (Salvat and Rives, 1991), but no other work on opisthobranchs in the Society Islands has been done. One objective of my work was to simply catalogue the species encountered on Moorea.

The distinctive coloration of many opisthobranch species has been speculated upon for years, especially that of the order Nudibranchia. Warning coloration has be suggested to explain the bright and conspicuous coloration of many nudibranch species (Wallace, 1889; Poulton, 1890; Crozier, 1916; Thompson, 1960; Edmunds, 1974; Rosenberg, 1989; Guliford, 1991). Warning or aposematic coloration is defined as an animal having dangerous or unpleasant attributes and advertising this fact by means of characteristic structures, colors or other signals that discourage predators from attacking them (Edmunds, 1974). The possibility of this condition occurring in nudibranchs has been tested with fish predators (Crozier, 1916; Thompson, 1960). Fish have color vision and are capable of learned responses

(Edmunds, 1991). Fish were shown to avoid nudibranchs, but only after the nudibranch had been dropped through the water column. Fish will bite at anything falling through the water (Thompson, 1960). These tests have demonstrated that nudibranchs are not palatable, but not that they are avoided because of their conspicuous coloration. Edmunds (1987) proposed four criteria that need to be fulfilled in order to demonstrate that a particular species is aposematic:

1.) It is distasteful to predators.
2.) It is conspicuously colored or advertises itself by means of some other signals.
3.) Predators avoid attacking it because of those signals.
4.) These conspicuous signals provide better protection to the individual or to its genes than would other signals.

Criteria one and two have both been demonstrated (Thompson, 1960), but sound evidence is lacking for the second two. In this study I attempt to demonstrate criteria three and determine if two conspicuous species of nudibranchs, *Gymnodoris ceylonica* and *Glossidoris hikueremsis*, are avoided by fish predators in natural situations.

Materials and Methods

All work was completed on Moorea, French Polynesia (17°30' S, 149°50" W) during October and November, 1994. In order to create a phylogeny of Moorean opisthobranchs, different locations around the island were explored (Figure 1), and alldiscovered organisms were collected, measured, drawn, photographed and preserved. A data matrix was set up using MacClade 3.01 and analyzed by four separate heuristic searches (Table 1) including consensus trees in PAUP 3.1.1. The matrix includes twenty-one taxa and twenty-seven characters (Appendices I and II). Characters were chosen only if they were mutually exclusive, had distinct states and were homologous in all taxa.
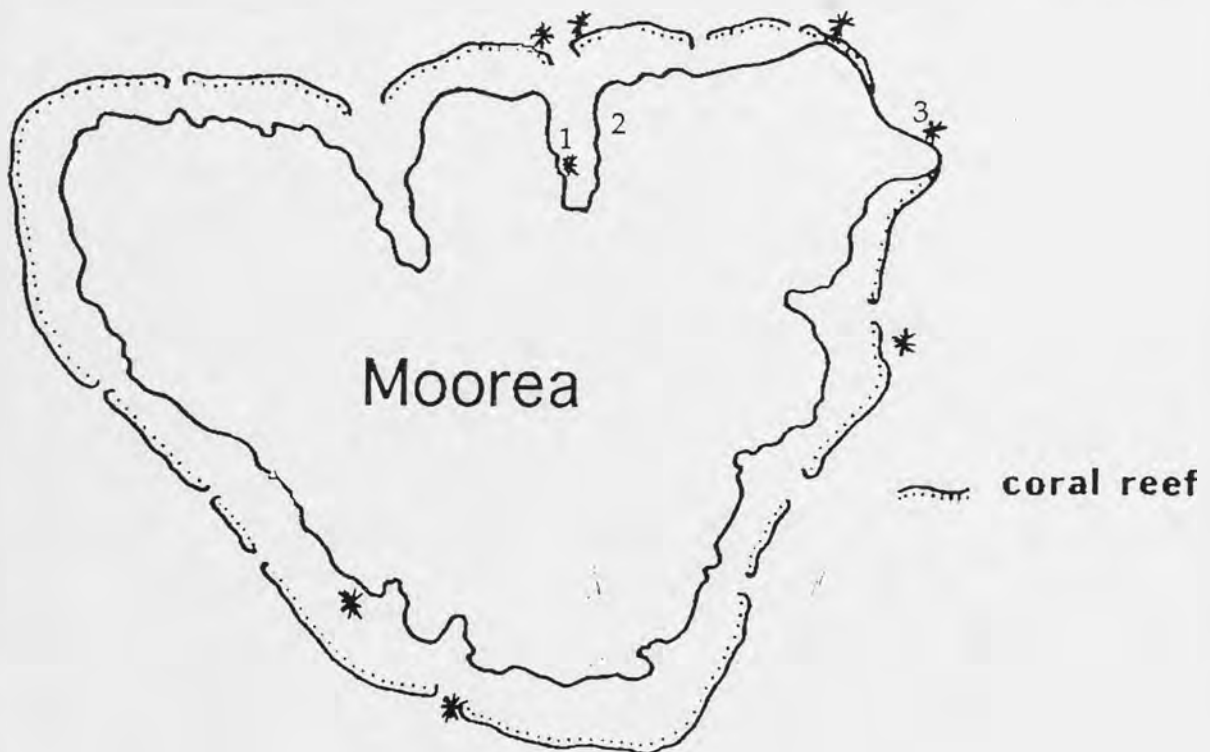
Figure 1. Sites for feeding experiments indicated by 1, 2 and 3
locations of opisthobranch discovery indicated by (*)

Character one, size, was not used in the analysis because the states: very small, small, medium, large and very large are continuous. This character was left in the matrix because it was a good way to store data and interesting to map on a completed tree.

General color is important in the classification of opisthobranchs. It helps determine if the organism is cryptic or conspicuous and may help answer questions about the evolution of these phenomena. This character, along with others involving color , was described using Part I of the Naturalist's Color Guide (Smithe, 1975). This guide helped keep the colors consistent throughout the matrix. General body color was described as the color of the opisthobranch underneath any pattern that may have been present. Usually this was the dominant color. Color was not linked to any other trait. For example, if the general body color was white the rhinopores were not always orange. Color and pattern have been shown to be descriptive in other gastropod phylogenies (Brunkhorst, 1993; Gosliner and Ghiselin, 1973).

Pattern and pattern color also play a role in the appearance of an animal to a potential predator. Pattern is usually what makes an organism stand out or blend in with its environment (Edmunds, 1974). Due to optics and the physics of light certain patterns are more suitable for specific purposes, like crypsis, than others (Cott, 1940). These patterns can be made up of dots, stripes or a combination of both. Foot color also may have an influence over the patterns seen by predators. If it is the same color as the body a pattern is not created. But if the foot is a different color it may create patterns and may change the way the organism is perceived. Some apparently cryptic nudibranchs may possess flash coloration. Flash coloration may involve exposing part of the body that are usually hidden. This type of warning device startles predators, but does not make the animal risk being conspicuous all of the time.

Rhinopores protrude from the bodies of opisthobranchs and are thought to have some sensory function, although their surface tissue does not differ greatly from that of the rest of their bodies. Some researchers believe that they are used for finding food or a mate (Behrens, 1980). Not all species of opisthobranch have rhinopores and some have two pairs. The number of rhinopores and their general morphology are very good indications of family, genus and species (Willan and Coleman, 1984). Four types of rhinopores are present in the opisthobranchs collected on Moorea. Four characters in the data matrix are dedicated to the rhinopores: presence, number, morphology and color.

The mantle is usually protected in gastropods by a shell, but in most opisthobranchs it is fully exposed and the most vulnerable spot for attack. It is also usually the most distasteful (Crozier, 1916). Mantle morphology changes the profile of many nudibranchs and therefore has a substantial effect on a predator's perception of its prey (Edmunds, 1974). Mantle color may assist in crypsis or aposematism more than any other colored part of the body of a sea slug. It defines the animal's outline and is the part that is viewed immediately next to the substrate on which the animal is found.

Gills are the primary respiratory organ of marine gastropods. They are another structure that can be used to differentiate between families in the opisthobranch sub-class. The gills can be exposed and raised on the dorsum, underneath the mantle on one side of the animal, a pair of flaps along the dorsal surface, or hidden beneath the shell. If exposed, as in all nudibranch species, there are five other characteristics that can be used to help identify different species and draw conclusions about the relationships between those species. These characters are whether or not the gills are rimmed along the axis, if the gills are arranged in concentric rings or are open in the middle, if the gills are retractable (cryptobranch) or not (phanerobranch), the general morphology of the gills and the gill color.

Data on egg masses for all species found were not available. However, the trait was included because spawn characteristics are specific to certain groups of opisthobranchs. Two major types of spawn mass were observed in Moorea. The

first takes the form of a ribbon attached along one edge to the substratum. The second is a capsule filled tube. Both types are laid in a spiral fashion (Thompson, 1976). Another minor type of spawn was observed that resembled haphazardly laid strings. Egg masses are so unique it is possible to identify to species just by viewing one mass (Wilan and Coleman, 1983).

Possessing a shell is a primitive characteristic in opisthobranchs (Faulkner and Ghiselin, 1983; Gosliner and Ghiselin, 1984). It is sometimes present in four orders of the eight orders that make up the opisthobranchia. The shells found in these orders are always reduced compared to the shells of other gastropods (Thompson, 1976).

Group size per 2 meters was not included in the analysis of this phylogeny. The character states for group size can depend on time of day, search effort, distribution of prey items and predator abundance. Because of this variability this trait is not descriptive.

The overall appearance of opisthobranchs, cryptic or conspicuous, can help answer some of the many questions about the evolution of aposematism. However, including this character in the analysis may bias the eventual tree. Instead, mapping the trait on a completed tree, along with a reasonable guess about the palatability of a species can demonstrate the evolutionary paths aposematism has taken.

The patch reef east of the Gump Biological Station, the patch reef west of Cook's Bay Hotel and the area within the barrier reef at Temae public beach served as the study sites in the test for nudibranch palatability (Figure 1).

Two species of nudibranchs, *Gymnodoris ceylonica* and *Glossodoris hikueremsis*, were fed to fish predators to test for learned behavior of the fish and to demonstrate distastefulness in conspicuous sea slugs. Each species chosen was locally abundant at one of the sites, *Gymnodoris* at Temae and *Glossodoris* at Gump station and neither was found at the Cook's Bay hotel site (Figure 1). At all three sites the fish predators were mainly six-bar wrasses, *Thalassomma hardwickii*, and damsel fish. At all three sites fish were fed paste, paste with bits of nudibranch inside and whole live nudibranchs. The paste was made up of flour and water mixed until the paste would stay together without being sticky. Each ball was approximately 2 cm in diameter. The nudibranch pieces were cut from organisms that had been relaxed in 10% MgCl and then rinsed in sea water. Every attempt was made to include part of the epidermal and dermal layer in each piece. If opisthobranchs are sequestering toxic chemicals they are usually stored in the skin. (Crozier 1916, Thompson 1960, Edmunds 1991) Plain paste balls and paste with nudibranch balls did not look any different. Live nudibranchs of comparable size, about 6cm were selected. Food was placed on a coral head in areas where fish were present. The amount of time it took a fish to bite the food was recorded. It was also noted if the food was eaten-1, bitten and rejected-2 or ignored-3 At each site ten replicates of each food choice; paste, paste plus nudibranch and nudibranch, were run for both *Gymnodoris ceylonica* and *Glossodoris hikueremsis*. Each set of replicates was repeated twice. In order to show a relationship between food type, site, time to first attack and reaction of the predator, four two-way analyses of variance were run.

Results

Four different searches were run on PAUP 3.1.1 (Table 1). If an outgroup was

Table 1. Variables in Tree Analyses

	Including Outgroup	Excluding Outgroup
Including Color Characters	1. Number of Trees = 7	2. Least Assumptions Number of Trees = 7
Excluding Color Characters	3. Most Assumptions Number of Trees = 24	4. Number of Trees = 24

included in the search it was made up of all species that were not nudibranchs, species 11, 12, 15, 16, 17, 20 and 21 from Appendix II. The inclusion of an outgroup did not change the tree structure. The same trees were found in searches one and two and the same trees were also found for searches three and four, showing that the distinction of a outgroup had no bearing on the final trees. When all characters were included in the analysis no assumptions were made. All characters were treated as equally important in answering evolutionary questions. These trees show two distinctive branches, one containing all of the non-nudibranch species. In the nudibranch branch five different clades have arisen and in the other branch the seven species have been divided into four clades. Figure 2 shows the tracing of rhinopore morphology and Figure 3 shows general color. Data analysis that did not
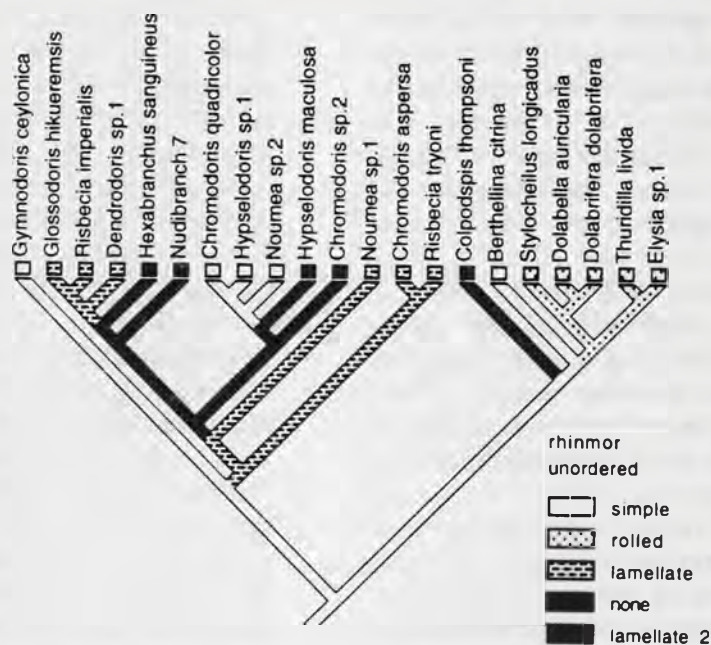
Figure 2. Phylogeny including all characters (rhinopore morphology traced)
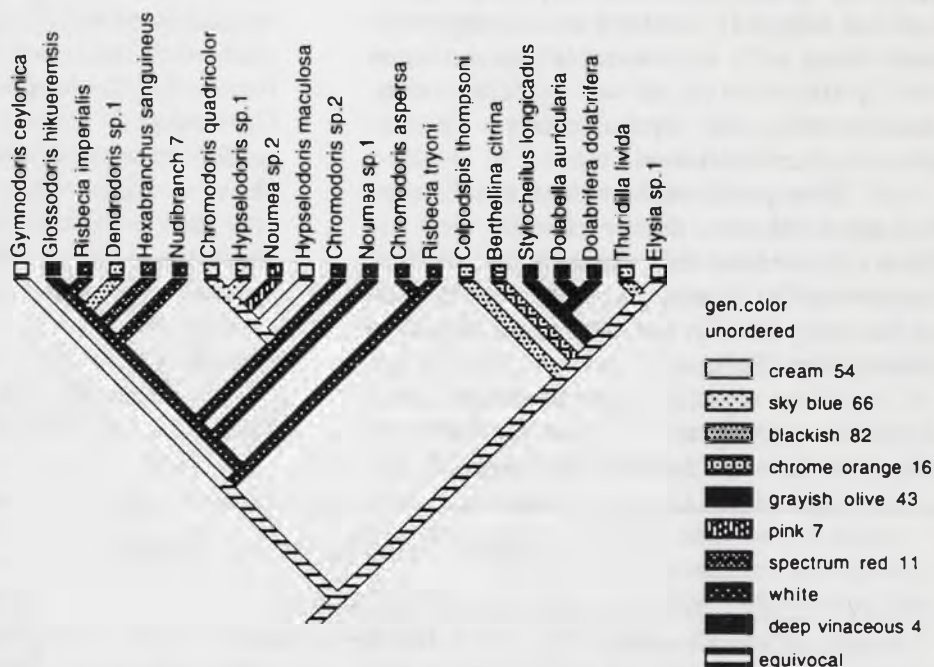
Figure 3. Phylogeny including all characters (general color traced)

include color characters assumed that color had a large impact on the formation of trees. This tree is not as defined as tree number one, it has one major branch that contains five clades, and one minor branch with only two species. Within the five clades of the large branch three include one species, one includes five species and one includes ten species. This large clade of five species is divided into two smaller

clades one of three nudibranch species and one of the seven non-nudibranch species. Figure 4 traces rhinopore morphology and Figure 5 shows trends in general color. Species used, characters and the completed data matrix are included in the appendices. A tree including all taxa and descriptive characters was used to trace overall appearance and assumed palatability (Figure 6).
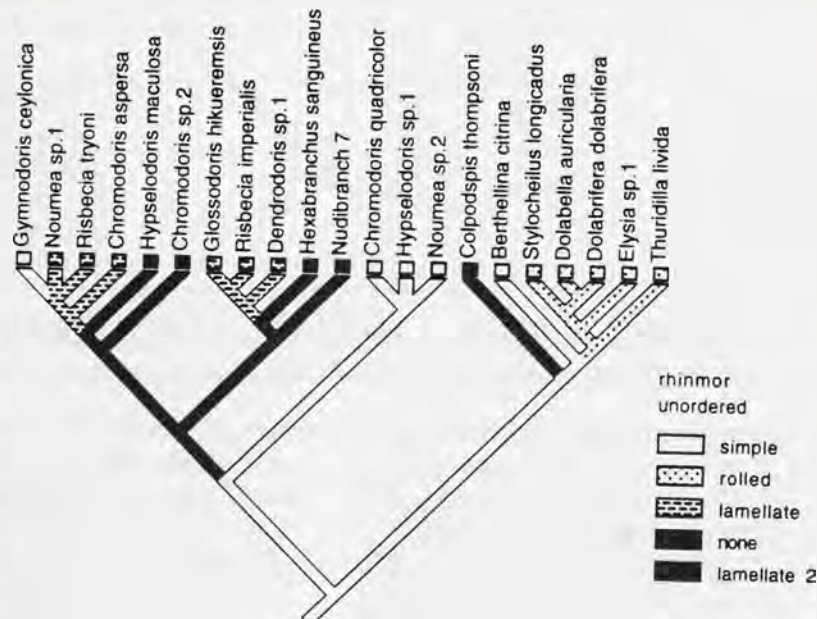
Figure 4. Phylogeny without color characters (rhinopore morphology traced)
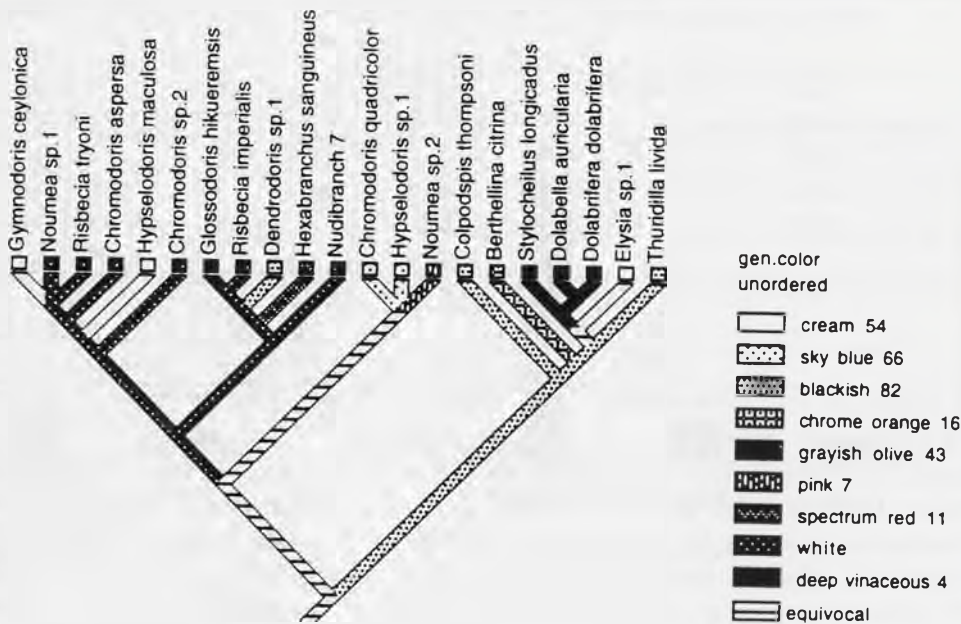
Figure 5. Phylogeny without color characters (general color traced)
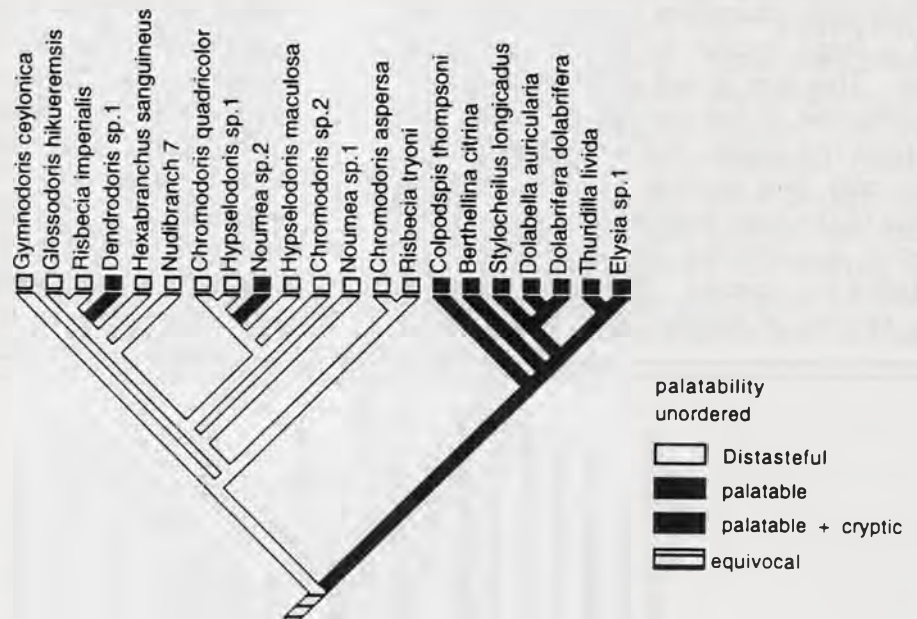
Figure 6. Phylogeny with palatability and overall appearance

The average time to first attack is showed for *Gymnodoris ceylonica* and *Glossidoris hikueremsis* (Figures 7 and 8). Live whole nudibranchs were rarely even tried and most often ignored. There was a slight, but significant difference in the time to attack on paste balls and time to attack paste balls with nudibranch bits, in both species. Food type was found to have a very significant effect on time to first attack in both species of nudibranch (Tables 2 and 3). The type of food offered also had a significant effect on whether or not the food was eventually eaten or not (Tables 4 and 5).
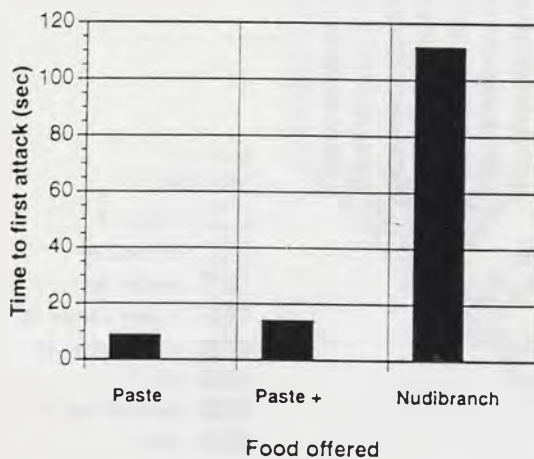
Figure 7. Attack rate on *Gymnodoris* sp.
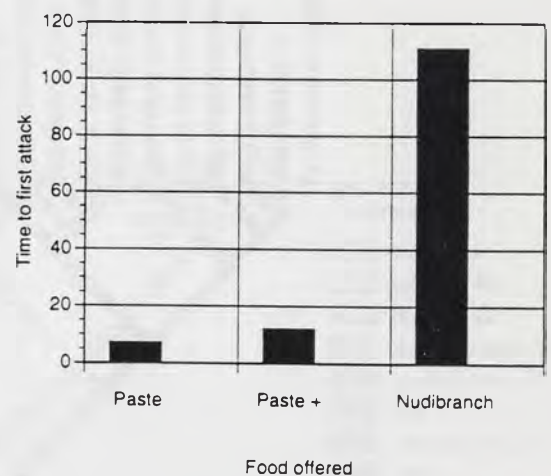
Figure 8. Attack rate on *Glossodoris* sp.

Table 2. Two-way analysis of variance. Shows effect site and food choice had on time to first attack on *Gymnodoris* Food choice very significant p<.0001

Analysis of Variance	sum of squares	df	mean square	f-value	tail probability
site	1757.7029	2	878.8515	3.22	0.0423
food	404366.96	2	202183.48	741.28	0.0001
interaction	1339.8606	4	334.9652	1.23	0.3008
error	46367.631	170	272.7508		

Table 3. Two-way analysis of variance. Shows effect site and food choice had on time to first attack on *Glossidoris*. Food choice was very significant p<.0001

Analysis of Variance	sum of squares	df	mean square	f-value	tail probability
site	1707.7010	2	853.8505	3.40	0.0357
food	417816.58	2	208908.29	830.87	0.0001
interaction	1438.4640	4	359.6160	1.43	0.2259
error	44000.650	175	251.4323		

Table 4. Two-way analysis of variance. Shows effect site and food choice had on whether or not *Gymnodoriss* was eaten. Food choice was very significant p<.0001.

Analysis of Variance	sum of squares	df	mean square	f-value	tail probability
site	0.8088	2	.4044	3.04	.0502
food	105.8852	2	52.9426	398.66	.0001
interaction	1.9458	4	.4864	3.66	.0069
error	22.5763	170	.1328		

Table 5. Two-way analysis of variance. Shows effect site and food choice had on whether or not *Glossodoris* was eaten. Food choice was very significant p<.0001.

Analysis of Variance	sum of squares	df	mean square	f -value	tail probability
site	0.0112	2	.0056	0.05	.9526
food	112.7343	2	56.3671	488.33	.0001
interaction	1.0093	4	.2523	2.19	.0725
error	20.2000	175	.1154		

Discussion

A final phylogeny of Moorean nudibranchs shown in Figure 9. This tree is a consensus of all taxa and all descriptive characters studied. All of the non-nudibranch species are grouped together in one clade. The most primitive of these species being *Colopodspis thompsoni* the only opisthobranch found that has a shell. The shell is retained from the full, heavy shelled ancestors of all opisthobranchs. This species is most closely related to *Berthellina citrina*, a notaspideian. *B. citrina* retains an internal shell. The

Gymnodoris ceylonica
Glossodoris hikueremsis
Risbecia imperialis
Dendrodoris sp.1
Hexabranchus sanguineus
Nudibranch 7
Chromodoris quadricolor
Hypselodoris sp.1
Noumea sp.2
Hypselodoris maculosa
Chromodoris sp.2
Noumea sp.1
Chromodoris aspersa
Risbecia tryoni
Colpodspis thompsoni
Berthellina citrina
Stylocheilus longicadus
Dolabella auricularia
Dolabrifera dolabrifera
Thuridilla livida
Elysia sp.1

Figure 9. Consensus phylogeny of all taxa and characters

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presence of this shell keeps this species toward the bottom of the tree, closer to a primate ancestor. The rest of the non-nudibranch species are grouped more because of the morphological differences that separate them from *C. thompsoni* and *B. citrina* than anything else that separates them from each other. The other species are continuously moved around in different trees because they are not very different from each other. The only main difference between the remaining five species is color.

The nudibranch portion of the tree is much more interesting. The species are mostly grouped together because of morphology. All of the species with similar gills, mantles and rhinopores are grouped together. The color characteristics vary and appear in many different branches of the tree. The color characteristics help to show that many different things may affect coloration that do not have any bearing on morphology. The groupings on this tree show that morphological characters are evolved in lineages, while color characteristics evolve independently again and again. The independent evolution of color and pattern reflect environmental differences thatnudibranchs may encounter. Whereas structures that are important in an opisthobranchs survival do not change very often in evolutionary time, the colors that it may need to do just that may change much more often. The opisthobranchs that have morphological characteristics in common may live in the same areas and deal with the same selection of prey items. This may lead to the allocation of resources, so that different species may begin to specialize on different prey. The differences in prey may lead in turn to changes in chemicals sequestered and colors obtained.

The feeding of *Gymnodoris ceylonica* and *Glossodoris hikueremsis* to fish predators demonstrated the distastefulness of these species. Paste balls with nudibranch inside were approached much more slowly than plain paste balls. The difference in attack time must be due to a chemical released by the nudibranch. Nudibranchs either gain chemicals from their food sources or manufacture them *de novo* (Faulkner and Ghiselin, 1983). These chemicals must be strong enough make a predator hesitant even when diluted in sea water. The whole live nudibranchs were completely ignored most of the time. This may be because the fish predators inherently know to avoid conspicuously colored items. It could also mean that the same chemical that slowed approach to the dough balls also warns predators when the nudibranch is alive and whole. The chemical warning would have to be much stronger in whole nudibranchs because all of the toxins are concentrated. These two species of nudibranch are from completely different parts of the island. It is presumed that they feed on different prey and in turn the chemical they utilize as defense are different. *Gymnodoris ceylonica* and *Glossodoris hikueremsis* seem to be equally noxious to predators.

The species were both found to be unpalatable and conspicuous, but this does not say for sure that they are aposematic. The colors of these nudibranchs may not evolve as advertisements for distastefulness, they may evolve along with the noxious qualities as another by-product of predation. Most cryptic nudibranch species achieve their camouflage by retaining pigments from their prey. It is possible that conspicuously colored species do the same. The benefit of the retention of these chemicals may be conspicuous colors that predators avoid. Further test would have to be done looking at a cryptic species with the same chemical defense. If the cryptic morph was eaten more often than the conspicuous one then aposematism would be favored, and selected.

The results of these two studies on Moorean opisthobranchs explore the use of color in two very different ways. The phylogeny shows the independent evolution of color, but does show that it changes the shape of the tree when excluded. It is an important character in this tree because of the limited number of characters. If more morphological characters were included, the relationships between taxa would be stronger. Other characters that should be explored are

radula morphology, jaw morphology, others pertaining to internal physiology and anatomy. The evolution of aposematism in this phylogeny does show that palatability is the exception and probably derived, although further study is needed here as well. The feeding experiment demonstrates a hesitancy on the part of a predator to eat a nudibranch even when color is hidden. The chemical aspect of aposematism is usually lost in all of the discussion of color and might be more important. Color has an important role in the life history of opisthobranchs and is seen many times to have more of a behavioral importance than a biological one. Before aposematism is declared the reason for nudibranch coloration, more work needs to be done on their biology. Perhaps, diet and coloration are the reason nudibranchs may be aposematic.

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APPENDIX I. CHARACTER STATE NAMES

1. size
   - 0: very small
   - 1: small
   - 2: medium
   - 3: large
   - 4: very large

2. gen.color
   - 0: cream 54
   - 1: sky blue 66
   - 2: blackish 82
   - 3: chrome orange 16
   - 4: grayish olive 43
   - 5: pink 7
   - 6: spectrum red 11
   - 7: white
   - 8: deep vinaceous 4

3. dots
   - 0: yes
   - 1: no

4. dot col
   - 0: spectrum red 11
   - 1: orange yellow 18
   - 2: spectrum violet 72
   - 3: cream 54
   - 4: blackish 82
   - 5: spectrum yellow 55
   - 6: none

5. stripes
   - 0: yes
   - 1: no

6. stripecolor
   - 0: blackish 82
   - 1: olive green 46
   - 2: white
   - 3: scarlet 14
   - 4: none

7. flashcolor
   - 0: yes
   - 1: no

8. foot color
   - 0: same
   - 1: different

9. rhinop
   - 0: yes
   - 1: no

10. rhinop2
    - 0: two
    - 1: four
    - 2: shovel
    - 3: none

11. rhinmor
    - 0: simple
    - 1: rolled
    - 2: lamellate
    - 3: none
    - 4: lamellate 2

12. rhincol
    - 0: cream 54
    - 1: scarlet 14
    - 2: blackish 82
    - 3: chrome orange 16
    - 4: grayish olive 43
    - 5: magenta 2
    - 6: spectrum red 11
    - 7: white
    - 8: spectrum orange 17
    - 9: sky blue 66

13. manmor1
    - 0: wavy
    - 1: straight
    - 2: none

14. manmor2
    - 0: flat
    - 1: raised
    - 2: none

15. man.color
    - 0: cream 54
    - 1: cyanine blue 74
    - 2: blackish 82
    - 3: chrome orange 16
    - 4: grayish olive 43
    - 5: magenta 2
    - 6: spectrum violet 72
    - 7: spectrum orange 17
    - 8: white

16. gills
    - 0: exposed
    - 1: side
    - 2: middle flaps
    - 3: hidden

17. gillmor1
    - 0: rimmed
    - 1: not rimmed
    - 2: none

18. gillmor2
    - 0: open middle
    - 1: rings
    - 2: none

19. gillmor3
    - 0: cryptobranch
    - 1: phanerobranch
    - 2: none

20. gillmor4
    - 0: moving
    - 1: still
    - 2: none

21. gillmor5
    - 0: branched plume
    - 1: flat
    - 2: tube
    - 3: none
    - 4: radial plume

22. gillcol
    - 0: cream 54
    - 1: scarlet 14
    - 2: blackish 82
    - 3: chrome orange 16
    - 4: grayish olive 43
    - 5: cyanine blue 74
    - 6: spectrum red 11
    - 7: spectrum orange 17
    - 8: white
    - 9: sky blue 66

23. egmor
    - 0: ribbon
    - 1: tube
    - 2: strings

24. egcol
    - 0: flame scarlet 15
    - 1: white
    - 2: orange yellow 18
    - 3: geranium pink 13
    - 4: raw umber 23
    - 5: scarlet 14

25. shell
    - 0: yes
    - 1: no

26. group size/2m
    - 0: one
    - 1: more

27. visual
    - 0: cryptic
    - 1: conspicuous

28. palatability
    - 0: Distasteful
    - 1: palatable
    - 2: palatable + cryptic

APPENDIX II. SPECIES LIST

1. Gymnodoris   ceylonica
2. Glossidoris   hikueremsis
3. Risbecia   imperialis
4. Chromodoris   quadricolor
5. Chromodoris   sp.2
6. Chromodoris   aspersa
7. Nudibranch   7
8. Noumea   sp.1
9. Hypselodoris   sp.1
10. Dendrodoris   sp.1
11. Berthellina   citrina
12. Stylochelius   longicadus
13. Noumea   sp.2
14. Hypselodoris   maculosa
15. Thuridilla   livida
16. Elysia   sp.1
17. Colpodspis   thompsoni
18. Hexabranchus   sanguineus
19. Risbecia   tryoni
20. Dolabella   auricularia
21. Dolabrifera   dolabrifera

APPENDIX III. CHARACTER MATRIX

Nudibranchs 1		1	2	3	4	5	6	7	8	9	10	11	12	13	14
		size	gen.color	dots	dot col	stripes	stripecolor	flashcolor	foot color	rhinop	rhinop2	rhinmor	rhincol	manmor1	manmor2
1	Gymnodoris ceylonica	1	0	0	0	1	4	1	0	0	0	0	3	1	0
2	Glossodoris hikueremsis	3	8	0	3	1	4	1	1	0	0	2	9	0	1
3	Risbecia imperialis	2	7	0	1	1	4	1	0	0	0	2	2	0	1
4	Chromodoris quadricolor	1	1	1	6	0	0	1	1	0	0	0	1	1	1
5	Chromodoris sp.2	0	7	1	6	1	4	1	0	0	0	4	1	1	1
6	Chromodoris aspersa	1	7	0	2	1	4	1	0	0	0	2	8	1	1
7	Nudibranch 7	0	7	1	6	0	4	1	0	0	0	4	7	0	1
8	Noumea sp.1	0	7	1	6	1	4	1	0	0	0	2	7	1	0
9	Hypselodoris sp.1	1	1	0	3	0	0	1	1	0	0	0	1	1	1
10	Dendrodoris sp.1	1	2	1	6	1	4	1	0	0	0	2	2	0	1
11	Berthellina citrina	2	3	1	6	1	4	1	0	0	2	0	3	1	1
12	Stylocheilus longicadus	1	4	0	6	1	1	1	0	0	1	1	4	2	2
13	Noumea sp 2	0	5	1	6	0	2	1	1	0	0	0	1	1	1
14	Hypselodoris maculosa	1	0	0	2	0	2	1	1	0	0	4	1	1	1
15	Thuridilla livida	1	2	1	6	0	3	1	0	0	0	1	2	2	2
16	Elysia sp.1	1	0	0	4	1	1	1	0	0	0	1	0	2	2
17	Colpodspis thompsoni	0	2	0	5	1	2	1	0	0	0	1	0	2	2
18	Hexabranchus sanguineus	4	6	1	6	1	4	0	0	1	3	3	2	2	2
19	Risbecia tryoni	1	7	0	2	1	4	1	0	0	0	4	2	0	0
20	Dolabella auricularia	4	4	1	6	1	4	1	0	0	0	1	5	-1	0
21	Dolabrifera dolabrifera	1	4	1	6	1	4	1	0	0	1	1	4	2	2

Nudibranchs 2		15	16	17	18	19	20	21	22	23	24	25	26	27	28
		man.color	gills	gillmor1	gillmor2	gillmor3	gillmor4	gillmor5	gillcol	egmor	egcol	shell	group size/?	visual	pal.
1	Gymnodoris ceylonica	3	0	0	0	1	1	4	6	1	0	1	1	1	0
2	Glossodoris hikueremsis	1	0	0	1	0	0	2	9	0	1	1	1	1	0
3	Risbecia imperialis	2	0	0	1	0	0	2	2	0	3	1	1	1	0
4	Chromodoris quadricolor	8	0	1	0	0	1	4	1	?	?	1	1	1	0
5	Chromodoris sp.2	5	0	0	0	0	0	4	1	1	5	1	0	1	0
6	Chromodoris aspersa	7	0	1	0	0	1	4	7	?	?	1	0	1	0
7	Nudibranch 7	6	0	1	0	0	1	4	8	?	?	1	0	1	0
8	Noumea sp.1	7	0	0	0	0	1	2	8	1	1	1	0	1	0
9	Hypselodoris sp.1	8	0	1	0	0	1	4	1	?	?	1	0	1	0
10	Dendrodoris sp.1	2	0	1	1	1	0	0	2	0	2	1	0	0	1
11	Berthellina citrina	3	1	2	2	2	1	3	3	?	?	1	1	0	1
12	Stylocheilus longicadus	4	2	2	2	2	2	3	4	?	?	1	0	0	1
13	Noumea sp 2	8	0	1	0	0	1	1	1	?	?	1	1	0	1
14	Hypselodoris maculosa	7	0	0	0	0	1	4	7	?	?	1	1	0	1
15	Thuridilla livida	2	2	2	2	2	2	3	5	0	5	1	0	1	0
16	Elysia sp.1	0	2	2	2	2	2	3	0	?	?	1	0	0	1
17	Colpodspis thompsoni	2	3	2	2	2	2	3	0	?	?	0	1	1	1
18	Hexabranchus sanguineus	8	0	1	0	0	1	0	6	0	3	1	0	0	0
19	Risbecia tryoni	6	0	0	0	0	0	4	6	?	?	1	1	1	0
20	Dolabella auricularia	4	2	2	2	2	2	3	4	2	4	1	0	0	1
21	Dolabrifera dolabrifera	4	2	2	2	2	2	3	4	?	?	1	0	0	1

Relationships between size and dominance order in the freshwater shrimp *Macrobrachium lar* (Fabricius)

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ABSTRACT. The behavior of the freshwater shrimp *Macrobrachium lar* was examined in the laboratory to find how great a role size plays in determining dominance order. Aggressive behavior defining dominance and submission made up a sizable portion, 27.98%, of all observed activites. A dominance order was definitely found to exist in a group sharing a tank, and was closely correlated (r = 0.866) to body length over a wide size range. A correlation was also found (r = 0.892 and r = 0.646) for dominance order determined by tournament-style individual matches over narrower size ranges. A difference in the slopes for the regression lines of the two size classes was highly significant. Size may not play as great a role in determining dominance in smaller *M. lar* as it does in larger specimens.

Introduction

Aggression is one of the most basic behavioral categories in animals and is present in both vertebrates and invertebrates. Among the many behaviors influenced by aggression are competition, territoriality, and feeding. Aggression has been well documented in the crustacean world (Dingle and Caldwell, 1969; Hazlett and Estabrook, 1974; Caldwell, 1975). Because aggressive action to the point of intraspecific physical combat is much more rare (Dingle and Caldwell, 1969), it is interesting to study when it is found.

A dominance order is the result of the addition of a social system to aggression and can thus be viewed as more advanced. It exists when, in a series of encounters between two individuals, one consistently takes the dominant role and the other is consistently submissive. Dominance order has been shown to be important in arthropods such as wasps (Pardi, 1948), crickets (Loher, personal communication), and crayfish (Bovbjerg, 1953). There have been some studies on factors (including size) influencing dominance order in crustaceans (Bovbjerg, 1956; Caldwell and Dingle, 1979), but none in freshwater shrimp.

This study examines the effect of size, as measured by body length, on the dominance order of *Macrobrachium lar* (Fabricius).

Materials and Methods

Species

Macrobrachium lar is a member of the same order, Decapoda, as lobsters and crayfish, and the same genus as *M. rosenbergi*, a shrimp grown for food worldwide in aquaculture. *M. lar* itself is regularly caught and consumed in the area where this study was conducted.

M. lar, like many other freshwater island species, has a diadromous life cycle: both saltwater and freshwater are required for development (Resh *et al.*, 1990). Eggs are washed out to the ocean where larval development is completed, and the maturing shrimp move into the streams for the adult phase. There is a trend to find a larger average size further upstream, but it is certainly not unusual to find mature adults close to the mouth. Communities at all locations examined were composed of varying sizes (personal observation).

Like all arthropods, *M. lar* must molt when it outgrows its exoskeleton. During the few days following a molt, the shrimp is particularly vulnerable to predation, including cannibalism. A refuge is required during such times and this could be a reason for the territoriality found in the species.

Collection

All shrimp were collected from stream sites in the Opunohu River

catchment, Moorea, French Polynesia (17°31′ S, 149°50′W):

Belvedere -- a small stream over boulders, reached by a trail behind and to the left of a concession stand at this well-known lookout point.

Marae -- a small stream over boulders and cobbles behind this anthropological site on the road to Belvedere.

Opunohu -- a large stream over cobbles, at the first and second bridges on the road from Opunohu Bay to Belvedere.

The Opunohu Valley is essentially a nature preserve (poaching is prohibited) and thus the streams, with the exception of a few bridges for roads, are relatively undisturbed.

Specimens were collected either by the traditional Polynesian method of scooping and draining with a pareo (large piece of cotton cloth) or by aggressively scooping and shaking of a 30 cm D-ring net under plants lining the stream's edge at lower elevations. The shrimp were then transported back to the laboratory in plastic bags. The facility used was the Gordon and Betty Moore Outdoor Laboratory at the Richard B. Gump Biological Station, University of California, Berkeley, on Moorea. Final length measurements and sexing for the animals used in the third phase (preserved in 70% ethanol) were done under a 9x dissection microscope at the University of California, Berkeley.

Experimental Design

General Behavior Observations

For the first phase of this study, approximately ten shrimp of sizes ranging from 2.5 cm to 6 cm were kept together in a glass tank, 49 cm x 24 cm. The tank was equipped with running water and a drain, keeping the depth at about 12 cm. Several stream cobblestones were in the bottom of the tank, providing limited refuges/territories.

For each observation period a focal individual was randomly selected (Altmann, 1973). Coordinates within the tank were chosen before each period from a table of random numbers; the shrimp closest to that point at the set starting time was the subject for the half-hour period. All of the subject's activities and interactions were recorded.

There were four broad categories of behavior for analysis purposes: aggression (grasping, striking, threatening, and avoidance -- these are further explained below), general locomotion around the tank, stationary action (including waving antennae, cleaning a claw, arching the tail, etc.), and other (including eating and simply standing still).

The observation periods took place at different times over the course of five days, including two at night.

Dominance Observation

The study's second phase took place in the same tank, described above, and involved fourteen shrimp. Each shrimp was labeled with a waterproof lab marker on the back of its carapace. By the method described above, a focal individual was chosen for a ten-minute observation period; ten minute rest intervals were taken between periods in order to maintain the level of vigilance required by the observer.

During each observation period, all aggressive interactions involving the focal individual were recorded by noting the label of the other shrimp, and what behaviors were seen in both animals. Four readily distinguishable categories of aggressive behavior were used (after Bovbjerg, 1953):

(1) Grasp -- One shrimp seizes another with its chelae (claw arms), and proceeds to hold it, "patting down" the other shrimp's body and legs, a motion similar to that of a police officer frisking a suspect. The other shrimp may struggle at first, but is motionless and submissive for the most part. This behavior seems to be a show and acknowledgment of dominance.

(2) Strike -- A shrimp hits another with its chela; usually backhand.

(3) Threat -- A shrimp approaches with chelae outspread in strike position. Threat and strike are both generally

followed by rapid retreat of the submissive shrimp.

(4) Avoidance -- While not in itself aggressive, this category indicates one shrimp prophylactically retreating from a more dominant shrimp coming near; or a less dominant shrimp going obviously out of its way to give wide berth to a more dominant one.

At the conclusion of this phase, the body length of each shrimp was measured from telson (tail segment) to end of eyestalk.

Dominance Matches
The final phase of the study was a tournament, set up in a "round robin" fashion with two size classes. The group of larger shrimp contained eight individuals and the smaller group was composed of six. Each shrimp met every other shrimp in its class exactly once, and each had not more than two matches per day with at least two and one-half hours between matches, usually more.

The matches for the larger group took place in a plastic tank, approximately 35 cm x 20 cm, with water depth about 8 cm; the smaller group's matches were held in a round plastic tank with an approximate diameter of 12 cm. The tanks were thoroughly rinsed and refilled after each match to eliminate, or at least dilute, lingering chemical signals that might influence the next pair. The tanks were bare of rocks and debris, and the partition was placed creating two symmetric areas. Thus when the partition was removed, a neutral arena was created. The shrimp were kept in individual labeled containers between matches; the water was changed twice each day.

A standard time schedule was used for the matches. One shrimp was placed on either side of a partition through the middle of a tank and allowed five minutes to acclimate. The partition was then removed. The shrimp were watched for ten minutes and the dominance outcome recorded. This determination was made by observing which shrimp took the dominant role in aggressive encounters significantly

more often, with greater weight on encounters toward the end of the time period. Occasionally, after this period, a more dominant shrimp could not yet be determined, i.e. dominance role fluctuating, or simply a lack of interaction; in such cases the observation was continued until an outcome was more definite.

Body lengths were measured from rostrum to telson.

Results

General Behavior Observations
During the course of six half-hour periods, a total of 218 activities and behaviors were recorded. Of these, 61 were part of aggressive encounters involving the subject shrimp. This makes up 28% of the total activities and behaviors recorded, with a median of 24%. The average rate was 20.3 aggressive behaviors per hour (Figure 1).
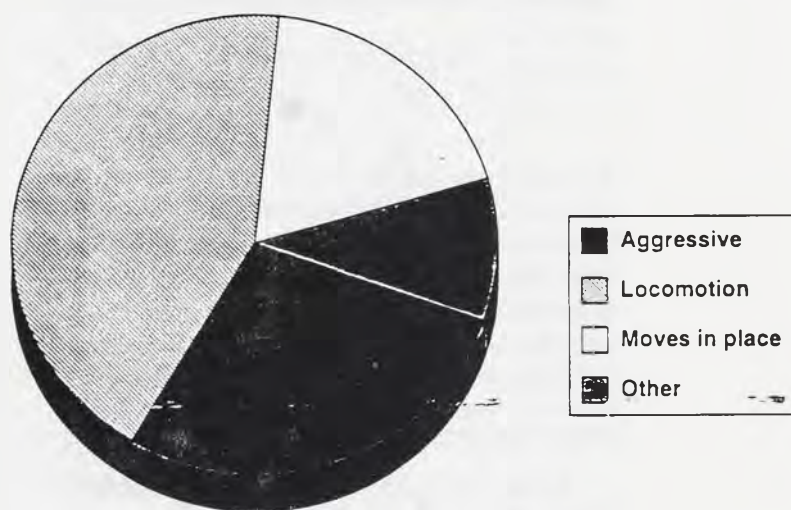
Figure 1. Activities observed

Dominance Observation
In each of the four behaviors -- grasp, strike, threat, and avoid -- clearly one shrimp is dominant and the other is submissive. Each shrimp's dominant role activities and submissive role activities were summarized in Table 1; these were summed at the end of each row and column to provide for each shrimp the total number of actions in which it was dominant and the total in which it was submissive. These

Table 1. Dominant and Submissive activities

	P	M	F	K	N	H	L	A	D	W	J	B	G	C	Total	% Dom
P		1	4	6	0	0	2	2	0	3	2	1	2	3	26	100.00%
M	0		0	0	4	3	1	1	3	6	1	10	6	1	36	92.31%
F	0	2		6	3	1	1	0	1	0	1	4	2	1	22	84.62%
K	0	0	0		0	6	4	9	3	7	14	7	9	7	66	79.52%
N	0	0	0	2		0	2	0	2	3	6	3	2	0	20	74.07%
H	0	0	0	0	0		2	0	2	0	4	5	0	0	13	56.52%
L	0	0	0	2	0	0		4	0	1	2	4	0	1	14	46.67%
A	0	0	0	0	0	0	1		1	0	1	0	4	1	8	28.57%
D	0	0	0	0	0	0	0	1		0	1	0	3	0	5	27.78%
W	0	0	0	0	0	0	0	0	1		3	0	2	0	6	21.43%
J	0	0	0	1	0	0	2	1	0	1		2	0	0	7	16.67%
B	0	0	0	0	0	0	1	2	0	1	0		2	0	6	13.95%
G	0	0	0	0	0	0	0	0	0	0	0	1		0	1	3.03%
C	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0.00%
Total	0	3	4	17	7	10	16	20	13	22	35	37	32	14		

raw numbers could not be compared because, due to the random nature of the focal individual selection, there was more data on some shrimp than on others. Percent dominance was then calculated for each shrimp by the following method:

$$\frac{\text{\# of dominant roles}}{\text{\# dominant + \# submissive}} \times 100$$

The individual body lengths ranged from 2.4 cm to 4.3 cm. Four of the smaller shrimp molted before the length measurements were taken, and thus lost their labels; an average of the four lengths was used for each of these shrimp. The lengths and percents dominance are listed in Table 2.

Table 2. Lengths & Percent Dominance

Shrimp	Body Length	% Dom.
P	4.1	100
M	4.3	92.31
F	3.7	84.62
K	3.1	79.52
N	3	74.07
H	3.2	58.33
L	3	46.67
A	2.4	28.57
D	2.58	27.78
W	2.58	21.43
J	2.9	16.67
B	2.6	13.95
G	2.58	2.94
C	2.58	0
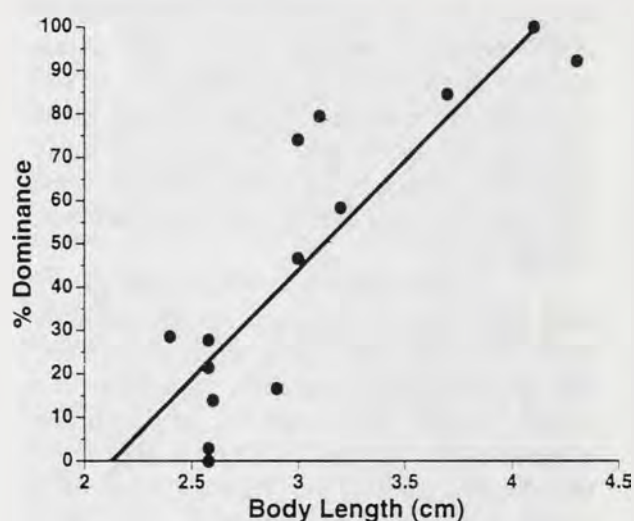
Figure 2. Aggressive Observation

A correlation was found between body length and percent dominance (r = 0.866). A regression line was also drawn (Figure 2).

Dominance Matches
The win-loss records were compiled for each shrimp, and they were ranked from least dominant to most dominant within the two size groups. When two shrimp had an equal number of wins and losses, their relative ranks were determined by the outcome of the match in which they met.
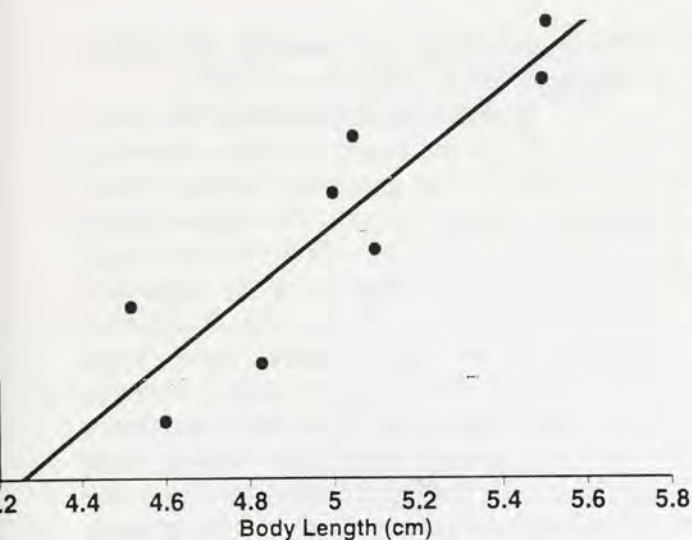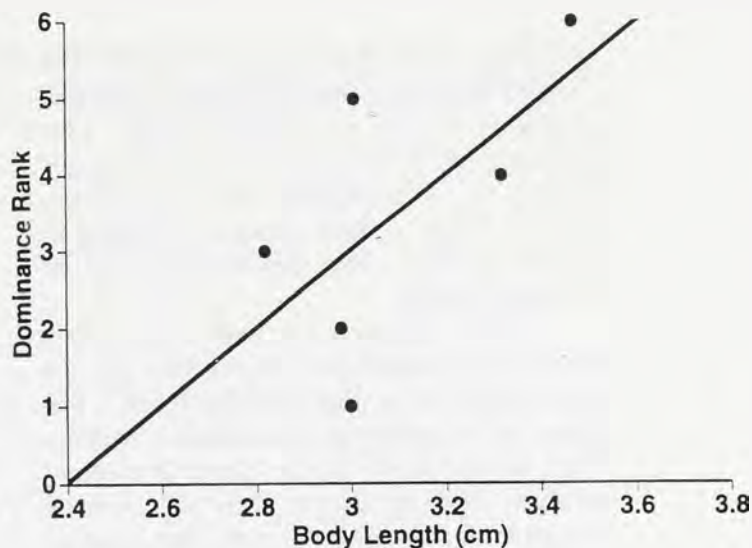
Figure 3. Large Shrimp

Figure 4. Small Shrimp

The dominance ranks were then compared with the body lengths for each shrimp, and correlations were found (larger shrimp r = 0.892, smaller shrimp r = 0.646). The regression lines are shown in Figures 3 and 4. The slopes of the two regression lines were found to be m = 5.960 for the larger group and m = 4.963 for the smaller group. These slopes were compared by a t-test (t = 3.0837, d.f. = 10, p < 0.01).

The results of the sexing showed all shrimp in this phase of the study to be female. Six of the animals in the larger group were ovigerous at some time during the tournament, as indicated in Table 2.

Discussion

General Behavior Observations

The results from this initial phase of the study show that aggressive behavior makes up a significant portion of observable activities in these shrimp each day (27.98%). The median of percentage of total activities was close to the mean -- showing that this level of aggressive behavior under these conditions is accurate for many of the shrimp observed, not merely for an exceptionally aggressive one.

This high prevalence of aggressive interactions (in which one shrimp is in a dominant role and the other is submissive) makes it worthwhile as a subject for study. In the natural stream environment, these shrimp are not contained with each other, and do not occur in such high densities with so few refuges. Such a high frequency of interactions may, then, be an artifact of the laboratory conditions. In any case, aggressive interactions do happen in the wild at some frequency and their outcomes are likely to be similar to those shown in a lab setting.

Dominance Observation

The lower left diagonal half of Table 1 is mainly zeros -- the dominance order was fairly consistent all of the way down the chain, with each shrimp assuming predictable roles (either dominant or submissive) in nearly every encounter. There is no question that a dominance order existed.

The correlation between body length and percent dominance is fairly strong; the correlation coefficient would probably be even closer to 1 if the four shrimp that molted had still been identifiable. This correlation shows that, over a wide size range, dominance order can be predicted rather well by comparing relative body lengths.

Dominance Matches

As seen in Figures 3 and 4, body length and dominance order were once again correlated, this time within narrower length ranges. Size affects dominance on a

finer scale, as well as on a gross level. The correlation in the smaller shrimp is not as strong as it is for the larger shrimp. This could simply be the result of a small sample size (n = 6), or it could mean that size truly doesn't relate to dominance as strongly in smaller shrimp. This possibility is further discussed below.

The difference between the slopes for the regression lines of the two groups was found to be highly significant. The slope is less steep for the smaller shrimp. This means that, for the same increment increase in body length, there is less of an increase in dominance for the smaller shrimp than there is for the larger. It may indicate that body size does not control dominance as tightly in the smaller *M. lar* as it does in the larger members of the species. This difference in slopes, along with the weaker correlation, could indicate that other factors play a greater role in determining dominance order for the smaller *M. lar*. Other factors not analyzed include claw arm length (not always related to body length, especially since some individuals lost one or both of these limbs before this phase), time from last molt, and the location from which they were collected (shrimp from further upstream could be more or less dominant), among others.

The two shrimp holding the ranks of 2 and 4 in the larger size class were the only two in that group not to have been gravid (carrying eggs) at some time during the study (Table 2). Both these shrimp have points appearing below the regression line in Figure 3 -- both held dominance ranks lower than would have been predicted by their body size. Perhaps gravid shrimp tend to be more dominant than non-gravid females to protect their offspring, or perhaps females that are more dominant are more likely to be gravid. Either way, this phenomenon certainly deserves further study.

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Emergence, Transit, and Foraging Behavior in Two Species of Pacific Island Gecko (*Lepidodactylus lugubris* and *Gehyra oceanica*)

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ABSTRACT. - The nocturnal activity cycles and foraging behavior of two species of Pacific island geckos, *Lepidodactylus lugubris* and *Gehyra oceanica* were documented in the field. The geckos were found to have a bimodal activity pattern. The time of emergence coincides with decreasing light intensity. The number of lizards using a clothes line to move between a diurnal retreat site and nocturnal foraging grounds was estimated to be 154.4 When offered a more direct route into the tree, over 90% chose the new route after only 8 days of observation. The line was removed for 2 days and *L. lugubris* found an alternative route into the tree. Various aspects of the general ecology of these species is also discussed including, diet, interspecific interactions, and predation.

Introduction

Although research has been done on various aspects of gekkonid biology, observations on nocturnal geckos during their natural period of activity are difficult to make and studies have been limited (Marcellini, 1977; Pianka and Pianka, 1976, Pianka and Huey, 1978). In contrast to most nocturnal species which are often secretive, Pacific island geckos offer an unusual opportunity to study activity cycles and foraging behavior. *Lepidodactylus*, for example, is considered a strongly homophilic species similar to the house mouse, roof rat and other human commensals (Sabath, 1981).

These gregarious lizards, began their trans-Pacific trek thousands of years ago, stowed away on Polynesian canoes (Petren and Case, 1994). Some of the earliest hitch-hikers were parthenogenetic species, in which all individuals are females capable of laying viable eggs without male fertilization. Increased shipping in the Pacific since World War II has dramatically augmented this colonization process.

Geckos are thriving in terrestrial ecosystems that are extensively modified. The establishment of buildings has provided new foraging surfaces as well as retreats for arboreal gekkonid species (Sabath, 1981). With the advent of electric lights, which attract and concentrate insects, the benefits of living near people have become even more pronounced.

This study presents field observations about how two species of Pacific island gecko (*Lepidodactylus lugubris and Gehyra oceanica*) travels through their environment and how this travel is influenced by light and dark cycles, temperature, habitat structure, and interspecific interactions. The activity patterns of these two species were monitored starting with emergence, transit to foraging grounds, and concluding with the return to diurnal retreat sites.

Methods

Study Site and Species

Fieldwork was conducted on the island of Moorea, French Polynesia, approximately 2 km NW of Pao Pao, near the mouth of Cook's Bay. All ecological data were collected on the property of the University of California Berkeley Gump Biological Station between 13 October and 17 November 1994.

The primary study site is located within a 120 m2 plot bordered on the east by the Station dormitory and on the west by Cook's Bay (Figure 1) The southwest wall of the dormitory has three large windows
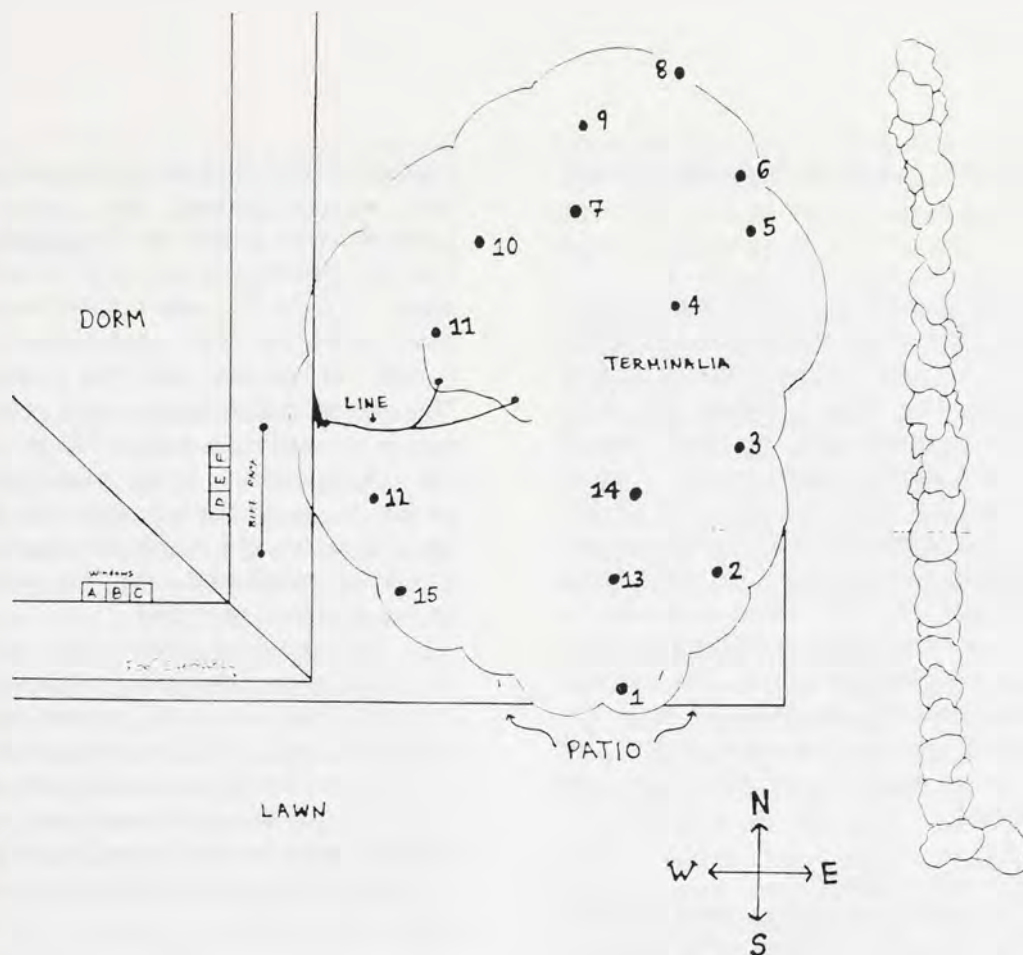
Figure 1. Map of Study Site, including sites 1-15 in tree

partially sheltered by the overhanging (slanted), shingled roof. A clothes line originating
from a descending arm of the roof, extends 2 meters to the west where it is attached to a branch of a mature *Terminalia* tree. The tree, which stands approximately 16 m high, extends over and shades the entire study site. The findings from this primary site were later compared with similar observations made at two other sites, also on the property of the Gump Biological Station.

Two species of Pacific island gecko, *Lepidodactylus lugubris* and *Gehyra oceanica*, occur syntopically within the study site. The occurrence of *L. lugubris* greatly outnumbers *G. oceanica*. Adult *L. lugubris* have an average snout vent length of 34-44 mm and hatchlings are approximately 15 mm from snout to vent (Zug, 1991). *L. lugubris* is a parthenogenetic species, although variations in reproductive strategies, such as bisexual groups and hybrids between the unisexual clones and bisexual groups have been documented within French Polynesia (Ineich, 1988 in Zug, 1991). *Gehyra oceanica*, in contrast, is a much larger, sexual species; adult average snout-to-vent length 59-84 mm and hatchlings 33-34 mm SVL (Zug, 1991).

The nocturnal activity and behavior of both, *Lepidodactylus lugubris* and *Gehyra oceanica*, was monitored from 1700 h to 2200 h and from 0300 h to 0500 h. Individuals were observed gradually emerging from diurnal retreat sights in the rafters of the overhang and shingles of the dormitory roof, moving as a group across the clothes line, and then feeding in the *Terminalia* tree.

Emergence

A 12 m transect was set up along the roof of the dormitory to evaluate the location and density of retreat sites, as well as to determine if individuals return to the same sites on consecutive nights During a two week period, the time and place of emergence from diurnal retreat sites was

recorded every 15 minutes between 1700 and 1800 hours.

Transit

Data on the movement of geckos across the clothesline were collected while sitting in a chair approximately 4 feet away from the line. When the first individual stepped onto the line, I noted the time and started a stop watch. During two minute intervals, for the next 90-100 minutes, the number of individuals passing a single point was recorded. A head lamp or a flashlight was used when necessary to illuminate a small portion of the line after it became too dark to count. Two weeks were spent making observations on a the undisturbed transport system before any lizards were marked or the line was manipulated.

Mark-Recapture Phase

On eight consecutive days between 24 October and 31 October 1994, both *L. lugubris* and *G. oceanica* were marked in order to estimate the number of individuals using the line to access arboreal feeding sites. Initially, every gecko crossing the line was caught by hand, gently marked with a stripe of white-out on its dorsal surface, and then released onto the trunk of the tree. Each following night, the number of previously marked specimens was recorded, as well as the number of newly marked individuals. This mark-recapture experiment was only conducted for eight days due of the stress inflicted by repeated disturbance. To calculate the population estimates, the following mark-recapture ratio was used:

$$N = \frac{M(n+1)}{(R+1)}$$

where N is the total number of individuals in the population, M is the sample of marked individuals, n is the second sample size of recaptures, and R is the number of recaptured individuals with markings.

Line Manipulations

In order to test the hypothesis that arboreal foragers, such as *L. lugubris* and *G. oceanica*, choose the most direct route from diurnal retreat site to nocturnal foraging site, an additional and more direct pathway was added to the existing line. The first attempt at creating an additional segment of the line was revised because the new pathway was significantly more bowed in contrast with the existing line. The second night the line was restrung so that it more closely resembled the original line. As a result, for the next 8 days, the geckos were presented with two lines of equal tension and disparate length. Each line was monitored and the number of geckos in transit recorded

In the final week of data collection the line was completely taken down. Alternate pathways and general responses were recorded. The line was left down for two consecutive days and then the original line, without the additional pathway, was restrung, and the number of lizards crossing was again counted during two minute intervals.

Foraging Behavior

Three windows on the west wall of the dormitory and three other windows on the south wall were used by the geckos as feeding sites. Individuals caught while foraging on the windows were marked with a distinct pattern using white-out or nail polish. Each marked individual was then assigned a number. Throughout the entire study, these windows were monitored and the spatial orientation of each numbered individual documented. Information about prey items was also noted when possible.

In order to analyze where the geckos forage in the *Terminalia* tree, fifteen sites were established. The sites were chosen based on accessibility, unfortunately the tree was to tall to thoroughly examine. Nine sites were located at the terminal ends of branches and the other six sites located in the interior of the tree. All sites were checked for presence or absence of *L. lugubris* and *G. oceanica*, between 22 October and 16 November. Active lizards were spotted using cues such as eye shine, body shine, and movement.

Ambient light intensity measurements were recorded by an Owl Weather Monitor System at the Station. Readings were available every 15 seconds on the computer

screen and hourly readings were printed out. Ambient temperatures (C) and wind speeds (kph) were also recorded by the weather station.

Results

Emergence

At approximately 1700 h, both *L. lugubris* and *G. oceanica* emerge from diurnal retreat sites in the shingles of the roof and rafters of the overhang. Initially, only the snout and head are visible; then over the course of approximately one hour, the whole body is exposed. At this point, lizards preparing to cross the line to feed, gradually move toward the descending arm of the overhang and wait until ready to cross. Throughout this emergence phase, multiple chirps were heard.

It is important to note that during the period of emergence the average ambient light intensity drops from 202.38 W/m2 to 0 W/m2; the steepest decline occurring between 1700 h and 1710 h (Figure 2). The average light intensity remains relatively

Figure 2. Light intensity over time
0 min = 1700 hr

constant between 1710 h and 1800 h, but then quickly drops down to 0 W/m2 at about 1810 h. Transit begins after the ambient light intensity drops to 0 W/m2.

A single *G. oceanica* and one *L. lugubris* were observed utilizing the space between the wall and the air conditioner as a diurnal retreat site. Based on distinct white-out markings and tail damage, these same individuals were recognized emerging from the same retreat sites each day. Whether other geckos inhabiting the shingles or rafters repeatedly emerged from the same site could not be determined.

Description of Movement

During exit and return, the flow across the line is unidirectional. While exiting, individuals approach the line with trepidation causing a back-up of geckos waiting to cross the line. After the first gecko ventures onto the line, small groups surge across, interspersed with periods of inactivity . During peak flow, when as many as 12 to 15 *L. lugubris* are on the line at once, they run over the backs of other individuals, run across hanging clothes, and use the underside to the line to facilitate faster transport.

The movement of *L. lugubris* consists of a series of discontinuous sprints, in contrast to *G. oceanica*, who remains in non-stop motion while on the line. *L. lugubris* moves at an average speed of .043 m/s, where as *G. oceanica* moves faster at approximately .10 m/s.

Starting Times

When the first gecko began to cross the line, either in the morning or the evening, the 'starting time' was recorded. A range of these times, means, and standard deviations are presented in Table 1.

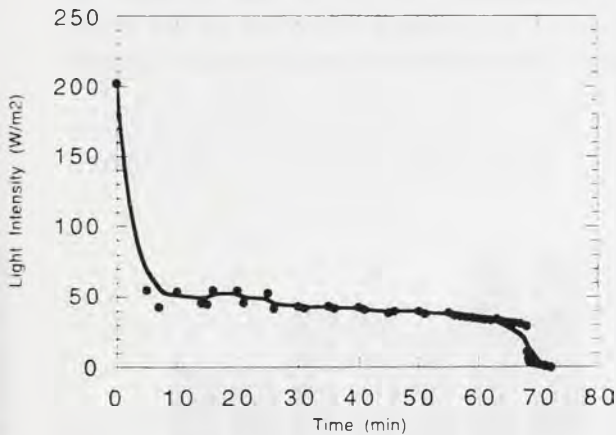**Table 1.** Starting Times

	Earliest Starting Time (hours)	Latest Starting Time (hours)	Mean Starting Time (hours)	Standard Deviation
EXIT	1753	1823	1811.5	7.34
RETURN	0359	0454	425.11	22.93

Table 2. Mark and Recapture Data

Total # Marked	R	n-R	N	# in Transit
*	75.0	29.0	*	104.0
104.0	77.0	12.0	120.0	89.0
116.0	102.0	10.0	127.3	112.0
126.0	102.0	13.0	141.9	115.0
139.0	113.0	11.0	152.4	124.0
139.0	80.0	9.0	154.4	89.0

All of the exit times occurred within 30 minutes of each other, in contrast to the return times which vary by as much as 55 minutes. Another difference in the pattern of transit between the exit and return phases is illustrated by Figures 3 and 4. The mean number of individuals in transit is graphed versus time (min) illustrating the general transit or activity pattern for the species. Figure 3 shows a steep increase until a maximum of 9.2 gecko/minute is reached. The graph declines as rapidly as it ascended. After approximately the 40 minute mark, the mean number of geckos in transit gradually approaches zero between 70-100 minutes. In comparison, a graph of the mean number of geckos using the line to return to the dormitory shows a less dramatic flow of activity (Figure 4). The maximum number crossing per minute is only half as large as the exit maximum. For the next hour, the curve fluctuates between 1 and 3.9 individuals/minute.

Ambient Temperature

No correlation between the ambient temperature and the total number of geckos crossing the line was found (R = .717).

Mark-Recapture Phase

In total, 150 geckos were marked on the line. During the first two days of frantic marking, the number marked was not recorded. In order to get a rough estimate of how many lizards use the line, the assumption was made that M, the sample size of marked individuals, was approximately equal to the number of marked individuals recorded on the third day. The number of freshly marked lizards from each day was then added to M = 75 + (n- R), until approximately 150 lizards were marked. For each day of observation,
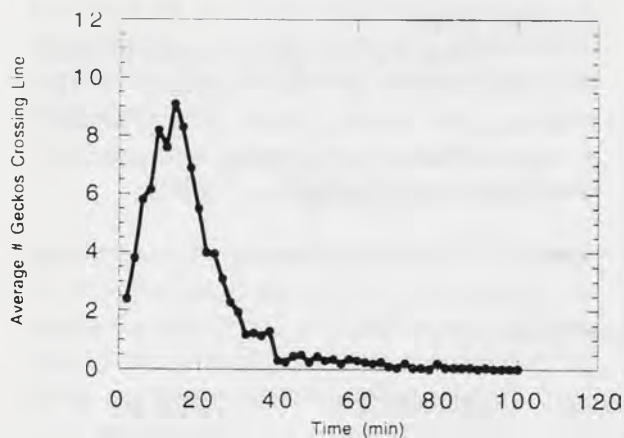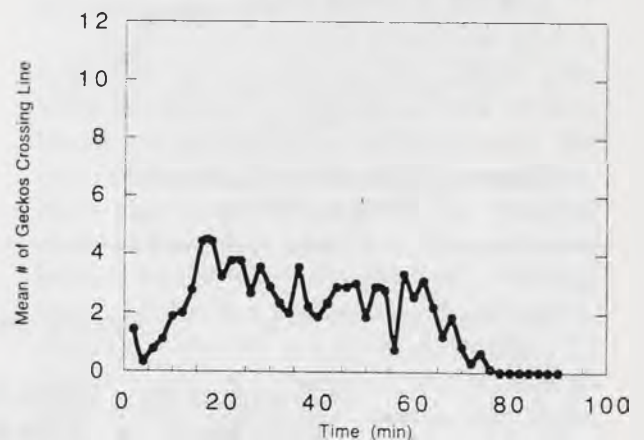

Figure 3. Departure Activity
(O min=1800h)

Figure 4. Return Activity
(O min=0400h)

Table 2 shows the total number of previously of marked lizards, the number of marked recaps R, the number of unmarked recaps (n-R), and the population estimate (N). The far right hand column is a list of the total number of geckos in transit during each observation period. Most of the transit number are within 30 lizards of the total population estimates (N). However, the final transit total differs from N by 65 individuals.

Line manipulation

An additional, more direct line was added to the existing system in order to test the hypothesis that geckos will choose the most direct arboreal pathway if given an option. The percentage choosing the more direct line during the exit phase is shown in Figure 5. On the first day, 4% chose the new path. On days 2 and 3, the percentage rose to over 60%, days 4-6 70%, culminating at over 90% on days 7 and 8. A few individuals of both species were seen initially choosing the original path, stopping, turning around, and then either backtracking towards the start of the new path, or jumping across and continuing down the new path towards the tree.

Figure 6. Microhabitat Selection

When the line was removed during the final stage of the project, the lizards emerged as usual, descended down to where the line was formerly attached, and then actively looked for somewhere to go. After about 40 minutes, over 30 geckos were still present on the descending arm. Several individuals went down another clothes line strung parallel to the house, but returned after going about .5 m. However, three geckos continued down the parallel line and jumped into a small hedge where they remained for the duration of the observation period. Geckos that were marked with a green stripe (indicating that they use the line) were seen feeding on the walls of the building and overhang.

Both nights that the line was down, individuals were observed jumping from the roof to the *Terminalia* tree. Previously several *G. oceanica* and a few *L. lugubris* were observed jumping up onto a branch overhanging the roof. During the two nights the line was down, the number of lizards attempting to jump to this branch noticeably increased. *L. lugubris* was also observed jumping off the roof attempting to land on site #11 (1.5 m across and .8 m down from the roof). This behavior had never been observed before.

Microhabitat Selection

The number of geckos found foraging at each of the 15 sites is shown in Figure 6.

Figure 5. Selection of More Direct Line

At sites 1-3, 5, 8, 10-12, and 15, all located at the ends of branches, a total of 35 lizards were found. At the remaining sites located in the interior of the tree, only one lizard was found.

The six windows on the dormitory wall, labeled A-F, serve as another primary foraging area in this system. The windows were mostly used by *L. lugubris*, but on several occasions *G. oceanica* was also seen eating insects concentrating around the light. Out of the 22 individuals caught and marked on the windows, 5 individuals reappeared on 6-9 different days, another 5 were present on 3-5 additional days, and 12 were only seen on 2 or less days.

Diet

Both *G. oceanica* and *L. lugubris* both have relatively general diets, feeding on a variety of different taxa. Although, no stomach content analysis was done in this study differences in diet were visible. *G. oceanica* were observed eating cockroaches and grasshoppers, where as *L. Lugubris* was observed eating very small beetles, ants and other tiny insects. Both species exhibited sit-and-wait predation behavior.

Interspecies Predation Incident

On the morning of 4 November a large *G. oceanica* was observed stalking *L. lugubris*. At 0424 h, a *G. oceanica* was waiting at the point where the new line attached to the tree. It crossed on the new line at 0425 h and then waited on the descending arm of the roof. At 0430 h, the same individual went back across the line towards the tree, but stopped at the fork between the new path and the old path. A *L. lugubris*, returning from the tree, saw the *G. oceanica* on the line, turned around and ran back toward the tree. After several minutes, the same *L. lugubris* came back and sprinted underneath the *G. oceanica*. At 0437 h the *G. oceanica* continued down the old path to the tree. It ran across the trunk to where the new line attached, got back on the line, and returned to the descending arm. At 0454 h, the *G. oceanica* turned around so its head was facing the point where the line attached. Meanwhile, many *L. lugubris* were

returning from the tree. At 0501 h, I heard a loud screech, shined the light on the *G. oceanica* and saw a *L. lugubris* in its jaws. The light disturbed the *G. oceanica* and it released the *L. lugubris* and retreated up to the rafters of the house. This was the only predation incident observed within the study site, although another student observed a *G. oceanica*, with only the hind legs and tail of another gecko sticking out of its mouth (Julie Person, personal communication).

Discussion

Emergence

Geckos, like most nocturnal animals, have acute vision. They have retinas composed of light sensitive rods, therefore they are capable of detecting light intensity or brightness (Marcellini, 1977). Studies on the relationship of the locomoter activity of *Coleonyx, variegatus* to changing light cycles suggest that light plays an important role in the activity pattern of nocturnal species (Evans, 1966). In contrast, emergence and activity patterns of diurnal species were shown to depend more on temperature.

Lepidodactylus lugubris and *Gehyra oceanica* were observed gradually emerging from diurnal rest sites at the same time the ambient light intensity was rapidly decreasing. At 1700 h, when the first geckos emerge, the mean light intensity is still 202. 38 W/m2. As the light intensity rapidly drops over the next hour, the number of emerging lizards steadily increases as it gets darker. This indicates that these species are sensitive to changes in light intensities, and other studies have shown that nightfall appears to be the most important determinant for the onset of activity. (Kingsbury, 1989)

During the gecko's hour long emergence phase, diurnal predators, such as Mynah birds end their activity cycle. Thus, by the time the lizards start to cross the line they have avoided this potential danger. Also, the hour of emergence enables the geckos to possibly synchronize movement to the Terminalia with conspecifics. The multiple chirp call, made by the *L. Lugubris* while emerging from the

roof, was also reported by Haake in 1969 (in Marcellini, 1977). Geckos are apparently unique among the lizards in possessing vocal cords and this allows them to produce complicated vocalizations (Gans and Maderson, 1973). Multiple chirps are given in a variety of contexts, but are most commonly heard during social interactions. It is possible that *L. lugubris* uses the multiple chirp calls to synchronize transit in this system, but this hypothesis would require a more detailed analysis of the effects of calls on conspecifics.

Activity

The activity pattern of both *L. lugubris* and *G. oceanica* is bimodal. Initially there is a burst of activity at dusk, a relatively centralized period of sit-and-wait predation, and then another peak in activity as the geckos return to diurnal retreat sites. In contrast, twelve species of nocturnal Australian geckos were found to be primarily active during the first 3 h following sunset, showing a unimodal pattern of activity (Pianka and Pianka, 1976). The researches, point out however that their data may be biased due to a heavier sampling effort earlier in the evening. It is possible that bimodal activity patterns may be necessary for geckos who maintain a diurnal retreat site at a separate location in relation to their primary foraging grounds.

Although both the exit and return are classified as periods of activity, there are distinct differences between the two phases. The exit curve ascends and descends more quickly and with less noise, whereas the return curve is more erratic and spread out. There are several possible explanations for the observed differences. Upon exit, all of the individuals haven't eaten for approximately 12 hours, so it is logical that they would all want to get to the feeding site as soon as possible. While feeding in the tree, certain individuals could reach feeding saturation before others and choose to return to the retreat sites, explaining the sporadic return pattern. When the geckos start to return in the morning it is still very dark and therefore, the asynchronous pattern in Fig. 5 could

also be due to the absence of a distinct change in light intensity.

Mark-Recapture

The results from the mark-recapture phase of this project an interesting question: What are the remaining geckos doing if only 75% went across the line that night? Geckos have extremely low metabolisms, and therefore it is possible that each individual doesn't need to feed every night. Banded geckos, for example have been found to be able to ingest enough food in four days to allow survival for 6-9 months in the laboratory without further feeding. (Bustard, 1967). The question could be addressed using radiotelemetry to track the movements of one individual over time.

Another explanation for the dissimilar totals between the number who exit and the number who return is that this system may have a small number of floating individuals. For example, an individual may find an adequate retreat site while feeding in the *Terminalia* tree one day, and choose not to return. On another day it may return choose to the dormitory. The hypothesis could be tested with more intense searches throughout the tree for lizards remaining behind during the day.

Line Manipulations

The results from the line addition and removal experiment clearly shows the behavioral flexibility of both *L. lugubris* and *G. oceanica.*. The fact that by the second night, already 60% were choosing the more direct path also indicates that a high premium is placed on finding the most direct or quickest way to get past the line, or bottleneck in the transit system. It is logical that geckos would want to reduce the amount of time spend in this highly visible, and therefore vulnerable position. The ability to adjust or develop new behaviors, observed when the transit system was altered, is one of the reasons that many gecko species thrive in urban environments throughout the Pacific.

Temperature

Although I didn't find a correlation between ambient temperature and the

number of active lizards it has been suggested that temperatures may strongly influence the behavior of nocturnal species (Kingsbury, 1989). It is possible that a correlation does exist but the trend wasn't evident in one months worth of data. Because the difference between the maximum and minimum temperature in the tropics is generally is so small the activity pattern and feeding behavior of these species are not limited by the ambient temperature.

Site Comparisons

In order to determine if the activity pattern observed at the primary field site was occurring elsewhere, two other sheds on the property were searched for the presence of geckos. *G. oceanica* and *L. lugubris* were both inhabiting the shingled roof of the first shed, located at the entrance of the dormitory driveway. At this site individuals were observed emerging from their retreat sites, moving down to the east corner of the shed, and then jumping .05 m onto the trunk of a large tree.

The second shed, which is less disturbed by human activity, is located across the road from the station, near the garden. The sides of the shed are covered with decayed thatching, used by *G. oceanica.* as diurnal retreat sites. *L. lugubris* was never observed there. This relationship between species composition and habitat type observed at the second shed parallels previous work, which states that *G. oceanica* becomes the dominant species with *L. lugubris* occurring more sporadically as habitats become more rural (Zug, 1991).

A long thick vine originating in the canopy of the surrounding trees, drapes down across the roof of the second shed. In order to test the hypothesis that the vine functions in the same fashion as the clothes line, data were collected during the emergence and transit phase of the *G. oceanica* activity cycle. In only 24 minutes of observation, 99 geckos were counted exiting the shed and running up the vine confirming my hypothesis. Surprisingly, at the same time the vine transit was occurring, 61 *G. oceanica* were observed jumping .37m onto the trunk of the nearest

tree. Because one group was constantly jumping, while another was running up the vine, an average of 6.67 *G. oceanica* /min were able to access the tree. It is clear that in a system with two viable modes of arboreal transit, the flow rate is higher and the activity peak is even more dramatic than seen at the primary site. The similar activity cycles and habitat use encountered at all three sites suggests that in order for either of these species to successfully occupy a building or shed, there must be a means of arboreal transit to a nearby foraging ground.

Foraging Behavior

Observations and experiments on foraging behavior detected differences in microhabitat selection. A total of 35 *L. lugubris* were seen actively feeding at the tips of a branches, whereas only one individual was recorded feeding in the interior canopy of the tree. This strong trend towards selection of microhabitats which are partially exposed, could be caused by the concentrations and distributions of insects, but more studies would need to be done to test this conclusion. It is important to note that all the sites monitored during this study were located in a thin layer of the low canopy and results may be biased.

Once a lizard was caught, marked, and released at one of the 15 sites, its presence or absence on that branch was monitored for the next several hours. In majority of the observation periods, the same individual would be present on the branch for 3-4 hours. This indicates that *L. lugubris* doesn't move nearly as far as other active foragers (Huey and Pianka, 1981). To confirm these observations, more sites in the upper part of the canopy would need to be established and individuals would need to be radio tracked.

Marked individuals were also monitored from day to day. Individual #6, for example was found at site 1 on six different days over a period of two weeks. This datum as well as other examples, suggests that *L. lugubris* regularly feeds in small general areas for at least 2 weeks and possibly longer. The small feeding ranges found in the tree, closely relate to other

observations made at the lab windows. Several individuals were seen feeding on the window panes as many as 10 consecutive nights. Other research has found that *L. lugubris* seems to establish dominance hierarchies, whereby larger individuals occupy the better feeding sites and smaller geckos the periphery (Zug, 1991). In the future it would be interesting to compare the mass, snout-to-vent length, and reproductive status of each gecko feeding in the lab windows to the rest of the population results.

Resource Partitioning

The two species of gecko inhabiting the dormitory roof make up what is defined as a "lizard assemblage" (Zug, 1991). The term is used to denote a group of lizards occurring syntopically, active at the same time, and potentially sharing some of the same resources (e.g., food and resting sites). This term does not imply any degree of organization or coevolution between the species. Both *L. lugubris* and *G. oceanica* were found to share the same temporal niche and use of space in this system, but there are several notable differences between them. The first and most obvious is body size. Species with larger heads, such as *G. oceanica*, tend to eat larger prey items than those with smaller heads (Pianka and Pianka, 1976). This was definitely observed to be true in the case of *L. lugubris* and *G. oceanica..* who were observed eating distinctly different sized prey items. Another difference worth noting is that *G. oceanica* reproduces sexually whereas *L. lugubris* is parthenogenic. Other studies have shown differences between the sexes in activity cycle and site specificity, there may be difference in habitat use between the two species as well as between different sexes of *G. oceanica* (Frankenberg; 1984, Kingsbury, 1989). Abundance of individuals of each species is another significant difference at this site and the presence or absence of conspecifics may effect the way each species uses its habitat. Approximately 8 *G. oceanica*, were monitored, where as there was well over 100 *L. lugubris* were watched. The higher proportion of *L. lugubris* is likely due to its preference for buildings in both urban and non-urban habitats (Sabath, 1981). It would be interesting to compare the abundance ratio of each species at a variety of habitats in further studies.

Interspecies Interactions and Predation

The most difficult observation to interpret was the 'predation incident' of *G. oceanica* on *L. lugubris*. It makes no sense that the two species would be part of the same assembly if one is feeding on the other. This leads me to believe that this behavior is rare and *G. oceanica* only preys on smaller lizards as a supplement to its main diet. This could be tested using gut analysis. It is also interesting that *G. oceanica* takes advantage of the bottleneck effect created by the line, in order to stalk prey.

On Moorea, in contrast with other islands like Hawaii and Guam, the geckos are free from major predators such as the mongoose (Pentron and Case, 1994). It is possible that the lack of predation pressure has been a key factor in the development of the observed transit behavior. It seems likely that in the presence of heavy predation, the diurnal retreat site and nocturnal feeding site would be separated. To test this hypothesis, more research would need to be done to see if the transit behavior observed at the three sites at the Gum Station is frequent on Moorea. The results would then need to be compared with data collected from islands where geckos are heavily preyed upon.

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Developmental Response of *Aedes polynesiensis* to Resource Limitation and Predation by *Toxorhynchites amboinensis* (Diptera: Culicidae) within Coconuts

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ABSTRACT. To determine the regulatory effects of resource limitation and predation within a cohort of larvae, *Aedes polynesiensis* first instar larvae were placed in rat-chewed coconuts. After 8 days, development rate, the proportion of emergent adults and pupae to the total larval population, [dev. rate = (a+p)/(a+p+l)] was taken as an indicator of resource limitation. A significant slowing of development time was seen within higher population densities (n=24; df=1, 25; p < .001). Greater *Aedes* wing lengths were noted in the presence of a larval predator, *Toxorhynchites amboinensis*, across each density category. Predation may have eased *Aedes* intraspecific competition, but due to small sample size, further studies of this trend are needed. Electrical conductivity and pH of the rainwater collected in 44 coconuts was measured, and no significant differences in water chemistry among subsets in the field and experimental subsets were noted, except in cases of a time-dependent function.

Introduction

Approximately half of all known viruses have been isolated from mosquitoes. While only a fraction of these are arboviruses, completing portions of their life cycles in both vertebrate and invertebrates, many of these have profound epidemiological consequences in humans. Conservative estimates of the morbidity and mortality from malaria worldwide are 270 million infected and one million deaths. Currently, two-fifths of the global population remains at risk. Both genera of vector mosquito, *Aedes* and *Culex*, are subject to biological control by the larval predator, *Toxorhynchites*. However, attempts to introduce *T. amboinensis* in the natural habitat have shown mixed results (Nakagawa, 1963; Gerberg and Visser, 1978; Focks *et al.*, 1982; Toohey *et al.*, 1985).

Recent research using a parasitic protozoan, *Lambornella clarki* (Ciliophora: Tetrahymenidae), showed a curious effect as the result of predation at higher host densities - those mosquitoes that survived to adulthood emerged with greater than expected overall fitness (Washburn *et al.*, 1991). Washburn and his colleagues believed that, within resource-limited environments, predation led to a reduction of intraspecific competition among the larvae. It has also been shown that the size of the adult is highly dependent upon larval food resources (Lounibos *et al*, 1985). Larger mosquitoes have greater longevity and, hence, more opportunities to ingest infected blood meals. Given these two responses, more must be known of the ecology of larval development before any biological control regime is undertaken.

To determine whether predation by *T. amboinensis* has a regulatory role on the size of emergent *Aedes* adults, this field study was conducted using coconuts as replicated microcosms. First, electro-chemistries of 44 coconuts were surveyed. Second, *Aedes polynesiensis* first instar larvae were placed in rat-chewed coconuts to determine which larval densities begin to experience resource limitation. As a final treatment, *T. amboinensis* was added

to half the coconuts. Distinct differences in *Aedes* wing length were measured as an index of the easing of intraspecific competition during the early stages of larval development.

Materials and Methods

Species

Aedes polynesiensis Marks (1951) is a geographic strain of mosquito first isolated at Atimaono, Tahiti. There has been debate as to whether it is simply a variant of *A. pseudoscutellaris*, with which it capable of producing fertile hybrid offspring. In any case, *Aedes* breed in containers and are able to tenaciously exploit a wide range of aquatic habitats close to human settlements. Prior to oviposition, adult females feed on the blood of mammalian hosts to nourish the fertilized eggs with protein. Thus, this genus serves as the main vector for vertical transmission of dengue fever and bancroftian filariasis in humans.

Toxorhynchites amboinensis (Dole-schall) was introduced to Mo'orea in 1975 as a biological control of *Aedes* (Riviere, 1979). Its larvae are aggressive predators within the same habitats favored by *Aedes*: rat-chewed coconuts, tree holes, and bamboo internodes (Steffan, 1975; Steffan and Evenhuis, 1981). Aerial oviposition allows them to survey potential breeding sites, as well as gain access to obstructed habitats (Furumizo and Rudnick, 1978; Benzon *et al*, 1988). Unlike their prey, *Toxorhynchites* females do not require blood to nourish their eggs and are, therefore, not responsible for disease transmission.

Larvae of both genera were raised (F>>20) within the Atimaono insectory, operated by the Institut Territorial de Recherches Médicales Louis Malardé in Papeete, Tahiti.

Cocos nucifera, common along the Mo'orean coast, is a large palm tree often reaching heights of up to 30 meters. In untended groves, the fruits are swept down by high winds or loosened by rodents. The fallen husks and broken shells collect the abundant seasonal rains and so provide

ovipositing sites for both *Aedes* and *Toxorhynchites*.

Locations and area descriptions

These experiments were conducted from 6 October to 17 November on the island of Mo'orea, French Polynesia. (GPS fixes were used to place sites on Mo'orea. The values obtained have been truncated to two decimal places due to measurement fluctuations). Wing length measures were performed on 2 December in the Entomology Laboratories at UC Berkeley. Analyses of development rate and wing length were completed using Berkeley Interactive Statistics Software.

Survey sites

Coconuts were sampled and collected from three distinct coastal regions:
1) The shoreline grove at Temae - 17°28.39' S, 149°46.51' W;
2) The Opunohu roadside - 17°30.39' S, 149°51.54' W;
3) The Vaiare roadside - 17°31.21' S, 149°46.49' W.

Experimental plot

Larval density experiments were conducted within the grounds of the Gump Biological Station. The site lay at 17°29.38' S and 149°49.63' W. It was five meters south of the driveway to the manager's office, and was approximately thirty meters from the island periphery road. Coconuts were placed in evenly spaced rows in a patch of cleared ground. The area has a northern exposure and rests on a gentle slope under a heavy canopy. The site was chosen because it closely matched the natural breeding conditions of *Aedes* throughout the island (Becker unpublished, 1992).

Field studies

Survey of breeding sites

The electrochemistry of collected water was measured in 44 coconuts from the three sites listed above. Individual fallen coconuts were selected using the following criteria: 1) the presence of a single chewed hole; 2) standing water; 3) intact husk.

Only those coconuts passing the visual inspection were used for study. Temperature, pH, and conductivity of the water were measured with a set of electronic probes. Once these readings were taken, the contents of coconuts were poured into white plastic pans and the larvae counted.

Effects of limited resources on development

To determine the conditions under which increasing larval densities create resource limitation, newly hatched *Aedes polynesiensis* first instar larvae (50, 100, 150, and 200 per replicate) were placed in rat-chewed coconuts. 150 ml of tap water was poured into each coconut along with 0.3 ml of 5% liver solution and a single yeast pellet as a nutritional supplement. The larvae were left to develop for 8 days.

Criteria used to select coconuts for the experiment were the same as for the electrochemical survey -- a rat-chewed entrance hole and water retention. Coconuts with an interior volume greater than 500 ml and less than ~ 200 ml were not used due to possible complications in nutrient density. Once they were taken from the field, the most promising of each truckload were placed upright on dry cement.

Half of the coconuts used for the experiment were steeped in boiling water for ~75 minutes, while half were simply rinsed out. Pouring boiling water in the coconuts simultaneously accomplished three things: 1) sterilized the site of previous larvae and eggs; 2) removed nutrients by leeching organics out of coconut meat; 3) indicated presence of holes missed on the initial field search. All coconuts were then assigned randomly to treatment groups (larval density and boiling).

After eight days within the plot, the contents of each coconut were poured in pans and individual larvae, pupae, and adult mosquitoes were counted. Development rate was measured as the ratio of pupae and emergent adults to the surviving *Aedes* within each coconut:

$$[\text{dev. rate} = (a+p)/\ (a+p+l)]$$

Daily internal temperatures were taken, and the time to pupation was noted. This was done to develop a time scale for mosquito development under the conditions unique to our particular experimental plot (mean daily ambient temperature of 24 - 28°C).

Effects of larval predation on adult size

To measure the degree of regulatory control exerted by the predator on its prey, half of the coconuts in this experiment were inoculated with a pair of newly hatched instar *Toxorhynchites amboinensis* larvae. Using two predators was a precautionary measure to ensure at least one survived the duration of the experiment. The remaining half was left without a predator. Both treatment groups were prepared as before (with 100, 150, and 200 larvae per replicate). To ensure standardization, all coconuts were steeped with boiling water.

Emergence traps were constructed of light-weight, clear plastic storage containers. The bottoms were cut out and replaced with fine Nylon mesh. The finished traps were securely affixed to the outer husk with water-resistant duct tape and a series of push-pins.

Aedes adults were allowed to emerge at their own rate. Lights and tapping caused the newly emergent adults to fly into the trap where they were collected for later censusing, sexing, and dissection. Since female *Aedes* are solely responsible for vertical disease transmission, measurements were made only of females. Males were used to practice and refine manipulations.

Wing length was measured from the insertion of the annular notch to the distal end of the wing. Wings were separated and handled under fixed magnification using an optical micrometer calibrated for scale.

Results

Coconut survey

Between the two subsets of coconuts in the field (those with larvae present and those without larvae), there was no significant difference in acidity (T= -1.066;

df=15; prob=0.303). None of H_3O^+ concentration variances were significant (Table 1).

Table 1 - Probabilities of pH Variations Among Four Data Sets		
Larvae	Present	Absent
Resource exp	.107	.297
Predation exp	.151	.387

Similarly, there was no correlation between conductivity and the presence or absence of larvae in the field (T=-0.136; df=15; prob=0.893). Comparing these subsets to the average conductivities for the predation experiment, there was, again, very little difference [larvae present vs. experimental (T=1.214; df=12; prob=0.248) and larvae absent vs. experimental (T=0.672; df=18; prob=0.510)].

Curiously, the conductivities found in our development rate studies were different than both subsets of field coconuts: [larvae present vs. experimental (T=1.800; df=15; prob=0.092) and larvae absent vs. experimental (T=2.227; df=26; prob=0.035)].

Resource limitation

As shown best in boiled treatment, the larval density in each coconut had a significant effect on the developmental rate (Figure 1). Larvae experiencing higher intraspecific competition developed significantly slower than larvae of lower densities (n=24; df=1, 25; p < .001). The rate within each category is expressed as a decimal proportion in Table 2. When data from all treatments are combined and compared by larval density, there is a slightly less negative regression slope (Figure 2).
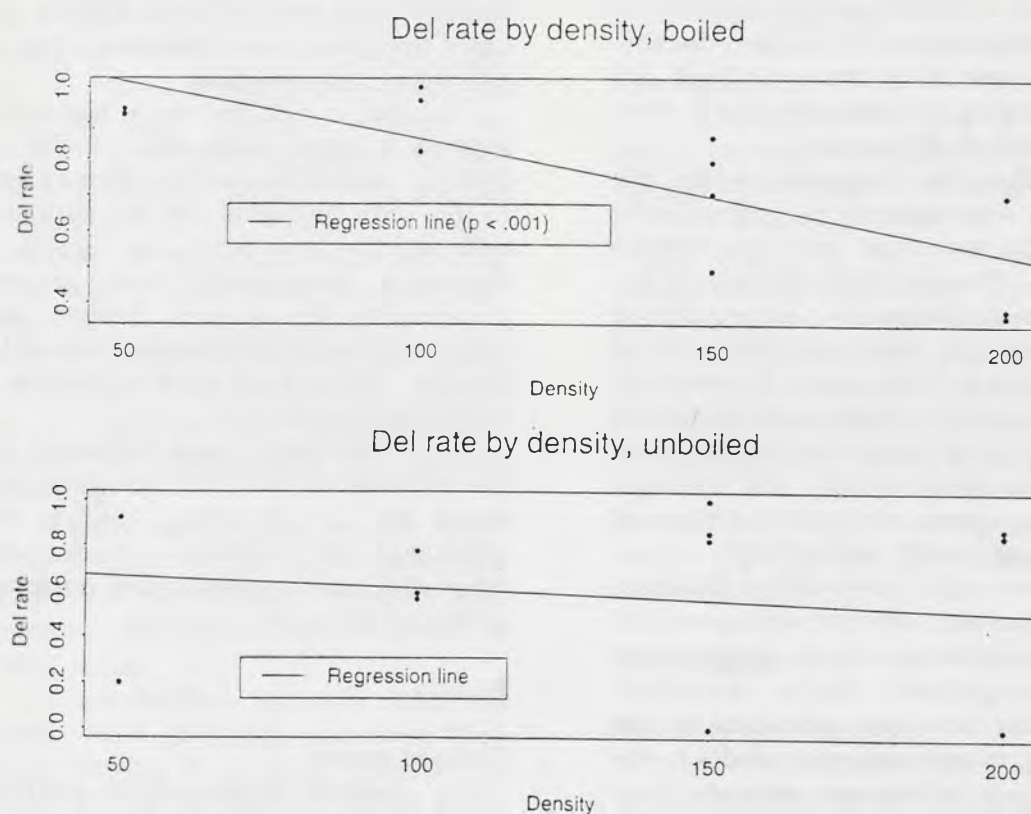
Figure 1. Boiling effect on larval density
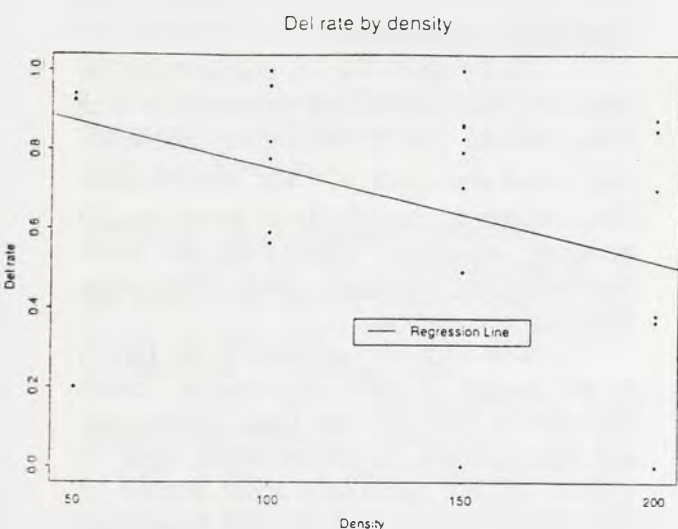
Figure 2. Comparison of larval density

Additionally, the boiling treatment played a critical role in stabilizing the internal environment of the coconut. Larval development rate was significantly more demarcated within boiled coconuts as compared to the unboiled ones (n=12; df=1, 12; p < .001). The rate of development in unboiled coconuts could not be significantly tied to initial larval density (n=13; df=1,12; p=0.64).

Table 2 - Mean Development Rates By Treatment and Density (Number of Surviving Adult Females in Each Category) [dev. rate = (a+p)/ (a+p+l)]				
Larval density	50	100	150	200
Boiled (+)	.93(3)	.95(4)	.71(4)	.48(3)
Unboiled (-)	.56 (2)	64 (3)	.53 (5)	.57(3)

Figure 3. Size-frequency distributions for various treatments

Predation effects

The mean wing lengths of the *Aedes* females that developed in the presence of *T. amboinensis* were larger compared to the average wing lengths in the absence of the larval predation (Table 3). Due to extremely high mortality at all treatment levels, sample sizes were small. No wing length data are available for the density level of 100 in the presence of the predator. Data for all six sets is shown in a series of frequency histograms (Figure 3).

Table 3 - Mean Female Wing length in mm By Treatment (Number of Surviving Adult Females in Each Category)		
Toxorhynchites Density	Absent	Present
100	2.72 (13)	N/A (0)
150	2.79 (7)	2.82 (3)
200	2.67 (7)	2.77 (5)

There were two outliers within the 100-larvae (uninoculated) treatment, and one was detected within the 200-larvae (uninoculated) treatment. Interestingly, both sets of outliers were centered around 2.2 mm. The outliers, within an original sample size of 35, cast a sizable influence on the means at the 200-larvae treatment level. The results with these outliers removed are shown in Table 4.

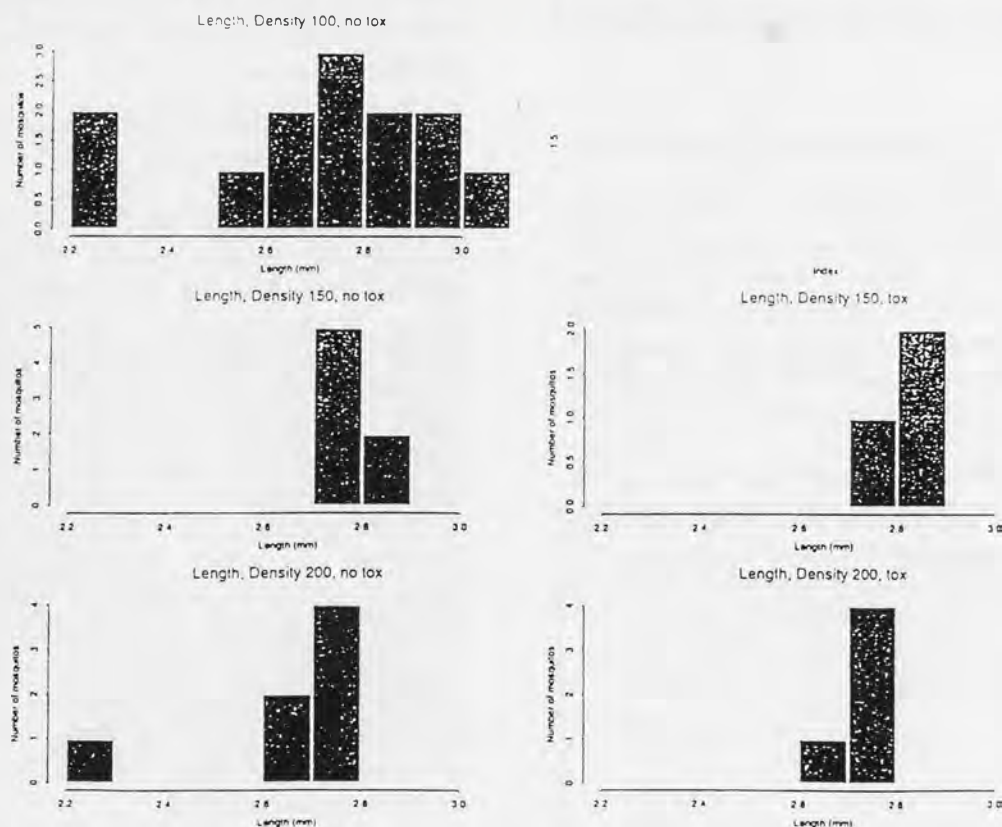| Table 4 - Mean Female Wing length in mm By Treatment, Outliers Removed (Number of Surviving Adult Females in Each Category)		
Toxorhynchites Density	Absent	Present
100	2.81 (11)	N/A (0)
150	2.79 (7)	2.82 (3)
200	2.74 (6)	2.77 (5)

Discussion

Equivalent chemistries

The search for an electrochemical basis for the habatibility of coconuts was inconclusive. Due to its logarithmic scale, only major shifts in H_3O^+ ion concentration (four orders of magnitude or more) would produce intolerable differences for these relatively hardy species. Such shifts were, however, uncommon.

Conductivity appears to be linked to the length of each experiment. Stark differences between the field survey and the development rate experiment were an artifact of the relatively short period of time the coconuts were exposed to adverse weather and the natural degredative processes within the nut. When the coconuts were allowed to sit in the plot for more than two weeks, as they did in the predation experiment, a greater similarity to the survey data was seen. This is reasonable given the duration coconuts, in untended groves, are exposed to the elements.

Resource limitation slows development

Nutrition clearly played a critical role in determining the rate at which larvae develop into adults. In addition, several other developmental variables are effected in tandem. A three-year survey of larval populations of *Aedes sierrensis* found mean pupal weight of females was inversely related to density (Hawley, 1985). While Hawley also showed that pupation success was not neccessarily density-dependent, his study didn't measure pupation as a function of time. However, the effects of time cannot be ignored. The longer larvae and pupae remain vulnerable to *Toxorhynchites*, predation effects will have a greater chance to manifest themselves. Thus, through its effects on time, nutrition contributes to predation effects, like those found in our experiment.

As a matter of protocol, boiling is essential to standardize the microcosms for any future experiments of this sort. As noted before, development rate in unboiled

coconuts showed no significant variation as a function of initial larval density (n=13; df=1,12; p=0.64). The use of this data, from the unboiled set, masked the significance of density-dependent effects when data from both sets were combined (Fig. 2). Preparation techniques do, in this case, make a difference.

Mortality under effective predation

There are two potential sources of the extremely high mortality seen in this study -- adverse weather and over-predation of *Toxorhynchites*.

Mean daily temperatures had fallen during this experiment (20 - 24°C) as a series of seasonal rainstorms swept over the site. The larval development was slowed across all treatment categories. Whereas, growth to adult emergence took 7-9 days at a daily average of 26°C for our resource experiment, it was nearly 15 days before the first adults settled into the trap. It is likely the lag provided the *Toxorhynchites* additional time to prey, and thus, the high *Aedes* mortality is a testament to the predatory abilities of *T. amboinensis*. This may be critical to the loss of the all inoculated replicates at the lowest density level.

In studies of *A. aegypti* and *T. rutilus rutilus*, *Toxorhynchites* larvae were added regularly (ca. every 10 days) to microcosms experiencing continuous recruitment of *Aedes* and *Culex*. The number of emergent adults was reduced by an average of 65% with a single predator and by 82% with two (Focks *et al.*, 1982). Throughout the course of their experiment, larger containers were used, and so even greater amounts of prey were available to the *Toxorhynchites*. Thus, the use of two *Toxorhynchites* within treatments of lower populations may have been more than sufficient to induce high mortality.

Aside from the temperature drop, the heavy rains, themselves, proved a more significant cause of the high mortality seen in all treatment categories. The rains, often reaching 20 cm hourly, poured water through the Nylon mesh covering, creating turbulence on the water's surface. These periods of disturbance may have been sufficient to deny larvae access to the surface, drowning many of them. Focks *et al* (1982) reported the average loss of 37% of pupal exuviae due to heavy rainfall and foraging ants.

Each of these factors, in combination with an already resource-limited environment, conspired to create an extremely small number of emergent adults. Thus, the presence of heavily weighted outliers within a sample size of 35 could be troubling. While it may appear unclear that this variation is truly the result of an easing of intraspecific competition, several investigators noted the same trend. Adult size is a fairly plastic characteristic, tightly correlated to larval resources (Wada, 1965; Klowden *et al*, 1988). Specifically, *Aedes* females from sites inoculated with *Toxorhynchites* showed slightly increased average wing length than females from other sites unaffected by predation (Rawlins, 1991).

Impact on disease transmission

Adult size variation has been shown to be strongly dependent on resources available (Mori, 1979; Gilpin and McClelland, 1979; Carpenter, 1983). This plastic characteristic, in turn, strongly influences both blood feeding success (Nasci 1986) and the potential to ingest infected blood meals (Service 1983). Thus, a reduction in larval intraspecific competition may increase the transmission potential of these mosquitoes. As evidence for this mounts, the whole notion of biological control must be re-examined in the context of proper predation ratios. A careful cost-benefit analysis may show biological control is doing more harm than good.

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The Reproductive Biology of *Rhizophora stylosa*:
an introduced mangrove on Mo'orea, French Polynesia

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ABSTRACT. The reproductive phenology of an introduced species, *Rhizophora stylosa*, was studied to determine the factors limiting its potential distribution on Mo'orea, French Polynesia, by observing the characteristics of its propagules including longevity, dispersal, and abundance. Mature propagules were placed in tanks of saltwater, freshwater, mixed salt and fresh water, and left to dry on a laboratory bench for up to 34 days. The very hardy and long-lived propagules were able to withstand the different water conditions and still remain viable. Dispersibility was monitored over two tidal cycles for both high and low tide releases with marked propagules released along the margin of the mangroves. The propagules showed a dispersal pattern of remaining under the parent plant, or dispersing beyond the 300m of the existing mangrove forest. Ten trees of the same relative height were monitored for different stages of floral buds, fruits and propagules over a four week period. No strong evidence was found to determine propagule abundance during a weeks time, over such a short study.

Introduction

The study of the reproductive phenology of a forest provides information on plant interactions with their environment, and helps elucidate the principal processes involved in forest regeneration (Jimenez, 1988). Processes such as distributional limits of a species, seedling colonization, and maintenance of existing forests can all be determined by studying a species' reproductive biology. The reproductive phenology about a specific species is especially important to understand when its introduction to an area changes the interactions with the environment and other established species.

Mangroves are the only trees among a relatively small group of higher plants which are successful in colonizing the intertidal zone, the interface between land and sea. These woody salt-tolerant trees characteristically occur along the more sheltered regions of tropical and subtropical coastlines, often being replaced at more temperate latitudes by saltmarshes composed of predominantly herbaceous species (Thom, 1982). The distribution of these forests extends eastward in the Pacific basin through Micronesia as far as Fiji, Samoa, and Tonga. It is, however, on the larger islands in the Western and Southwestern Pacific that the greatest development is noted (Merrill, 1945) (Figure 1).

Two characteristics of mangrove forests, dispersal in water and vivipary, pertain to their propagules. Their dispersal over long distances is an excellent example of water dispersal, but there are relatively few studies of the patterns and processes of dispersal of mangrove propagules. Vivipary has been described as "the zygote, once formed, develops uninterruptedly through the embryo into the seedling without the intervention of any resting stage" (Macnas, 1968). Gill and Tomlinson (1969) also discuss the continuous development of the embryo without any dormant period, and the fact that there is no 'true seed.' Essentially, the dispersal unit is a 'small tree,' for which the term propagule is convenient. The continual growth of the embryo during dispersal is a unique aspect of mangrove establishment.

The family Rhizophoraceae, contains four exclusively Old World genera of mangroves and a group of twelve upland genera (Hou, 1960). *Rhizophora* is a genus of circumtropical distribution containing about seven species (Hou, 1960). *Rhizophora*, the characteristic genus often being called 'the true mangrove' trees, is
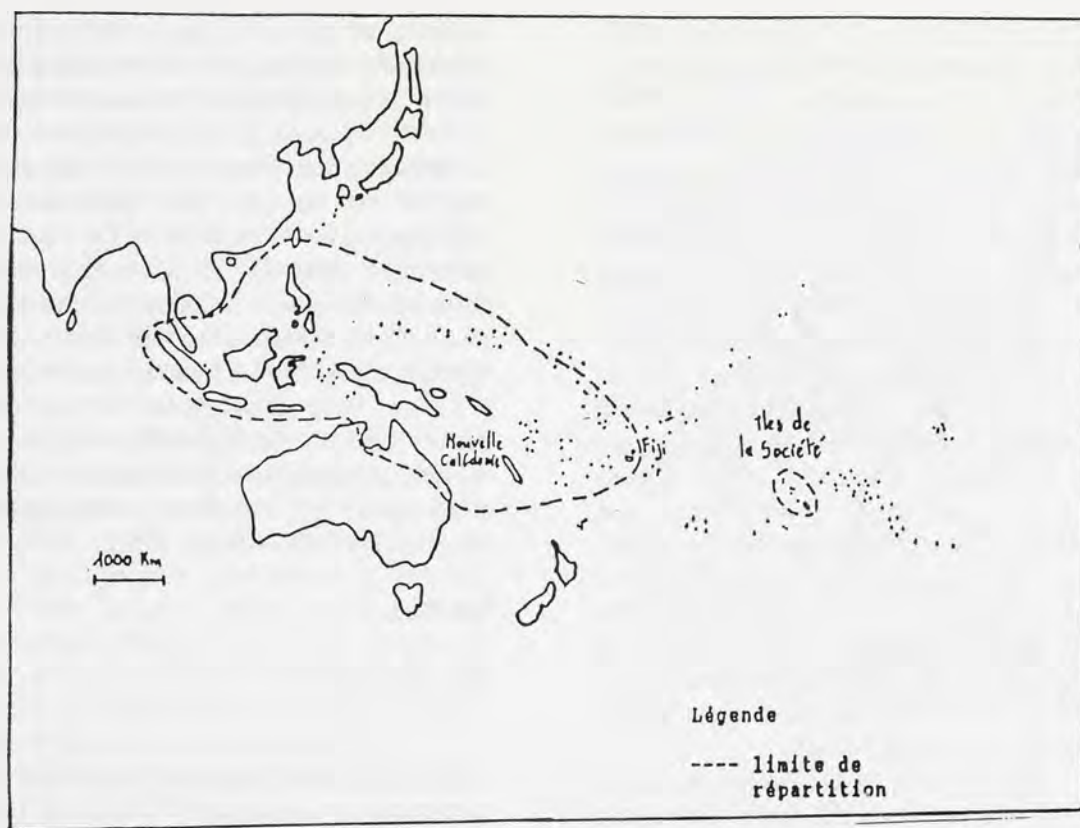
Figure 1. Natural Distribution of *Rhizophora stylosa* (from Cavaloc, 1987).

quickly identified by its extensive prop-root system.

Propagules of *Rhizophora* are shaped like rods with pointed ends and superficially resemble giant green beans. They have elongated, floating hypocotyls, produced by extensive vivipary on the parent tree. This is a form of parental care in the plant world. The cotyledons, fused into a ring, are left behind in the fruit when dispersal begins (Gill and Tomlinson, 1969). The mechanism for propagule establishment is still under debate. Egler (1948), noting the discovery of 'J' shaped hypocotyls on wild seedlings, suggested that the propagules strand themselves in a horizontal position, grow roots, and pull themselves upright, an indication that the propagules become erect after rooting. Davis (1940) reported that the propagules float vertically, their sharp tips embed themselves in the substrate by abrasion. While LaRue and Muzik (1951) suggest

that the propagules fall from the tree and implant themselves in the soil like little spears, noting that most seedlings bear straight hypocotyls, indicating that they root while erect.

The distribution of *Rhizophora stylosa* ranges from the island of Formosa throughout Malaysia to Melanesia, Northern Australia, Fiji and Micronesia, and is exclusively found along sandy shores and on sand-covered coral terraces facing the open sea (Hou 1960). *R. stylosa* disperses primarily in January and February, with floral development periods occurring during the wet season beginning in November (Duke *et al.*, 1984). The propagules are large, those of *R. stylosa* being larger and heavier than *R. mangle*, but smaller and lighter than *R. harrisonii* (Rabinowitz, 1978).

R. stylosa was introduced to Tahiti, Mo'orea, and Bora Bora, it can also be found on Huahini, Tahaa, and Raiatea in

the Society Islands (Woodroffe, 1987; Personal observation, 1994). Its introduction to Mo'orea's Vaianahe Bay, first in 1930 then again in 1935, from New Caledonia was with the hopes of cultivating oysters on the buttressing roots. Although this project failed the mangrove trees remained, spreading over the ensuing 60 years to new sites on the island. By 1987, *R. stylosa* had established itself on approximately one-fourth of the coastline of Mo'orea. These sites occur in more favorable locations with a few trees located in less favorable areas (Cavaloc, 1987). Cavaloc (1987) argues that the mangroves will continue spreading exponentially around the island because there are many unoccupied favorable habitats. The majority of the mangroves are located on the South-West shore where the most favorable sites occur, protecting them from the dominant winds coming from the North-east.

The majority of work that has been done on Mo'orea, aside from Cavaloc's (1987) description of the ecological consequences of mangrove colonization, was done by Kramer (1992) who showed a correlation between *Paspalum vaginatum* grass clearing and *R. stylosa* tree height.

Neither of the studies pertained to the reproductive biology of *R. stylosa*, and how this affects distribution around the island.

The goal of this paper is to better understand the distributional limits of *R. stylosa* on Mo'orea by determining its reproductive limits. To partially determine this we can asses the viability, distribution and quantity of propagules that will be released for distribution. The specific questions asked in this study are: (1) how long propagules remain viable under certain ecological conditions, (2) number of propagules produced in one weeks time and (3) distance and direction propagules travel in the field.

Methods

Site Description

All experiments took place during the months of October and November in the mangrove forest located North of Haapiti on the South-West shore of Mo'orea, French Polynesia (17°30'S and 149°50' W) (Figure 2). The Haapiti site, north of the original introduced stand in Vaianahe Bay, is younger and is one of Mo'orea's more

Figure 2. Established mangrove sites on Mo'orea in 1987 (from Cavaloc, 1987)

extensive. The canopy is not completely closed by mature trees, but the shoreline has formed a monospecific zone of *R. stylosa* ranging from 10m to 50m inland. Heading east, the inland population is composed of *Rhizophora stylosa* with an understory of *Paspalum disticus* grass. The roadside is lined with *Hibiscus tileaceus*, a few *Thespesia populnea*, and *Coco nucifera palmier* trees are also present. Two seasonal rivers drain into this area from the mountains located on the east.

The length of this mangrove forest is roughly one-fourth of a mile long, with a gift shop located to the north and a school to the south, both containing breakwaters (2' to 3' wall to prevent erosion of the soil from wave action) creating a barrier demarcating the end of the mangrove region. *R. stylosa* occurs on coral sand, on mud, and in depressions in the grassy areas inland.

The average temperature is 27°C and the average precipitation levels are high during the rainy season. The mangrove is also located on the windward side of the island, causing a higher precipitation level and freshwater input.

Seed Morphology and Natural History:

To better understand *R. stylosa's* propagule, I sectioned 20 propagules with razorblades and made sketches. I also observed and noted floral buds and arrangements, leaf and flower morphology, and fruit development. A dissecting scope was needed to clearly see the tissue layers (Figure 3).

Seed Viability

Mature seeds were collected from the original mangrove site in Vaianahe Bay located on the south side of Mo'orea. Mature seeds were identified by those that had an abscission zone (1/2" or greater) and were still attached to the fruit on the parent plant. Fifty seeds were placed in an outdoor saltwater tank at the Richard Gump Biological Station on Mo'orea. The sea water system at the station allows a constant supply of fresh sea water to flow into the tank. Observations on the conditions and buoyancy of the seeds were made every few days. After 17 and 34 days,
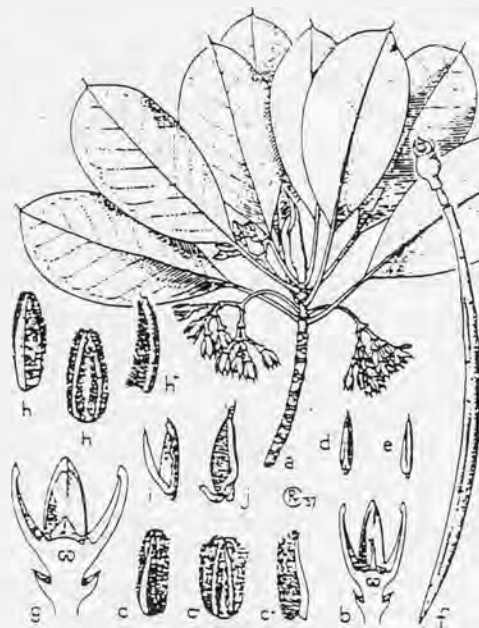
Figure 3. *R. stylosa* propagules (Chapman, 1954)

25 seeds were selected and replanted in the Haapiti mangrove. A week later, viability of the seeds were assessed by the presence or absence of budding primary roots.

Ten mature seeds, collected from the mangroves at Haapiti, were each placed in ziplock bags. One contained 50% sea water and 50% freshwater in equal parts (18 ppt). The other contained 100% freshwater (0 ppt). The water was changed daily, and the bags were left open for the air to circulate. Five seeds were dissected from each bag after 7 and 14 days. The general condition and possible viability of the seeds were then assessed.

Ten mature seeds, collected from the Vaianahe Bay site, were placed in an air-conditioned room (25°C) without water. These seeds were left to dry, and the general condition and viability were assessed after 14 and 34 days.

Dispersal of Seeds

Dispersal of seeds during high and low tide was assessed over a 48 hour period

along the margin of the Haapiti mangroves using a mark and recapture method. One hundred mature seeds were collected and tagged with 2" of florescent orange spray paint on the epicotyl end. All were marked with a number using liquid paper on the hypocotyl end. One hundred seeds were released in groups of ten from ten different sites along the mangrove border at high tide and again at low tide. The sites of seed dispersal were the same for both experiments, and chosen by following the border of the mangrove and using the farthest branch out above the water as the dispersal site. Branch and water height, along with the number of seeds that landed in the ground below were recorded. Wind speed and direction and current speed and direction were also noted.

Visual searching for the marked seeds occurred along the entire margin of the mangrove and 20m outward towards the ocean. Observations were made on the distance and direction traveled from dispersal point after 24 and 48 hours.

Fruit Set

The number of floral buds, flowers and fruits for *Rhizophora stylosa* were followed for one month at weekly intervals on ten trees (range 1.97- 2.64 m) in the Haapiti mangroves, located on the South-West shore of Mo'orea. The amount of buds, flowers and seeds were counted to determine the number of seeds produced per week.

Buds, flowers and seeds were classified into six categories based on the stages of seed development. They are as follows:

Unopened buds were defined from immature green buduals to yellow mature buds. Non-pollinated flowers were buds that had opened to flowers that had not been pollinated. Pollinated flowers ranged from the pollination of the flower when the petals and anthers dropped to the formation of the brown fruit coat (<1/4"). Young seeds ranged from >1/4" fruit to the development of the hypocotyl of the new seed. Partially developed seed were defined by the presence of the hypocotyl to the formation of the dehiscent zone. Fully developed seeds ranged from the formation of the dehiscent zone to the abscission of the mature fruit.

Results

Propagule Viability

The propagules placed in the saltwater tank were all considered viable after replanting in the Haapiti mangroves for one week. After 17 and 34 days all propagules showed signs of root buds or primary roots; some primary roots reached 2" long. The propagules that were left for 34 days began to grow primary roots in the tank at the station before they were replanted in the mangroves. Change in propagule buoyance was observed in the saltwater tank. Initially, all but 2 percent of the propagules floated. After 7 days, 36 percent were floating vertically while 54 percent had sunk. By 34 days all had floated vertically, some sank, and many had sprouted roots (Figure 4). Wild Rhizophora propagules have been observed
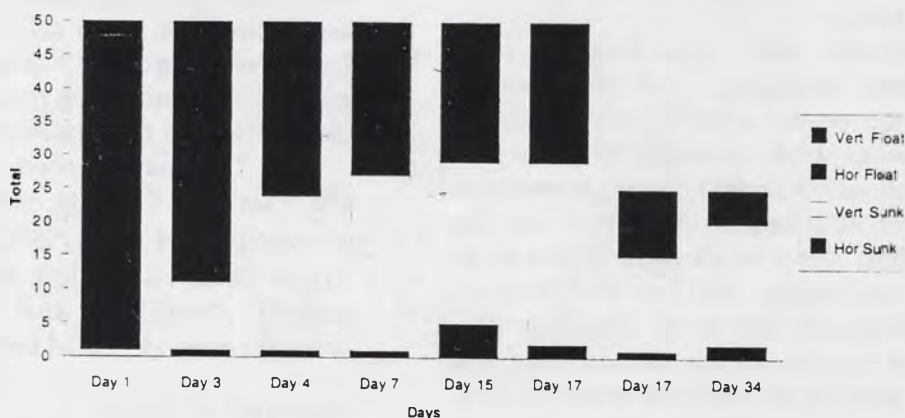

Figure 4. Change in propagule position
for 50 *R. stylosa* propagules in saltwater over 34 days

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Table 1. Propagule viability

	100% Saltwater Seeds			
	Hor Sunk	Vert Sunk	Hor Float	Vert Float
Day 1	0	1	47	2
Day 3	1	10	32	7
Day 4	1	23	14	12
Day 7	1	26	5	18
Day 15	5	24	3	18
Day 17	2	27	2	19 100% 25/25
Day 17	1	14	1	9
Day 34	2	18	0	5 100% 25/25

	50%/50% Seeds	
	Method	Viable
Day 7	razorblade	100% 5/5
Day 14	razorblade	100% 5/5

	100% Freshwater Seeds	
Day 7	razorblade	100% 5/5
Day 14	razorblade	100% 5/5

	Dried Seeds	
Day 14	razorblade	100% 5/5
Day 34	razorblade	100% 5/5

Table 2. Propagule observations (low tide)

Low Tide		
Distance (m)	Number After 24hrs	Number After 48hrs
0 0-1.0	36	22
1.1-2.0	4	1
2.1-3.0	2	0
3.1-4.0	2	1
4 1-5.0	0	1
5.1-6.0	0	0
6.1-7.0	1	1
7.1-8.0	1	0
8.1-9.0	0	1
9.1-10.0	0 46/59=78%	0 27/40=68%
10.1-11.0	1	0
11.1-12.0	1	1
12.1-13.0	2	0
13.1-14.0	0	1
14.1-15.0	2	0
15.1-16.0	1	2
16.1-17.0	1	2
17.1-18.0	0	0
18.1-19.0	1	1
19.1-20.0	0	0
>20	4	6
	Total= 59	Total= 40

to float horizontally when they first fall from the parent tree. The change in propagule position did not effect the viability or the amount of primary root growth.

The propagules that remained in the ziplock bags, both 100% and 50% seawater, remained viable after 7 and 14 days. There was no evidence of primary root growth in the bags, but upon dissection all appeared to be in good general health.

The dried propagules looked healthy but partially dehydrated. After dissection the propagules were observed to have lost some water (they were not as moist as the others in the other experiments), but only needed to be rehydrated for proper growth (Table 1).

Dispersal

Low Tide

Of the 100 propagules released at low tide 59 were recovered, all of which were found within 100m, and no recordings were made beyond 100m of the dispersal point. Of the 59 observations made after a 24 hour period, 95% of the propagules were found with-in 10m of the dispersal point. After 48 hours (two tidal cycles), 68% of the total recovered were found within 10m of the dispersal point No observations were made beyond 100m with the greatest distance being 90m. (Figure 5, Table 2) The other 41 propagules were not found, either they were washed into the understory of the
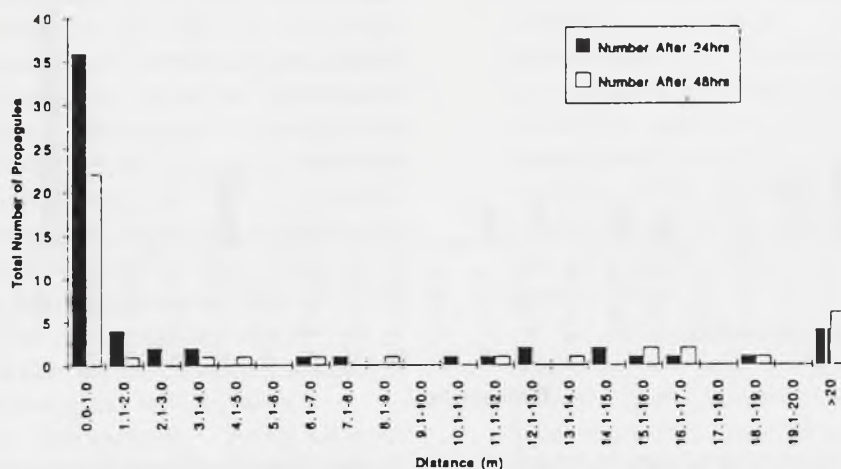
Figure 5. Frequency of propagules found at low tide after 24 hrs (n=59) and 48 hrs (n=40).

Table 3. Propagule obs. (24 and 48 hrs.) high tide

High Tide		
Distance (m)	Number After 24hrs	Number After 48hrs
0.0-1.0	13	7
1.1-2.0	3	4
2.1-3.0	2	1
3.1-4.0	2	0
4.1-5.0	0	1
5.1-6.0	0	0
6.1-7.0	1	0
7.1-8.0	1	0
8.1-9.0	0	0
9.1-10.0	1	0
10.1-11.0	1 23/32=72%	1 13/19=68%
11.1-12.0	0	0
12.1-13.0	0	0
13.1-14.0	0	0
14.1-15.0	0	1
15.1-16.0	0	0
16.1-17.0	2	0
17.1-18.0	0	0
18.1-19.0	0	1
19.1-20.0	0	0
>20.0	6	3
	Total: 33	Total: 19

Recovery of propagules was highest at lower tides when the poor tidal flushing would allow the seeds to remain entangled in the mangrove roots.

High Tide

Fewer recoveries were made on the high tide experiments. Of the 100 released seeds, 33 propagules were recovered. Seventy-two percent of those were within 10m of their dispersal point. After 48 hours, 68% remained within 10m. No observations were made outside of 100m. The greatest distance traveled that was observed was 62m. (Figure 6, Table 3) The other 67 propagules were never found and are believed to be in the understory or beyond the mangrove stand.

Fruit Set

There were no significant changes on the trees for buds, flowers, or seed growth over the four weeks. However, there was a slight decrease in the total number of buds, flowers, and young fruits probably due to abortion of seeds at different stages (Figure 7).

parent trees, or were carried beyond the mangrove stand.
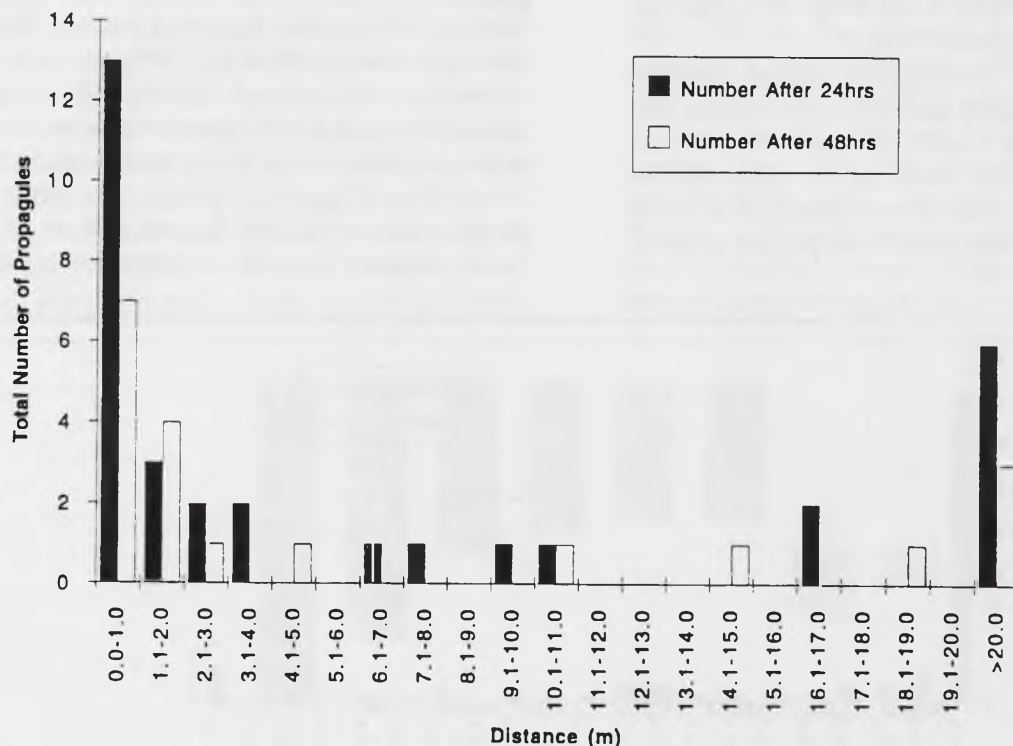
Most propagules were deposited at the recovery site within 2 tidal cycles.

Figure 6. Frequency of propagules found at high tide after 24 hrs (n=33) and 48 hrs (n=19).
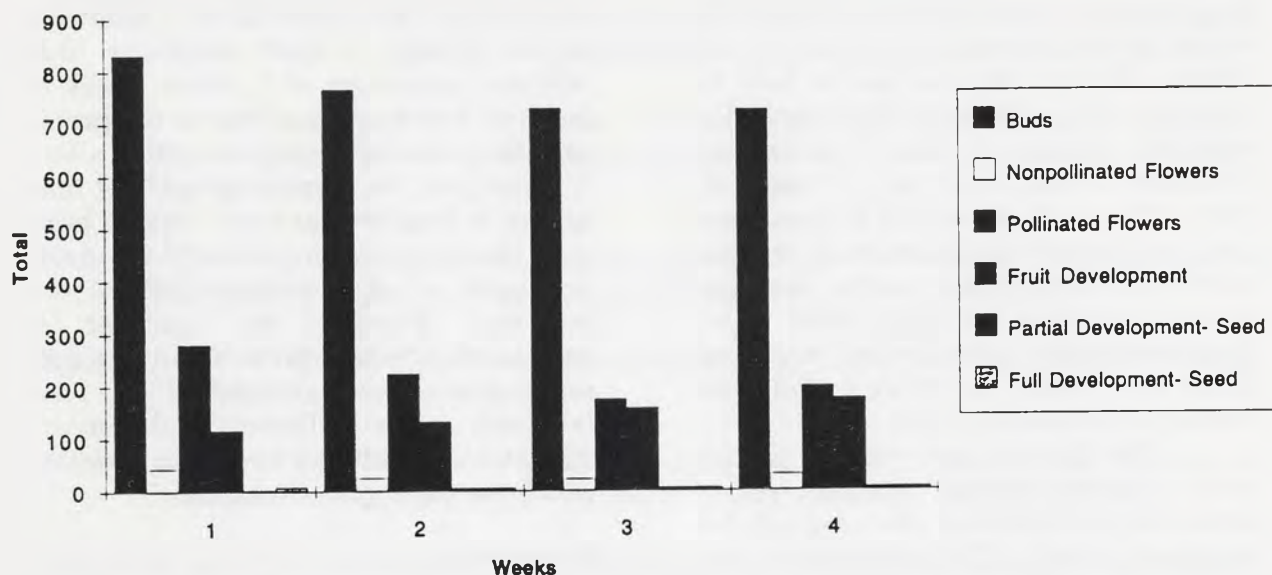
Figure 7. Number of floral buds, flowers and fruits (n=10)

Discussion

Rhizophora stylosa has a hearty and long-lived propagule, able to withstand many changes in the environment. Propagules kept in saltwater for 34 days remained viable and even started to root in the tank without a substrate being present. Davis (1940) reports that propagules of *R. mangle* were kept floating or submerged for 12 months or more grew when planted. This phenomenon was also proven with *Rhizphora* in the understory of Panama (Rabinowitz, 1978). Propagules also remained viable when placed in a mixture of salt and freshwater or all freshwater for up to 14 days. Frequently mangrove forests are inundated with freshwater or have a freshwater stream nearby. Propagules of mangroves are more likely to root in or near estuaries where salt-tolerance is lower (Clarke, 1993). Furthermore, dried propagules were able to root even without the presence of water for 34 days. LaRue and Muzik (1954) reported that propagules kept on a laboratory bench for 68 days lost a third of their weight but grew when planted.

Wild *Rhizophora* propagules have been observed to float horizontally. When the mature propagule is released from the parent tree, it gradually drops to a vertical floating position as it becomes denser, until it finally sinks (Davis, 1940). Larger propagules can regain buoyancy after an initial sinking phase (Rabinowitz, 1978), but this was not observed. If this is the tendency of a mature propagule, to float for a second time, this property would permit long distance dispersal after a few weeks' unsuccessful attempt at local establishment.

Mangrove seedlings that grow from large propagules (more than 10g fresh weight) have low mortality rates(Rabinowitz, 1978b.) Rabinowitz (1978b) further suggests that photosynthetic assimilation is being outstripped by respiration, and that the seedlings die from gradual exhaustion of embryonic reserves. The vivipary and viability of *R. stylosa's* dispersal unit can be attributed to the parental care given to the propagule while still attached to the parent plant.

As is common in tropical trees with large fruits, only a small proportion of flowers gives rise to mature fruits. Very little work has been done on the floral and fruiting phenology of *R. stylosa*, while no work has been done on the amount of

propagules produced at any given time, as shown in Duke et al's (1984) study of the mangroves in North-Eastern Australia. *R. stylosa* has a maximum appearance of open flowers during the months of July to December, the period of predominantly dry weather leading to the wet season, November to May on average (Duke et al, 1984). The maximum number of propagules was also shown to be dispersed during the months of February to April after the rainy season, allowing the propagules to be distributed under optimal water conditions (Duke et al , 1984). My study provided no relevant information to this.

The dispersal patterns of *R. stylosa* show a strong tendency to either remain under the parent tree, or move beyond the mangrove stand. This experiment was designed for the margin of the mangrove. More propagules were likely to land and remain in the mud below if they were released at low tide rather than high. If the propagule fell from a considerable height, it would be more likely to remain below the parent plant if the water level was not significant. The amount of water below the propagule, height it was released from, and the presence of obstacles under it (ie: roots or other seedlings) determines weather it will land in the substrate below or be carried out by the tide. Propagules released on the interior of the mangrove forest are more likely to be entangled within the lower parts of the existing mangrove trees, thus protecting them from being carried away by the incoming and receding tides.

Clarke (1993) found that newly released propagules are mostly moved on the initial flood tide and strand at the high tide mark less than 500m from their point of release. Seeding establishment under the parental tree would maintain existing mangrove stands, while propagules that disperse beyond the mangroves tend to colonize new sites.

The propagules of *R. stylosa* are hearty, long-lived and can be dispersed over long distances. Cavaloc (1987) found that the spread of this mangrove species is colonizing the island of Mo'orea exponentially. After studying the reproductive biology of *R. stylosa*, I believe that this species will continue to spread over the island and colonize further sites. A propagule, the dispersing agent of this species, is long-lived and can disperse over great distances, having already acquired one-fourth of the existing coastline on Mo'orea. Most of this coastline is considered to be more favorable an area, but some trees have established in less favorable areas. Therefore the main distributional limit will be the substrate on which the propagule establishes.

Future Work

There are several possible projects that could be completed pertaining to the Mangrove forests on Mo'orea. Here are a few:

1.) Looking at the Reproductive Biology on the other strands of younger and older ages. (i.e. the original site and a newly establishing site.)
2.) Further mapping of the extent of colonization if the mangroves on Mo'orea.
3.) Finding a correlation (if any) between height of *R. Stylosa* and seed set per week.

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The Vegetation of Reef Islands (Motus):
A Study of the Ecological and Anthropogenic
Effects on the Motu Temae

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ABSTRACT. This study of the flora of the reef island (Temae) of Mo'orea, is a continuation of the work done by Carolyn Cartier (in press). Understanding the ecological factors that determine the plant distribution on motus provides information for conservationists of unique floras of the world. This study is the groundwork for future research on the vegetation types of motus, the biological specialization of strand plants, and the effects humans have on them. The motus host a diversity of strand plants with many specialized native plants that are not found on the main Island, Moorea. Humans have utilized these motus, but cultivation is limited due to ecological factors such as salt stress, lack of freshwater, wind, and wave action. Yet the species found on the motu Temae result from human impacts, including cultivation and accidental dispersal. Temae is the largest and most inhabited of all the motus in Mo'orea.

Introduction

Mo'orea is surrounded by a protective barrier reef that hosts five reef islands (motus). These reef islands are defined as sand cays with shingle platform (Murphy and Stoddart, in press). In an already stressed environment on the barrier reef the addition of humans can have immense impacts. There are many lessons to be learned about resource limitation and management strategies necessary for the survival of a stressed environment. Motus provide an opportunity for the study of the vegetation that effects the morphology of the reef island and the study of how the reef island dictates where the plants grow. They are excellent environments for analyzing dispersal by both natural and human forces (Cartier, in press).

The vegetation of French Polynesia is presently an unstudied species. In the late 1700's expeditions from England and France began in the South Pacific. Naturalists and in some cases botanists were present on these voyages. Yet very little about the native flora of the Society Islands or general description of individual plants was documented. Botanists George and John Forester, on the second voyage of Captain Cook to the Society Islands (1773), produced a narrative on the flora of Tahiti, Huahine, and Raiatea. From this time to the early 1900's a handful of expeditions continued, yet little documentation of the species present on these Islands occurred. A partial flora was published on the Society Islands in 1974 by Martin Grant, Raymond Fosberg, and Howard Smith. Classically, most work on the flora in the Society Islands was on Tahiti rather than Mo'orea.

Until the late 1980's there was no documentation of Mo'orea's reef islands flora. In 1989 a group of researchers from the Geography Department at the University of California at Berkeley made an expedition, survey and collection on the Mo'orea's three motus; Tiahura, Fareone, and Ahi. They found fourteen different species of trees, seventeen species of shrubs, twenty-seven species of herbs, and twelve species of grasses. Carolyn L. Cartier has compiled this information in her paper on the vegetation of the motus of Mo'orea (in press).

Island flora is very different from continental flora due to a large degree of separation from a diverse continental plant source. Plants with specialized dispersal mechanisms are found on these islands. The diverse geography to a small area of Pacific islands as well as its isolation fosters a high level of endemism. The location of the Society Islands constitutes the easternmost range of many Pacific

island genera (Grant *et al.*, 1974). Consequently, the western islands of the Pacific have many species in one genera while the Society Islands may have only one. Thus a decrease in plant diversity from the western to the eastern pacific occurs.

Atolls and motus contrast the Islands they surround by an overall less diverse flora, very few endemic species, and a diversity of strand plants (Fosberg, 1949). The uniqueness of the flora is characterized by strict zonation formed in concentric rings that progress from the seaward shore to the lagoon shore (Fosberg, 1949). Each zone explicates the different environmental factors and stresses which each vegetation type can withstand. There is no set form for the width or the locations of these zones. Thus a mathematical approach to understanding the plant species diversity will not work consistently across these boundaries. These environmental factors are plastic and vary for each individual motu based on location, geomorphology, weather patterns, and freshwater lens.

This study is an extension of previous work on the vegetation of motus in Mo'orea by Carolyn Cartier (in press). Through the documentation of species found, their location, and seedling density on Temae relationships are seen between the location of certain plants, the effects of human use, and ecological factors. The species lists from the motus studied by Carolyn Cartier and similar sampling in this study of the motu Ahi reveal how the ecological factors and the human impacts effect these motus in comparison to their effect on the motu Temae. This is the background for further research on conservation strategies for the native flora of Mo'orea and a documentation of the specialized plants that are found on the motus.

Location

Mo'orea (latitude 17°30'S, longitude 149°50'W) is located in the windward group of the Society Islands of French Polynesia. It lies approximately 25 km northwest of Tahiti, the largest and most populated of the windward islands.

Mo'orea is surrounded by a fringing reef and a barrier reef. Figure 1 shows the location of the five reef islands on the barrier reef. Typically, the motus have a seaward, loose or cemented conglomerate platform, and a lagoon side made up of coral rubble and coral sand (Murphy 1993).
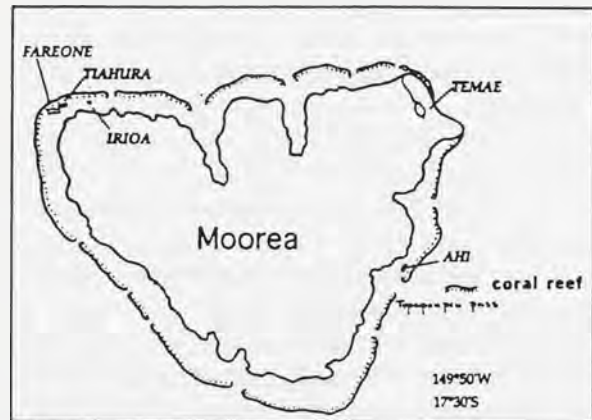
Figure 1. Motu of Mo'orea

Temae, located off the northeastern shore of Mo'orea, is the largest of all the motus (97 ha). It is connected on its southeastern end to the main island. Originally Temae was completely separated from Mo'orea by a lagoon until early Polynesians burned and cleared the adjacent valley for agriculture (Murphy, 1993). It was subsequently filled in when an airport was built in the mid 1900's. Northwest of the connected area, on the side of the motu that faces the main island, there is a brackish lake and a salt marsh. On the eastern ocean facing side of the motu is found the conglomerate platform. Temae has the smallest portion of the seaward conglomerate platform of all the other motus in Mo'orea (Stoddart and Murphy, in press). The study site on the northwestern corner of the motu was chosen because it was the furthest from the inhabited end of the island (southeastern end and central section), and had the most intact strand community.

The motu Ahi is located off the southeastern shore of Mo'orea. It is near the Tupapaupau Pass. It the second smallest of the motu (3.1 ha). Ahi's seaward conglomerate platform is extensive, especially in comparison to Temae. The lagoon side of the Ahi consists of mostly coral rubble. There is only one dwelling on Ahi, located on the northwestern shore.

Materials, Methods, Collection and Records

Temae Transects

For the motu Temae I followed closely Carolyn L. Cartier's methodology on her transect work for the other three motus (Ahi, Tiahura, and Fareone). I placed three 150 meter parallel transects that bisected the motu from conglomerate platform to the marsh. The transects were 50 meters apart and thus covered a 150 meters squared area of the motu Temae. The third transect ended at 110 meters when the swamp edge was reached and sampling was impossible. Along the transect I sampled every 10 meters with a 5 square meter plot on alternating sides of the transect line. Due to the narrowness of the vegetation zonation and the weedy vegetation on Temae, the frequency and size of the plots along the transect were increased from Cartier's sampling methods. In each plot, for each species of plant, the number of individuals and estimated percent cover was taken . For vines and rhizominous plants, the presence was noted and the percent cover taken. The nature of the growth of these types of plants makes it virtually impossible to tell individuals apart. At each plot the soil type and general surroundings were also noted.

Temae Height Determinate Plots

There are three distinct communities of different overstory plants. Two of the communities are dominated by introduced trees; the coconut plantation and the casuarina woodland. The third community that contains the most native plants is the strand community. From each of these three communities I ran a 25 meter transect line. Due to the smallness of the

communities, with the exclusion of the coconut plantation, the transect line ran the length of the community parallel to the tide line. The coconut plantation transect line bisected two distinct dominant understory types. Along each transect line using a random number table I selected three random plots. Each plot had a radius of 5 meters. For each species within the plot, the number of individuals, height, and percent cover was measured. In this case height is used as a measurement of age. I will refer to them as height determinate plots.

Temae Collection

I made a collection of plants identified on the transects, with the exceptions of well know and documented species or single sited species. A total of 32 species were collected in triplicate. These plants are being mounted and labeled and a set will be sent to the University of California Herbarium, the second set to the Richard Gump Research Station in Mo'orea; and the third set will be divided between the Bishop Museum Herbarium and ORSTOM in Tahiti.

Ahi Height Determinate Plots

The expedition to Ahi was for a comparison in succession of similar communities on two different motu. I also made note of the different strand trees found on Ahi that were not located on Temae. These plots were placed similarly to the height determinate plots on Temae. Because the coconut plantation on Ahi is smaller and overgrown with *Lantana camara*, sampling of this area was impossible. For comparison to Temae, I chose six coconut trees in different locations, described the surrounding understory shrubs and trees, and their percent cover. I sampled the lagoon side and the ocean side strand communities and the casuarina community in the same manner as on Temae.

Bishop Museum Herbarium

I spent two days in the Bishop museum Herbarium checking my species list with the herbarium specimens collected on the Eastern Pacific Islands. I also checked the plants that I had not found on Cartier's

(in press) species list and on Francis Murphy's (1993) species list to see if any of my unknown specimens were previously collected.

Observational Study

I visited and made observations on two of the northwestern motu of Mo'orea, Fareone and Tiahura. Here I noted the dominant community types and found them to be similar to the motu Ahi with the exception of the casuarina woodland which appeared to cover a larger area on these two motu.

Results

Temae transects

I collected and identified 32 species of plants on the three transects combined. I observed another 5 species outside of the study area on the northwestern corner of Temae. Of the 37 species only 6 are not keyed out to date. Table 1 (Appendix) lists the species based on general vegetative categories trees, shrubs and grasses. Table 2 (Appendix) compares the species list found on Temae with the species list on the three motu studied by Carolyn Cartier (in press). Figure 1 shows the major plants as they rise and fall in dominance along the transect showing the different zonation from the high tide line inland towards the salt marsh. Figure 2 shows the changes in understory dominance in the coconut plantation. Figure 3 shows the total number of species to area sampled for each of the transects on Temae.

I follow Cartier's (in press) classification for describing the different communities found along the transects. The first vegetative type encountered from the high tide line inland on the first transect is the *Pemphis* scrub community dominated by *Pemphis acidula*. On transects two and three the first community encountered is a casuarina woodland dominated by *Casuarina equisetifolia*. The second vegetative type encountered on all three transects is a beach-crest scrub dominated by *Morinda citrifolia*, *Tournefortia argentea* and *Scaevola taccada*. The third vegetative type encountered along the transect is the interior woodland which in an undisturbed motu would be a broadleaf tree community. On Temae this community is almost entirely a coconut plantation. There are two types of dominant understory in the coconut plantation. In transect one the dominant understory of the coconut plantation is *Chamaesyce atoto*, *Morinda citrifolia* and *Bidens pilosa*. In transect two the dominant understory is a mixture of *M. citrifolia* and *B. pilosa*. Transect three is similar to the second transect with the addition of *Tricholaena rosea*, which fades out further inland and closer to the marsh, as the marsh is approached *B. pilosa* and the native sedge *Fibristylis cymosa* increase in number.

Temae Height Determinate Plots

The three dominant communities sampled on Temae are found there and not necessarily on the other motu. Few of the individual species found on Temae can be followed consistently through each community. Conclusions based on the scatter plots and observations can be made on each plant individually.

Morinda citrifolia is one of the few species found in all three communities on Temae. In each of the three community plots a larger amount of seedlings are found than adult plants with one exception; in the third plot of the coconut plantation a greater amount adult plants are found (Figure 4).

Bidens pilosa is found predominantly in the coconut plantation. The plantation plots show a larger amount of *B. pilosa* seedlings than adult plants. The number of plants of this species far exceeds that of other weeds in the coconut plantation.

Chamaesyce atoto is found only under the coconut plantation overstory. In the three plots in this community it is found in only one. Unlike *Morinda citrifolia* and *Bidens pilosa*, *C. atoto* has few seedlings and mostly adult plants.

Species 2 is found in both the beach crest community and the coconut plantation. In this sampling *Species 2* is found mostly in the second plot with in the coconut plantation community. This species behaves similarly to *Bidens pilosa* and
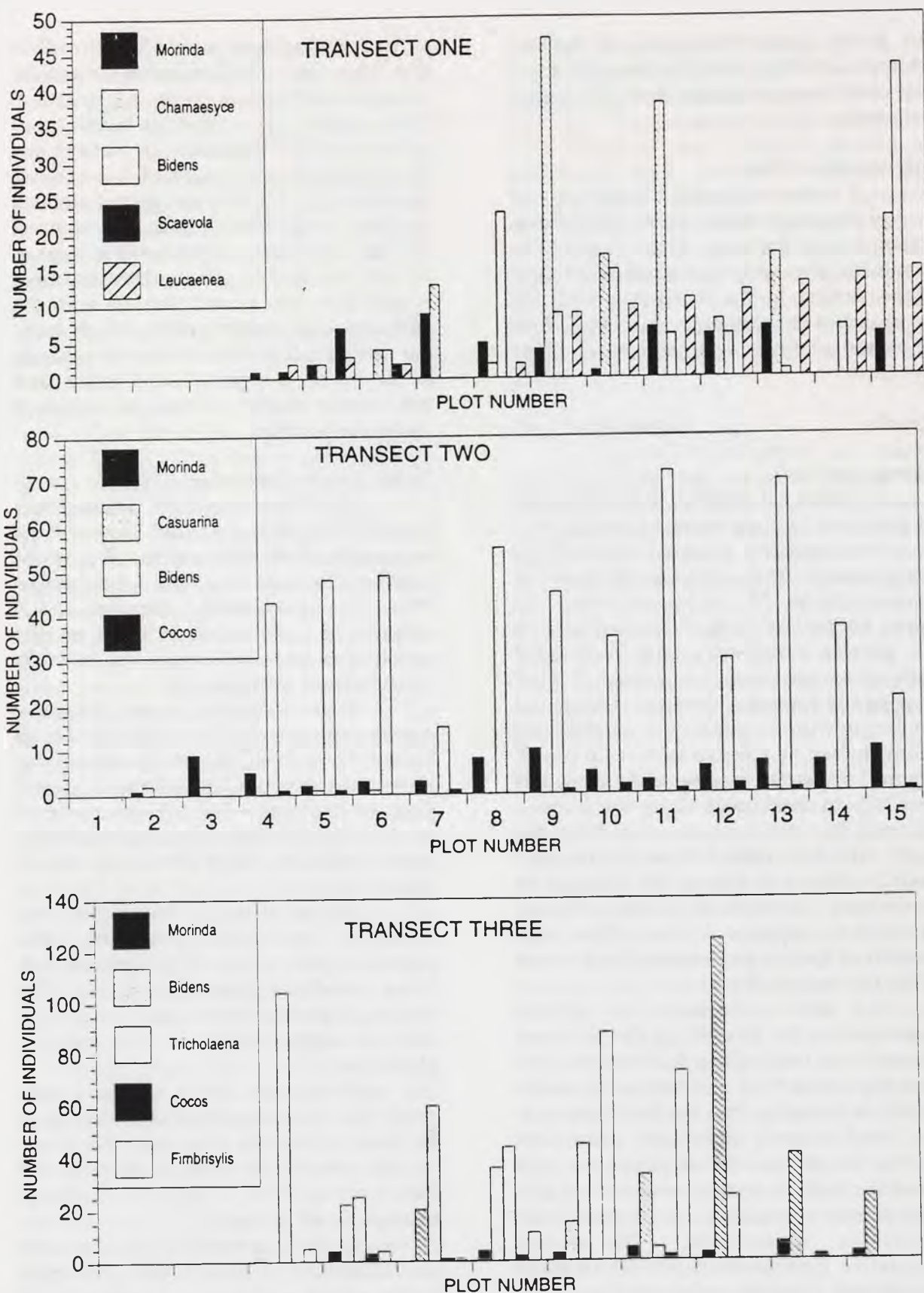
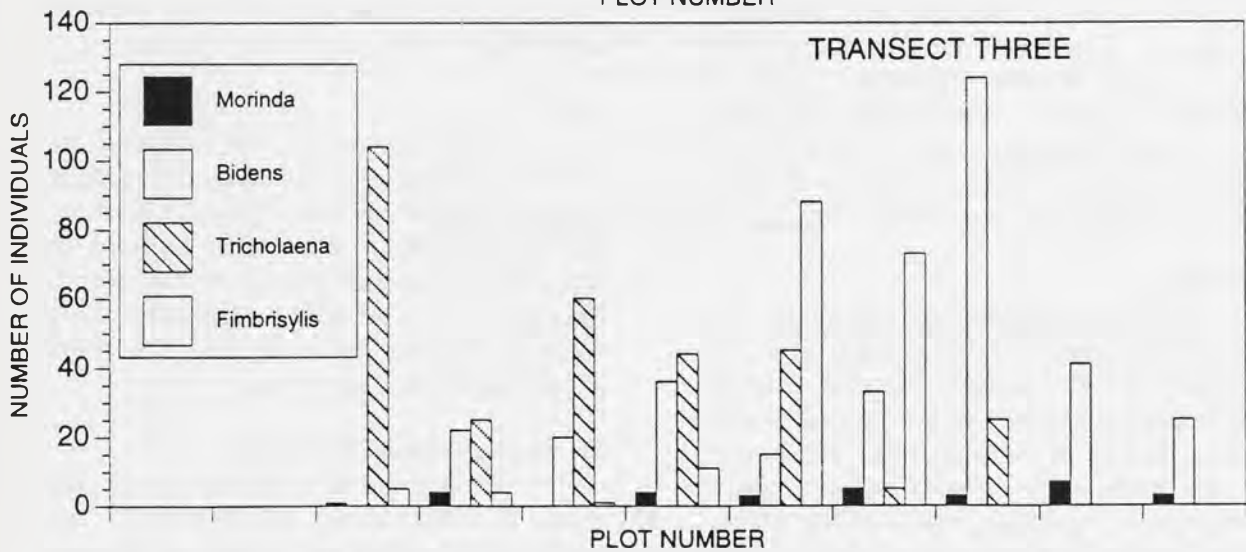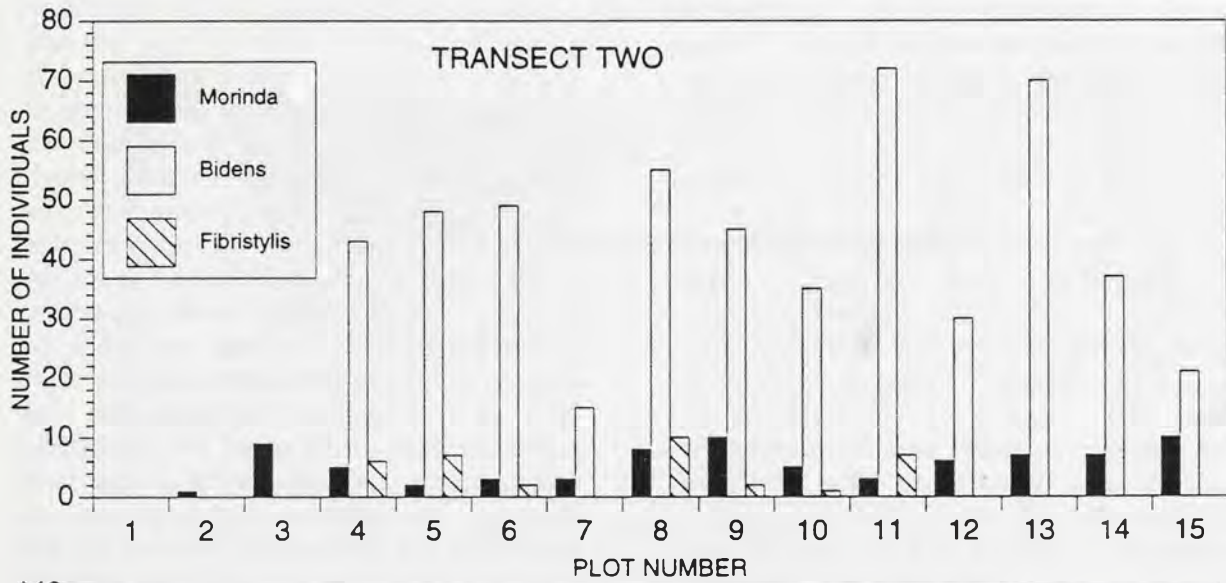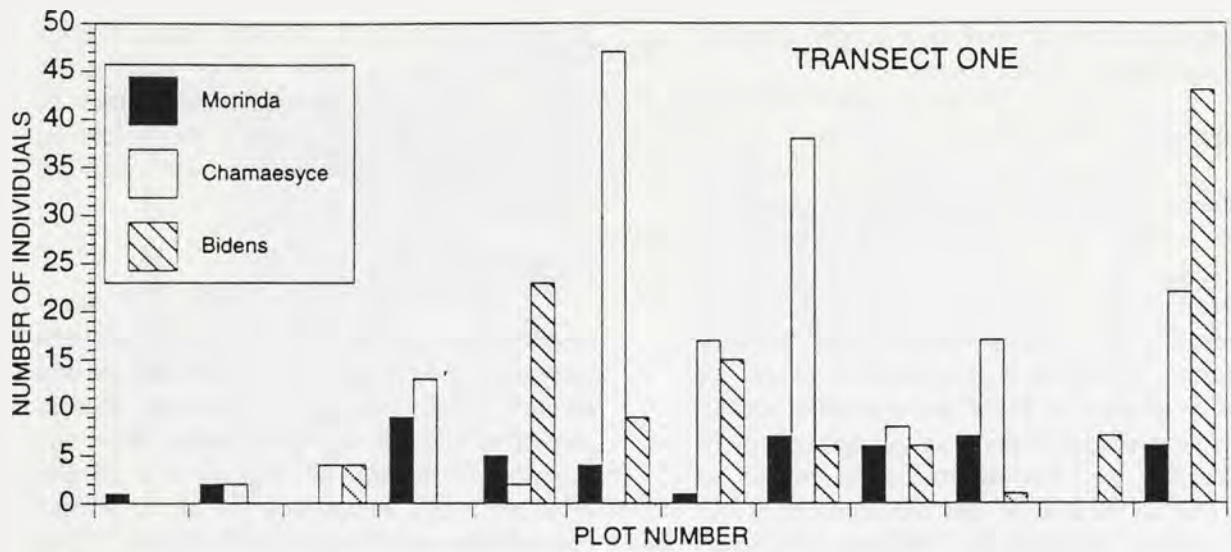**Figure 2.** Dominant plants found in the three transects of Temae.

Figure 3. Dominant understory plants of three transects on Temae.

Morinda citrifolia; it has a larger amount of seedlings to adult plants.

Vegetation and Ecological Factors

The vegetation types on the motu of Mo'orea are unique. The flora of motus in the Pacific are defined as pantropic or Indo-pacific strand species and non-native introductions (Murphy and Stoddart, in press). As stated earlier, the Society Islands constitutes the eastern realm of many genera of these Indo-pacific plants. Consequently, there is a decrease in diversity and endemism. The motus of Mo'orea, situated on the barrier reef, are in a stressful, high energy environment. Each of the five motu are effected by different degrees of these ecological factors. These factors affect the types of plants found as well as their location on the motus. Of the introduced species there are both Polynesian introductions and post contact European introductions. A variety of cultivated plants are presently planted in the centers of the motus. The pemphis scrub and beach crest strand vegetation types dominate most of the motus around Mo'orea except for Temae. *Pemphis acidula* is considered the pioneer species of the motus. The pioneer vegetation and the subsequent successional vegetation that follows stabilizes the reef island thus providing a resistance to erosion and the catcher mitt for sedimentation (Murphy and Stoddart, in press). The motu Ioria is completely made up of *Pemphis acidula* and of *Fibristylis cymosa*. Without soil buildup and a large enough freshwater lens the motu Ioria may never support a diverse plant community.

Salinity

Due to the frequent sea spray, the occasional storm washing over, and the smallness of the motus, there is a large percentage of salinity in the ground water and in the soil of these Islands. The plants of the motus are specialized for these conditions. However, many of the plants that humans cultivate are unable to deal with this stress, hence the areas of allowable cultivation are limited. Often on the Mo'orean motu cultivation occurs in the interior of the motu were there has been

a greater buildup of soil and deeper freshwater lens. This varies with each motu and is not necessarily an indication of the islands area but perhaps an indication of geomorphology, current patterns, and the frequency of storms.

Freshwater Lens

The freshwater lens (Ghyben-herzberg lens) is formed on motus when rain percolating through the course and porous soils displaces the saltwater below. Due to the structure of the freshwater lens the interior of the island will have a deeper layer of fresh water and the outer strand community will have a narrow layer. This is a source of freshwater for the vegetation above that can be drawn by root systems. The lens is dynamic, rising and falling in response to the tides, due to the buoying of the freshwater by the salt water below it (Murphy, 1993). For strand plants, which are physiologically able to cope with the stress of inundation and salt spray, the size of the lens is not as essential as it is for the larger shrub and tree species. Characteristically, motus are able to support broadleaf trees with a shallow root system. The depth of this freshwater lens varies for each of the motu and will effect where plants are found with deeper root systems. For example root crops such as arrowroot are profoundly effected by the salinity of the water and will only grow in areas where the water is the freshest.

Soil

When a motu is first colonized by the early scrub communities and sedges there is little or no soil. Through erosion, and leaf litter the humus begins to build up usually toward the center of the island. Eventually the reef island supports a more diverse community including broadleaf shrubs, small and large trees.

Wind, Waves and Currents.

Each motu is subjected to varying levels of wind, waves and currents. The storm tracts across the Island of Mo'orea from October to March are the Northeast Trades. In the winter the Southeast trades dominate (Murphy, 1993). The motus in the line of these storm tracts experience greater
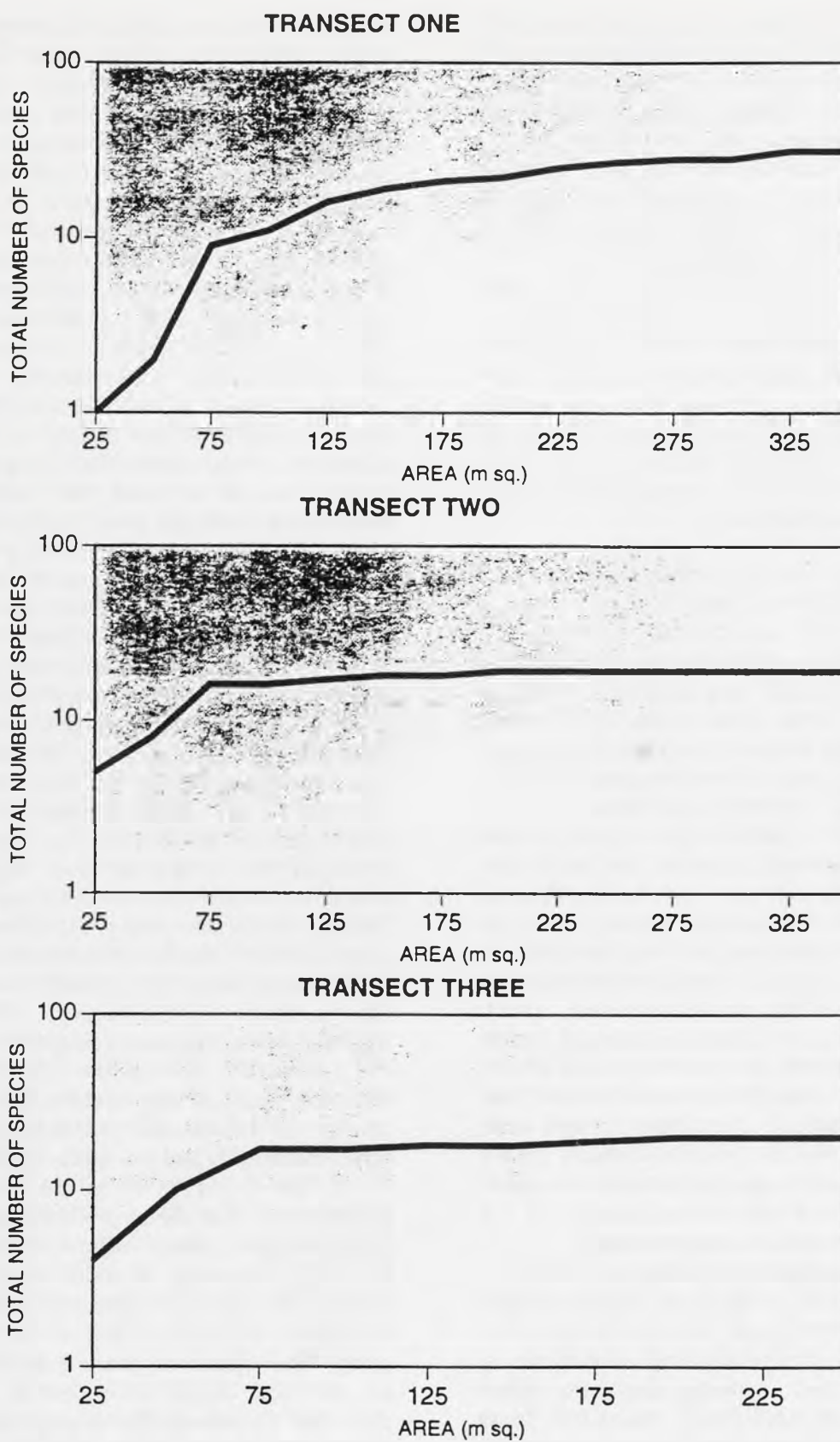
Figure 4. Total number of species per area: three transects on Temae.

amounts wind blown salt spray and wave inundation. Cyclones from the northwest occasionally affect the Island of Mo'orea. "The eastern flank of these storms is the high energy side, with the system rotating clockwise and moving south, and they therefore still have a considerable effect on northern and western exposed coasts." (Murphy and Stoddart, in press).

As a cause and effect the wind generated currents will vary on the motu as well. The northwestern motus, Fareone and Tiahura, are hit by strong wind generated currents. The wind drives these currents in the lagoons and creates waves or surges on the beach that may transform the beach front and hence the vegetation (Murphy and Stoddart, in press).

Discussion

Temae

The conglomerate platform of Temae is smaller per area of the island than any of the other motu on Mo'orea. This may be in part an explanation for the limited extent of the pemphis scrub community. On the other motus it forms extensive stands up against the conglomerate platform and the beach flat. *Pemphis acidula* is a salt tolerant scrub and is often inundated during the high tides. It has a tough wood utilized by Polynesians to make carved objects, parts of canoes, and fish hooks (Whistler, 1980). The small size of this community on Temae is partly due to the encroachment of the casuarina woodland into areas that normally host *P. acidula*. Further east, down the beach from my study site I observed no *P. acidula*; this may be due to clearing from the construction of the dwellings that run along the beach.

The beach crest scrub community on Temae forms a narrow band on the northwestern corner of the motu. The patches cover approximately a 10 meter by 20 meter area. In areas along the beach crest where the beach crest scrub is expected, stands of casuarina woodland grow. On the northwest corner there are approximately three stands of casuarina woodland and few strand plants growing in the understory. The narrowness of this community and the lack of the strand trees, which typically are found inland from this community and interdigitated with this community, is probably due to clearing for the coconut plantation. "The number of tree species will have been reduced on larger islands with the eradication of certain vegetation types." (Stoddart, 1975). Despite these pressures on this community, it still contains the most native plants of all the communities on the Mo'orean motus. The strand community is a specialized community with plants adapted to high salt, wind, wave stress, and nutrient poor soil. Throughout the history of human habitation on the motus, this community is rarely cleared or used for cultivation because of nutrient poor soil (Stoddart, 1975). Subsequently, there is a loss of diversity from the invasion of casuarina woodland and also because of the interior clearing for the coconut plantation.

The coconut plantation is a planted mono-culture of the tree *Cocos nucifera*. *C. nucifera* is planted principally for the exported cash crop of copra. It was and is also used by Polynesians for food, drink and traditional medicines (Whistler, 1980). The coconut plantation has probably replaced the broadleaf tree vegetation found on other uncleared motus in the Pacific. Ahi has many broadleaf trees inland from the beach crest scrub community even though there are planted coconuts in the interior. Occasionally, I found sightings of this remnant community within the coconut plantation on Temae. *Guettarda speciosa* was found in the second transect at the border of the beach crest scrub community and the coconut plantation.

In order to plant coconut plantations, considerable clearing of the pre-existing vegetation must have occurred. Presently, burning is used to clear the vegetation. This is deduced from the frequent burn marks found on the coconut trees. The repetitive clearing and burning of the plantation provides a perfect substrate for weedy herbaceous plants to invade the area without the competition from the native species (Stoddart, 1975). Typically, there is an increase in weeds. On Temae the weeds are from the Asteraceae family (*Bidens pilosa* , *Species*

I, and Species O). It has also been found on other Pacific atolls and motus that *Morinda citrifolia* is the primary understory plant found in a secondary succession after burning (Cartier, in press). This would explain the occurrence of *Morinda citrifolia* throughout the coconut plantation on Temae.

In the study site chosen on the northwest corner of Temae there are two different understory types found under the coconut plantation (Figure 3). The first transect lies adjacent to a cultivated area and dwellings. In this first transect there is a greater diversity of plants and a higher frequency of single sight plants. Six single sight plants are found only in the first transect compared to one single sight plant found for each of the other two transects. The area along the first transect appears to be unmaintained or not cleared as frequently as the other two transects. This can be inferred from the larger biomass and height of the plants in this first transect. In the second two transects there is a similarity between the plants that are dominant and their abundance. In calculating the total number of species per area (Figure 4), it is apparent that in the most recently cleared areas a loss in plant diversity occurred. The graph of total number of species per area for the second two transects shows a sharp drop off in new species once the area of the coconut plantation is included (Figure 4). After intense clearing the same weedy plants establish themselves which explains the lack of new species found in the coconut plantation and the lack of diversity.

The height determinate plots conducted on Temae reveal differences in seedling recruitment and seedling density in the three different communities. Within the beach crest strand community the type of seedlings correspond with the adult plants of this community. The dominant seedlings found were *Morinda citrifolia*, *Species U*, and *Tournefortia argentea*. In the casuarina woodland there were few seedlings found. Those found correspond with the adjacent beach crest strand communities such as *Morinda citrifolia* and *Scaevola taccada*. In the coconut plantation there is difference between

species ratios of adult plants to seedlings. This is an indication of recruitment ability. In the first transect adjacent to cultivation area one of the dominant plants *Chamaesyce atoto* has mostly of adult plants (Figure 4). This indicates that *C. atoto* is not recruiting and may have reached its peak successionally as part of the coconut understory. It may be that there will be a subsequent increase in native strand shrub plants, yet it remains to be seen over time. In the area that has been more recently cleared the graphs indicate that *Bidens pilosa* and *Species 2* are successful recruiting. The number of seedlings is much greater than the number of adult plants found. This is to be expected of a plant that is either established or in the later phase of establishment. In Polynesia *Bidens pilosa* is commonly found in areas that have been recently disturbed. It is found throughout the coconut plantation but is prolific in the more recently cleared areas. The range of *B. pilosa* does not extend into the strand community. It is seen near the periphery of the border between the strand community and the coconut plantation. Normally, weedy plants are both adaptive and good colonizers, but the lack of their presence in the littoral zone suggests that these introduced weedy plants are not surviving or competitive under the stress of the beach crest strand community.

The casuarina woodland, which consists predominantly of Casuarina *equisetifolia*, is replacing portions of the pemphis scrub community and the beach crest strand community. *C. equisetifolia* is native to Northern Australia and is found in the littoral zone on dry sides of islands. It is found on the main island of Mo'orea as well as the motus on the barrier reef. *C. equisetifolia* is a fast growing tree that sometimes reaches heights of 12 meters in ten years (Merlin, 1977). The tree is used for a variety of functions in Polynesian culture and is often planted as a wind break on the coast line. Its ability to grow in high salinity and dry environments are part of the reasons for its success. Due to a variety of factors very few strand plants grow in its understory. It is also noted that very few of the casurina seedlings are found in the

understory of the adult trees. These large trees cause a great degree of shading and deposit a dense leaf litter, making seedling recruitment virtually impossible. There is also a probable increase in soil pH which makes seedling survival slim in an already stressed environment, therefor the seedlings that are able to recruit have limited chances of survival.

Ahi and Temae

The height determinate data gathered on the two motus reveal varying results. There is a significant difference in the composition of strand communities species on the two motus. On the seaward facing shore of Ahi there are stands of mono-species shrub plants similar to Pemphis *acidula*. One of these plots is the shrub plant *Sophora tomentosa*. *S. tomentosa* is in the Fabaceae family and is frequently found on sandy shores of high islands and atolls. It forms exclusive stands and recruits heavily in it's understory. Another plant which according to Stoddart and Murphy (in press) is extraordinarily abundant is *Suriana martima*. It forms a similar dense stand as *P. acidula* and *S. tomentosa* on the seaward side of the motu just inland from the conglomerate platform. These types of mono-stand plants on the seaward edges are also found on Tiahura and Fareone. It is not found in the study site on Temae except for the stand of *P. acidula*. Further west down the beach from my study site there are two small (10 meters by 10 meters) plots of *S. maritima*. The lack of this feature is perhaps due to the clearing in front of the dwellings and the clearing of the strand community during the establishment of the coconut plantation.

Humans

Since the early existence of Polynesians in Mo'orea it is probable that the reef islands surrounding the Island were occupied. There is some evidence of this. For example, old basalt fire stones brought over from the main island have been found in historic sties on the lagoon side of the motu Tiahura (Stoddart, personal communication). On the motus, due to the harsh environment, the amount of human introduced plants and land modifications is limited (Murphy, 1993). Many of the native strand species found on the motus were utilized by early Polynesians for tools, boats, and medicine (Murphy, 1993). Root crops were found in areas that "...had been modified by excavating and composting. The areas thus transformed were generally small relative to total island size." (Rappaport, 1965). In these areas of all five motu the cash crop (coconut plantation) has been planted in the last 100 years. The cash crop plantations replace a diverse native broadleaf tree community. There is a limit to where the coconuts can grow and it seems that most of the weed introduction both incidental and deliberate (through cultivation) occurs almost exclusively in this already disturbed area. *Casuarina equisetifolia*, planted by early Polynesians, has had direct effect on the beach crest scrub community. This tree has the potential to greatly reduce the established and somewhat stable strand community. As Stoddart (1975) said on his work in the Aitutaki motus "...perhaps it needs to be stressed that on many Pacific atolls we are no longer dealing simply with patterns resulting from natural immigration and extinction, but with vegetation actively managed by man."

Temae, of all the motus on Mo'orea, is heavily impacted. Most of the motu has been cleared and dwellings have been established. Where there are not homes in the center of the motu, there are coconut and gardenia plantations (*Gardenia taitensis*). Temae's overall structure has been greatly modified by land fill and the airport. These recent modifications are the continuation of the filling in of the marsh area which began when early Polynesians cleared the adjacent valley on the main island. What is left on Temae are the remnants of the original plant communities before the human modifications of the land.

Conclusions

This study is the ground work for a more extensive study including the other three motus not sampled; Tiahura, Fareone, and Ioria. Height determinate plots similar to the one on Ahi and Temae would reveal how the different ecological factors

of each of the motus determine recruitment and seedling density for plants on each of the motu. Similarly transects bisecting the different plant communities and species area curves would reveal the differences in plant diversity based on theses same ecological factors. There is also hope that studies will take place that investigate the biology of some of the seaward facing drought tolerant scrub communities before they are forced into extinction by other communities.

Understanding the rules that govern plant diversity on these small islands will be helpful to understanding the basic concepts needed for successful conservation (Cox and Moore, 1973). The motu of Mo'orea provide an encapsulated ecosystem from which studies can be made of how human must manage and preserve and environment already under stress from limited resources and natural phenomenon.

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APPENDIX

Table 1. Vascular Plants Found On Temae: Species List*

Category	Introduction	Native name
TREES		
Carica papaya	I	
Casuarina equisetifolia	I	aito, ironwood
Cocos nucifera	I/N	ha'ari
Guettarda speciosa	N	tafano
Tournefortia argentea	N	tohonu
Pandanus tectorius	I/N	fara
Leucaenea lucocephala	I	
Ricinus communis	I	
SHRUBS		
Gardenia taittensis	I	tiare tahiti
Morinda citrifolia	I	nono
Pemphis acidula	N	miki miki
Scaevola taccada	N	naupata
Suriana martima		'O'uru
Stachytarpheta urticifolia		
Lantana camara	I	
Chamaesyce atoto?		
Species 2		
Species U		
HERBS		
Bidens pilosa	I	
Cassytha filiformis	N	taino'a
Catharanthus roseus		
Emilia fosbergii		
Ipomoea littoralis	N	papati
Ipomoea pes-caprae	N	pohue
Passiflora foetida		
Portulaca sp.	N	aturi
Vigna marina	N	pipi
Tacca leonteopetaloides	I	pia
Wollistonia sp.		
Species R		
Species I		
Species Q		
GRASSES		
Cenchrus echinatus		
Fibristylis cymosa	N	pakopako
Lepturus repens	N	nanamu
Sporobolus ferilis		
Tricholaena rosea		

* The list was compiled from the Hawaiian flora and species lists from Carolyn Cartier and Francis Murphy.

Table 2. Comparison of species found on four Motus.*

CATEGORY	MOTU			
Herbs				
Bidens pilosa	Fareone	Tiahura		Temae
Boerhavia tetrandra		Tiahura		
Cassytha filiformis	Fareone	Tiahura		Temae
Catharanthus roseus	Fareone	Tiahura	Ahi	Temae
Conyza bonariensis	Fareone	Tiahura		
Davallia solida		Tiahura		
Dendrobium sp?	Fareone			
Desmodium incanum?		Tiahura	Ahi	
Dodonaea viscosa		Tiahura		
Emilia fosbergii	Fareone	Tiahura		Temae
Euphorbia hirta	Fareone	Tiahura	Ahi	Temae?
Ipomoea littoralis	Fareone		Ahi	Teame
Ipomoea macrantha	Fareone	Tiahura		Temae
Ipomoea pes-caprae			Ahi	Temae
Lipidium bidentatum		Tiahura		
Nephrolepis hirsutula	Fareone	Tiahura	Ahi	
Oxalis corniculata		Tiahura		
Passiflora foetida	Fareone	Tiahura	Ahi	Temae
Phyllanthus debilis?		Tiahura		
Polypodium scolopendria	Fareone	Tiahura	Ahi	
Portulaca oleracea	Fareone	Tiahura	Ahi	Temae
Vigna marina	Fareone	Tiahura	Ahi	Temae
Vernonia cinerea	Fareone	Tiahura		
Tacca leonteopetaloides	Fareone	Tiahura	Ahi	Temae
Triumfetta procumbens	Fareone	Tiahura	Ahi	
Spathoglottis plicata	Fareone			
Zephyranthes sp.?			Ahi	
Grasses				
Cenchrus echinatus	Fareone	Tiahura		Temae
Cyperus javanicus	Fareone	Tiahura		
Dactyloctenium aegyptium	Fareone	Tiahura		
Digitaria setigera	Fareone			
Eleusine indica		Tiahura		
Eragrostis amabilis	Fareone	Tiahura		
Fimbristylis cymosa	Fareone	Tiahura	Ahi	Temae
Lepturus repens	Fareone	Tiahura	Ahi	Temae
Melinis minutiflora	Fareone	Tiahura		
Stenotaphrum micronthum		Tiahura		
Thuarea involuta		Tiahura		
Tricholaena rosea	Fareone	Tiahura		Temae
Trees				
Carica papaya	Fareone	Tiahura	Ahi	Temae
Calophyllum inophyllum	Fareone	Tiahura	Ahi	
Casuarina equisetifolia	Fareone	Tiahura	Ahi	Temae
Cocos nucifera	Fareone	Tiahura	Ahi	Temae
Cordia subcordata	Fareone	Tiahura	Ahi	
Guettarda speciosa	Fareone	Tiahura	Ahi	Temae
Hernandia sonora	Fareone	Tiahura	Ahi	
Hibiscus tiliaceus	Fareone	Tiahura	Ahi	Temae
Pandanus tectorus	Fareone	Tiahura	Ahi	Temae
Pisonia grandis	Fareone			
Plumeria rubra	Fareone			
Terminalia catappa	Fareone		Ahi	
Thespesia populnea	Fareone			
Tournefortia argentea	Fareone	Tiahura	Ahi	Temae
Shrubs				
Colubrina asiatica	Fareone		Ahi	
Cordyline fruticosa		Tiahura		
Gardenia taitensis	Fareone		Ahi	Temae
Hibiscus ornamental hybrid	Fareone			TEmae
Lantana camara	Fareone	Tiahura	Ahi	Temae
Morinda citrifolia	Fareone	Tiahura	Ahi	Temae

Pemphis acidula	Fareone	Tiahura	Ahi	Temae
Premna serratifolia	Fareone	Tiahura		
Ricinis communis	Fareone			Temae
Scaevola taccada	Fareone	Tiahura	Ahi	Temae
Serianthes myriadena?	Fareone		Ahi	
Sophora tomentosa	Fareone	Tiahura	Ahi	
Stachytarpheta urticifolia	Fareone	Tiahura	Ahi	Temae
Suriana maritima	Fareone	Tiahura	Ahi	Temae
Tecoma stans	Fareone	Tiahura	Ahi	
Wikstroemia coriacea	Fareone	Tiahura		
Waltheria indica		Tiahura		

*The list is from Cartier (in press). Temae is included from species list on table 1.

Traditional Medicine in Mo'orea, French Polynesia: A Study of its Uses, the Practitioners, and their Plants

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ABSTRACT. This study presents information on Tahitian healers, the traditions that accompany the Mo'orean healing practices, the plants that are being used to make the medicines, and how they are employed. This paper also contains results of a study of two villages, Temae beach and Paopao Valley. These results suggest that Temae inhabitants grow, prepare, and use more medicinal plants than inhabitants in Paopao Valley and that there is an inverse correlation between the use of Tahitian medicine and the possession of French medical insurance. In sum, 100% of the twenty villagers who were interviewed used French medicine at some time, 90% also use Tahitian medicine, 90% have medicinal plants in their gardens (half of which were intentionally planted), and 70% of the villagers made their own medicines. From this data it appears that even with the availability of French medicine (75% of the people were insured for it), Tahitian medicine is still widely used on Mo'orea.

Introduction

One in four modern Western medicines was either originally discovered in plants and then synthesized, or is still extracted from their plant sources (Bird, 1991). The commercial value of these plant-derived products worldwide is more than $20 billion per year (Myers, 1992). Currently, there are more than 200 pharmaceutical companies who are investing millions of dollars searching the tropics for plants with medicinal value (Hodgin, 1991). To date, scientists have done an intensive screening of 1 in 100 plants and a cursory screening of only 1 in 10 of tropical forest plants (Myers, 1992). Unfortunately many plants, particularly in the tropics, are becoming extinct each year (Myers, 1992). The worlds dependence on medicinal plants provides a critical incentive for Western interest in biological conservation.

The knowledge of which of the earth's 280,000 plants hold medicinal value is frequently held only by the indigenous population of a region (Myers, 1992). Fortunately, medicinal plants are still used today in many areas including Polynesia. Cox (1991) states:

"There are scientific reasons to believe that the plants used in Polynesian medicine may indeed be efficacious in treating disease. A recent survey of 74 plant species used in Samoan herbal medicine showed that 86 percent demonstrated pharmacological activity in either a broad *in vitro* or *in vivo* screen".

However in many places, indigenous knowledge of medicinal plants rapidly fading as a result of Western influenced political, social, and economic changes (Myers, 1992). For example, in French Polynesia, French controlled island governments both inadvertently and overtly discourage the practice of traditional medicine through their educational institutions and medical establishments which along with economic incentives contribute to demising incentives to learn traditional medicine:

"Training in Polynesian ethnopharmacology is lengthy and offers little prospect of financial reward to young people in the increasingly monetized culture of Polynesia" (Cox, 1991).

In view of these circumstances, I chose to study and document traditional medicine use in Mo'orea, French Polynesia. Mo'orea provides an interesting ethnobotanical study sight because of the presence of both traditional Tahitian medicine and French (Western) medicines. There are several publications (i.e. Petard, 1986; Cox, 1991) concerning Polynesian plants and people but they don't

thoroughly document the tradition, the plants involved in Tahitian medicine or the opinions of the people who choose whether or not to use it. The first part of this paper describes the traditions that accompany the Mo'orean healing practices, the plants which are used to make the medicines, and how the medicines are used by healers. The second part of the paper presents the results of twenty interviews in Paopao Valley, which is primarily an agricultural area, and the village of Temae, which is a beach community where many of the inhabitants work in the hotel industry. The interviews provide data concerning the preferences between Tahitian or French medicine and how widespread the knowledge of traditional Tahitian medicine is within the general Mo'orean population.

Materials and Methods

In order to gather information on traditional Tahitian medicine, I interviewed eight healers and twenty Tahitians who were not previously known to be healers. The majority of the interviews were conducted in French; however, in cases where the interviewee spoke only Tahitian, Hinano Murphy, a local resident and teacher, served as a translator. The names of those interviewed are omitted and relabled with numbers due to the sensitivity of the subject matter. During initial interviews, I recorded the conversations on audio tape as well as with hand-written notes. However, I stopped using a tape recorder because it made interviewees apprehensive.

Part 1: Interviews with healers were made possible by Tahitian acquaintances who took me to the homes of their friends or family members who were traditional healers. Healers were asked general questions (Table 1) which were designed to extract information about Tahitian medicinal traditions including which plants are used to treat various ailments. Interviews were conducted during the day and generally lasted thirty minutes to an hour.

Table 1 - Interview Questions Asked of Known Medicinal Healers

1. What plants do you use for medicine?
2. Where do you get them?
3. How do you use them?
4. How did you learn Tahitian medicine?
5. How do you feel about French medicine?
6. Do you receive compensation for your healing?
7. What do you perceive as the cause of disease?
8. How effective is Tahitian medicine?
9. Does every family have a healer?

Part 2: The second part of my research tested several hypotheses about the current state of Tahitian and French medicine in two villages, Temae and Paopao Valley:

(1) More inhabitants of Temae will have French insurance because of their tendency to work in the hotel industry while less Paopao inhabitants will have insurance due to their tendency to be independent farmers.

(2) There will be an inverse correlation between ownership of French medical insurance and the use of Tahitian medicine.

(3) Temae villagers will use more French medicine because they are in closer proximity to the hospital and urban influence, and also because of Hypothesis 1. Paopao inhabitants would use and prepare more Tahitian medicine due to their distance from the hospital and urban influence in addtion to Hypotheses 1.

(4) Paopao gardens will have a wider variety and number of medicinal plants due to their agricultural lifestyle, whereas Temae would have less due to the seemingly less vegetated coastal area.

The twenty interviews with villagers who were not previously known to be healers were divided into two categories: ten were interviewed door to door in the coastal village of Temae and ten were interviewed in the same manner in Paopao Valley. These twenty people were asked about their use of Tahitian medicinal plants and their opinions about Tahitian verses. French medicine (Table 2).

Interviews were conducted during the day and lasted from five minutes to an hour.

Table 2 - Interview Questions Asked of Villagers in Temae and Paopao

1.	Do you have medicinal plants in your garden?
2.	What do you use them for?
3.	Did you plant them?
4.	How much time do you spend caring for them?
5.	When you or your family are sick, do you prefer Tahitian or Tahitian medicine?
6.	If you do make Tahitian medicine, how did you learn it?
7.	Do you have French medical insurance?
8.	How many members in your household?

Part 3: With the aid of local informants, I made a voucher collection of medicinal plants which are available at the U.C. Berkeley Herbarium. The plants for the were selected according to (1) a list of popular Polynesian medicinal plants in the book *Plantes Utiles de Polynesie*, (2) the plants which were shown to me by villagers and healers who use them and (3) the plants which were on display by the director of the governmentally funded Opunaho medicinal garden (*l'Economie Rurale*). The plants were collected, pressed in a plant press, dried in a dry box, and labeled with the Tahitian name (provided by the people showing me the plant), the botanical name (Petard, 1986), the date, and the location where it was found.

Data and Discussion

Diseases and Medicines

Tahitian medicines are all named according to the ailment which they are designed to heal. The categories for ailments are complicated, if not impossible, to translate (Cox, 1991). The classifications are broad and often cover a wide variety of ailments. The three most common medicines (*raau*) were *raau hea, raau ira, and raau fati. Raau hea* means "that something bad is in the organism" and it is generally used to clean or purge the body including to cure internal infections and to relieve menstrual problems. It may also be used as a preventative medicine for fetuses and children. *Raau ira* is primarily used as a preventative or curative medication for convulsions in children, nervousness, or fever. *Raau fati* is generally used for fractions, contusions, and broken bones (Grepin, 1984). Although modern Tahitians are generally aware that bacteria and viruses cause many illnesses, spirituality is still a major influence in Tahitian medicine. Some healers say that some illnesses, mostly mental, are caused by evil spirits.

There are also healers who claim that there is an element of magic in the preparations of Tahitian medicines and if a recipe were prepared by someone other than the healer, it would not be effective due to the lack of proper magic and prayer. Herbal remedies are regarded as personal property and are generally made by or under the direction of the healer to whom it belongs. Although most healers insist on preparing all their own medications to ensure that it is done correctly, there are some healers who will give out a simple recipe for a patient to prepare for themselves.

There are traditional medications for almost any ailment ranging from cancer and H.I.V. to babies who drool excessively. The precise recipe for most maladies differ between healers; however, there are many fundamental similarities. Coconut water forms the base of most medicines along with several ingredients from freshly gathered vascular plants. However, some remedies are prepared in advance and stored in glass containers for up to six months. Some fermented medicines are passed on through generations of healers and if the healer uses some of the liquid, he or she refills the bottle with additional green coconut water to replenish the medicine.

If all the necessary medicinal plant ingredients are not available in his or her garden, the healer may have to search for it in the mountains or may ask someone for it if it can be found in their garden. It is considered improper to refuse the request of a healer for a plant which is on your property because they are a gift of nature.

Some medicinal plants, such as the antibiotic *tiapito (Ophioglossum reticulatum)*, are almost extinct and can only be found in the governmentally funded medicinal garden at *l'Economie Rural*. These plants are available to healers for use as medicines free of charge. The healers also noted that medicinal plants must not have any pesticides and other added chemicals on them.

Bees from local apiaries are also used as a form of medicine. The bees are used to sting particular places on the body (acupressure points) to alleviate muscle pains and disorders.

Treatment

Most Tahitian medicine is taken for three consecutive days. The first day is to train the body to react to the medicine. On the second day, it becomes apparent as to whether the medicine will be effective, and the third day is for the cure. If a treatment is for a chronic disease, the medicine may be taken for three days, stopped for three days or three months, and then continued for another three days, and so forth.

There are also many dietary restrictions that accompany the use of Tahitian treatment. The patient is not allowed to eat salts, oil, canned or preserved foods, beef, fish from outside of the lagoon, or drink alcohol or coffee. Patients are advised to follow the traditional Tahitian diet, composed of local foods such as raw fish and breadfruit which are both eaten raw or boiled rather than fried. Exercise and cleanliness are also considered important in maintaining good health.

If the medicine does not work, it is usually said that it is because it was prepared improperly or because the patient strayed from the proper diet. However, it is also true that effectiveness varies from healer to healer and a patient may try several healers before he or she finds one with a cure which responds well with his or her body.

Tahitian and French Medicine

Apparently, Tahitian medicine is not widely respected by French doctors. According to one healer, Tahitian medicine was banned until recently because the French believed that the Tahitian healers were not qualified to practice medicine and were therefore dangerous. However, the same healer also stated that Tahitian medicine has recently become somewhat more acceptable than it was a few decades ago.

It is forbidden to mix Tahitian and French medicine because it is said that neither remedy will be effective and that the ailment may worsen. One must choose either French or Tahitian medicine and continue to use only that type of treatment. However, it is possible to be treated with French medicine and if it proves to be ineffective, one can completely cleanse himself of the French medicine and apply Tahitian medicine which may then prove to be effective.

Most healers say that French medicine is only necessary if there is some kind of major accident. A major accident includes a car accident or something more urgent and severe than a broken bone. One healer said that she will attempt to cure a patient with Tahitian medicine first but if it is ineffective, they will advise the patient to resort to French medicine.

Traditions

Although donations and gifts are accepted, patients are rarely charged for Tahitian medical treatment. There are some healers in Papeete who are charging money, but tradition deems that there is no reason to charge money because the knowledge is passed down through the family and the plants are free. One medicine woman has been invited to be a paid healer in the United States of America, but refused because she prefers to stay in Mo'orea and help people in the traditional Tahitian manner, free of charge.

Most Mo'orean families have a medicine person in their family. It is usually taught by a mother or father to a daughter or son, but children-in-law, nieces, nephews, and friends may also learn if they are interested. The education process is gradual and is often taught experientially. The healer will teach his

or her apprentice as the child is growing up. When the child or another patient is ill, the child watches and learns as the healer prepares the medicine. Knowledge is also recorded in big books of Tahitian medicine which are also passed down through the family.

When asked how their mentor learned Tahitian medicine, most healers will say that the knowledge has come from a long line of ancestors leading back to their family "tahua" or priest. The tahua is considered to be the person who discovered and passed on the medicinal recipes for that particular family. Although healers may attribute their knowledge to the ancient family tahua, my data shows that healers are currently using modern plant introductions (Table 3) and that there are new remedies for modern diseases such as HIV and diabetes (Appendix A), which implies that healers are constantly discovering new recipes independent of their mentors. Table 3 provides information on the current uses of medicinal plants for a wide variety of modern ailments.

Table 3. Common Medicinal Plants and their Uses

NPM*	Tahitian Name	Botanical Name	Medicinal Uses
?	Ahi	*Santalum insulare*	double tongue
P?	Ahia, Paa Ahia	*Eugenia malaccensis*	canker sores, lung ailments
P	Aito	*Casuarina equisetifolia*	kidney stones, double tongue
?	Anani	*Citrus sinensis*	teething, post-birthing, baths, colds
N	Ati	*Calophyllum inopyllum*	nervous children, chicken pox, eczema, acne, and seeds can be burned to ward off mosquitoes and nonos
P	Aute ute ute	*Hibiscus rosa-sinensis*	chicken pox, teething, boils, breast cancer, nervousness,
P	Auti, Ti	*Cordyline frutcosa*	broken bone (cast), hemorrhoids, post-birth, drooling babies, preventative medicine forbabies, bronchitis
M?	Avaava	*Nicotiana tabacum*	centipede stings, bites, cuts
?	Avaro	*Premna obtusifolia*	sore throat
?	Corossol	*Annona muricata*	nervousness (especially children and babies)
N?	Haari, Niu, E aa (ute ute) (red) (ere ere) (black)	*Cocus nucifera*	Base of most remedies, purging, Hea, mosquito bites, congestion
?	Hutu	*Barringtonia Asiatica*	broken bones, hemorrhoids
P or M?	Maniota	*Manihot esculenta*	hemorrhoids
N	Mati	*Ficus Tinctoria N*	abortion, purge, female problems
?	Matie	*Brachiaria paspaloides*	diabetes
P	Meia Rio	*Musa sapientum N or P?*	stop bleeding, back pain

P or M?	Metuapuaa	*Phymatosorus sp.*	broken bones, boils, teething, cold, tuberculosis, headache, stomach ache, upset babies, swelling
?	Miri	*Ocimum basilicum*	fever, negative thoughts, cuts
N?	Miro	*Thespesia populnea*	fever
P or M?	Moemoe	*Phyllanthus spp.*	weak babies, water in the ear
P?	Nono	*Morinda citrifolia*	stonefish stings, burns, acne
P or M	Oporo	*Capsicum frutescens*	boils, pimples
P or M?	Ora	*Ficus prolixa*	cancer, preventative medicine for babies
?	Painapo	*Ananus Comosus*	stomach ache
N or P?	Patoa Avaava	*Oxalis corniculata*	Hea, tonsillitis, contusions
?	Patoa Purahi	*Rorippa Sarmentosa*	ulcer, Hea, contusions
?	Pia Tahiti	*Tacca leontopetaloides*	hemorrhoids
N or P?	Piripiri	*Cenchrus echinatus*	cancer
N or P?	Purau	*Hibiscus Tiliaceus*	colds,
?	Rea Tahiti	*Safran d'oceanie*	tetanus (post bleach)
N or P?	Tahinu	*Tournefortia argentea*	sore throat
?	Tamore	*Polygonum dichotomum*	liver ailments, antibiotic
?	Taporo	*Citrus aurantiifolia*	liver ailments, stomach ache, urchin stings, sore throats, hemorrhoids
P	Tiairi	*Aleurites moluccana*	acne and eczema
	Tiapito	*Ophioglossum reticulatum*	antibiotic
P	Tiare Tahiti	*Gardenia taitensis*	ulcer, cancer, fever, chronic (sinus headache), nervousness, stomach ache, medicine for babies
?	Tiatiamoua	*Davallia solida*	broken bones, boils, cold headache, stomach ache, tuberculosis, fractures, swelling
P	To	*Saccarum officinarum*	purge, raau hea, anti-fatigue
N?	Tou	*Cordia subcordata*	purge, female problems
N or P?	Tuava, Tuava	*Psidium guajava*	tonsillitis, abortion, diarrhea
P	Uru	*Artocarpus altilis*	sore throat
N or P?	Vaianu	*Adenostemma viscosum*	broken bones, boils, cold headache
P or M?	Vi Popaa	*Mangifera indica*	children's ailments, asigaterra, food poisoning
P	Vi Tahiti	*Spondias Dulcis*	lung ailments, upset babies, raau hea

*NPM refers to Native, Polynesian introduction, or Modern (European) introduction.

Part II. Surveys of two villages -

Temae and Pao Pao

The results from these interviews reveal some interesting trends (Appendix B).

Temae

The average person interviewed in Temae was a 43 year old female representing a household of 6.2 people. They spent an average of .41 hours per week caring for their 11.4 types of medicinal plants, of which 40% were intentionally planted. There was a total of 92 plant species in all the gardens combined. All interviewees used French medicine at some time (although only 70% had French medical insurance) and Tahitian medicine (although only 90% can prepare some themselves).

Paopao Valley

In Paopao valley, the results were slightly different. The average person interviewed was a 44 year old female representing a household of 7.1 people. They spent an average of .47 hours per week caring for their 10.2 types of medicinal plants (of which 50% were intentionally planted). There was a total of 114 plant species in all the gardens combined. All interviewees used French medicine at some time (although only 80% had French medical insurance). Tahitian medicine is used by 80% of the Paopao villagers (although only 70% can prepare some themselves).

Comparison between Paopao Valley and Temae

Although the difference between the results of the Temae and Paopao surveys are minimal (Figures 1 and 2), it is interesting to note that my hypotheses were fairly incongruous with the results of this research. I had hypothesized that the Temae inhabitants would be more likely to be insured, more likely to use French medicine, and less likely to grow, prepare, or use Tahitian medicines than people in Paopao Valley. Instead, the results showed that although everyone in both villages uses French medicine

sometimes, and that Temae inhabitants grow, prepare, and use more medicinal plants than people in Paopao (although there was a larger variety of plant species found in Paopao).

I had also hypothesized that the tendency to use Tahitian medicine would increase with the decrease in French insurance, due to the expense of paying for the French medicine compared with the free traditional alternative and the data does indeed support this theory. The surveyed people in Temae had less insurance and used more Tahitian medicine than those in Paopao Valley.

Perhaps the Temae villagers use more Tahitian medicine because they have less insurance but it may also due to a stronger sense of tradition in their area because of the close proximity of the houses and the general cohesiveness of the community. The people in Paopao Valley are more spread out and each household appears to remain rather reclusive. However, to properly analyze these results, it would be necessary to have more information (including the economic status) about the interviewees.

The results of the interviews with the villagers is not only interesting when comparing the two villages, but it can also be regarded as a general survey of the Mo'orea population. Although 100% of those interviewed used French medicine at some time, 90% also use Tahitian medicine, 90% have medicinal plants in their gardens, half of which were intentionally planted, and 70% made their own medicines. From this data it appears that even with the availability of French medicine (75% of the people were insured for it), Tahitian medicine is still very popular and practical on Mo'orea.

Tahitian and French Medicine

The results of the interviews indicate that most people prefer to use Tahitian medicine but are often forced to use French medicine for immunization shots (for diseases such as elephantitis), surgery, or ailments which are undiagnosable by a Tahitian healer. Also, if a government employee needs to take sick leave from work, it is mandatory that he or she get an
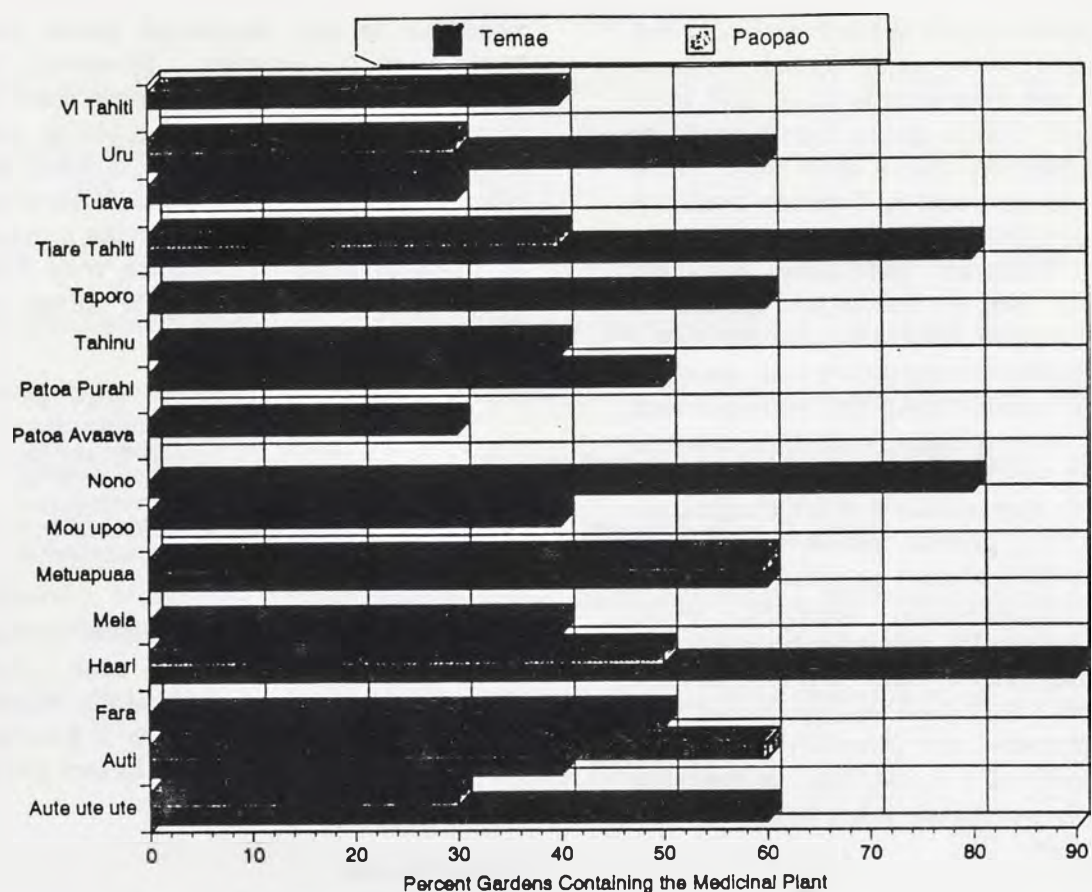
Figure 1. Eleven of the most common medicinal plants in the gardens of Temae and Paopao
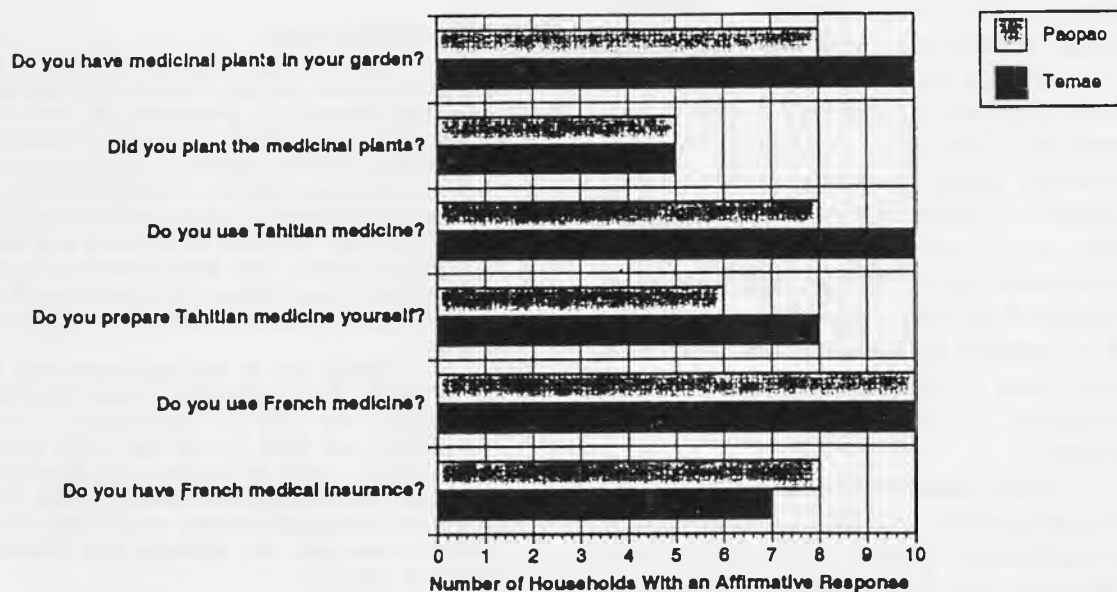

Figure 2. Results of Some Survey Questions: Temae vs. Paopao

excuse from a doctor at the French hospital. Some interviewees prefer French medicine because they believe it is faster and more convenient. Others dislike French medicine because they say that it only heals on the surface, as opposed to Tahitian medicine which cures the inside as well.

Tahitian medicine is most commonly used for babies and children's. The children's medicines (usually called *raau hea*), both preventative and curative, are most often used for nervousness, hyperactivity, malaise, excessive mucous, and other minor illnesses. Another common use of Tahitian medicine is for purging the body. Other general ailments which are treated with Tahitian medicine are cuts, fevers, headaches, eczema, acne, conjunctivitis, colds, sprains or broken bones, and hemorrhoids. There are also several people who had medicinal recipes to treat cancer, diabetes, and infertility. However, a few people didn't use Tahitian medicine because it tastes bad, takes too long, or is too difficult.

Conclusion

Tahitian medicine has not yet been lost to Western medicine in Mo'orea. Despite the high accessibility of French medicine, many ailing people are still asking healers for cures and traditional healers are continuing to prepare Tahitian medicines with local plants. Tahitian medicine is evolving with the modern age of disease as is evidenced by the remedies for new diseases such as HIV and diabetes. However, Tahitian medicine is not necessarily going to remain as strong and successful as it currently is. Some medicinal plants are close to extinction, and the preservation of medicinal knowledge is endangered by the younger generation's lack of interest in learning the medicinal secrets (due to the absence of financial incentives in a monetized Western economy).

More research needs to be done, in Tahiti and other tropical regions, before the medicinal plants and indigenous knowledge become extinct. There is tremendous potential for the world of

medicine in the medicinal plants and healers of the tropics. However, no bioassays or tests have ever been done on some of the most widely used plants, such as Tiare Tahiti (Cox, 1991). If medicinal plants are discovered and deemed profitable, then they may provide a means of preserving an area which may have otherwise been deforested or ruined for monetary profit:

> "Medicinal plants play an important role in preventing destruction of tropical lands because they can be considered potential extractive reserves (products which can be harvested and sold by the local community without contributing to severe environmental degradation" (Ryan, 1991).

Perhaps in the coming decades, Western medicine will incorporate more plant ingredients, and the tropics along with its people will be perceived as a precious resource which must remain in tact and be properly cared for.

Future Studies

In the future, there needs to be more research and bioassays on the chemical properties of Tahitian medicinal plants. Also, it would be interesting to monitor the success rate of the healers by recording the percentage of patients who are successfully cured by Tahitian medicine.

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Appendix A
Tahitian Medicinal Recipes

Due to the sensitive and confidential nature or the material, I have chosen not to publish the recipes which were given to me by the healers. Copies of the recipes may be furnished upon request. Following is a list of the ailments for which I have medicinal recipes.

Abortion:
Acne:
AIDS:
Bad spirits and negative thoughts:
Blood problems:
Boils:
Breast Cancer:
Broken bones:
Burns:
Centipede stings:
Chicken Pox:
Congestion:
Conjunctivitis:
Cuts:
Diarrhea:
Double tongue:
Eczema:
Female problems (Raau Hea):
Fever:
Fractures:
Fungus:
Head cold:
Hemorrhoids:
Hyperactivity:
Insomnia:
Kidney stones:
Leukemia:
Liver problems:
Migraine headache or sun stroke:
Mosquito bites:
Oral herpes:
Post birth (for mother):
Pulmonary problems:
Purging:
Sore muscles:
Sore throat:
Stomach ache:
Stonefish sting:
Swelling:
Teething:
Tetanus:
Tonsillitis:
Tuberculosis:
Ulcer:
Urchin spines:
Urchin stings:
Water in the ear:
Weak muscles:

Appendix B
Table 4 - Results of Interviews in Temae

Family #	1	2	3	4	5	6	7	8	9	10	Avg	%
Approximate Age	40	60	40	35	35	30	45	70	35	40	43	N/A
Sex	F	F	F	M	F	F	F	F	F	F	N/A	90 F
# People in Household?	7	12	5	3	3	4	5	10	7	5	6.2	N/A
# Medicinal Plants in Garden	3	14	14	12	9	21	14	11	9	7	11.4	N/A
Planted Intentionally?	No	Yes	Yes	No	No	Yes	Yes	No	No	No	N/A	40
Hours Spent Caring for Plants (hours)	0	1	1	0	.5	1	.2	.25	.1	0	.41	N/A
Use Tahitian Medicine?	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	N/A	100
Prepare Tahitian Medicine?	Yes	Yes	Yes	No	Yes	Yes	Yes	Yes	Yes	Yes	N/A	90
Use French Medicine?	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	N/A	100
Have French Medical Insurance?	Yes	No	Yes	Yes	Yes	Yes	No	No	Yes	Yes	N/A	70

Table 5 - Results of Interviews in Paopao Valley

Family #	1	2	3	4	5	6	7	8	9	10	Avg	%
Approximate Age	40	40	60	45	30	40	45	40	60	40	44	N/A
Sex	F	F	F	F	M/F	M	F	F	F	F	N/A	80 F
# People in Household	8	15	9	4	11	2	5	10	2	5	7.1	N/A
# Medicinal Plants in Garden	9	0	16	4	0	41	1	11	10	10	10.2	N/A
Planted Intentionally?	No	No	Yes	No	No	Yes	No	Yes	Yes	Yes	N/A	50
Hours Spent Caring for Plants (hours)	0	0	1	0	0	2	0	1	.5	.2	.47	N/A
Use Tahitian Medicine?	Yes	Yes	Yes	No	No	Yes	Yes	Yes	Yes	Yes	N/A	80
Prepare Tahitian Medicine?	No	Yes	Yes	No	No	Yes	Yes	Yes	Yes	Yes	N/A	70
Use French Medicine?	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	N/A	100
Have French Medical Insurance?	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	No	No	N/A	80

Table 6 - Number and Types of Plants In Paopao Gardens

Family #	# of Plants	Medicinal Plants Found in Paopao Garden
1	9	Auti, Uru, Patoa Purahi, Metuapuaa, Meia, Tuava, To, Vi Tahiti, Haari
2	0	She says that she doesn't have any
3	16	Mou upoo, Tiapito, Patoa Purahi, Taataahiara, Metuapuaa, Auti, Taporo, Haari, Ofeofe, Ora, Hehaa, Piripiri, Tiare Tahiti, Corossol, Tuava, Vi
4	4	Metuapuaa, Tiatiamouaa, Auti, Miro
5	0	He says that there aren't any.
6	41	Ahia, Moemoe, Ora, Uru, Corossol, Avota, Taporo, Te Tumu Anani Popaa, Rea, Auti, Metuapuaa, Tiatiamoua, Patoa Purahi, Purau, Haari, Kava, Pistas, Taofe, Opuhi, Litchi, Croton, Pohue, Teriveti, Tamiomao, Miri, Hutu, Oporo, Maa pape, Tiare Tahiti, Aute, Miro, Otime, Tou, Ame, Ati, Nahe, Fouka, Fara, Mou upoo.
7	1	Mati
8	11	Metuapuaa, Taataahiara, Patoa Purahi, Tiare Tahiti, Iita, Toroura, Otime, Hehaa, Moemoe, Aloe, Mou upoo.
9	10	Amoa, Aute, Auti, Metuapuaa, Tuava, Patoa Purahi, Meia, Vi Tahiti, Evi, Haari.
10	10	Rea, Uru, Aute, Haari, Auti, Tiare Tahiti, Mou upoo, Vi, Iita, Nono.
Total	92	

Table 7- Number and Types of Plants In Temae Gardens

Family #	# of plants	Medicinal Plants Found in Temae Garden
1	3	Tiare Tahiti, Nono,
2	14	Hutu, Aute, Haari, Miro, Tiare Tahiti, Taporo, Metuapuaa, Auti, Uru, Nono, Aito, Meia Rio, Tiapitu, Tamore
3	14	Tiare Tahiti, Metuapuaa, Vi Tahiti, Avaro, Corossol, Iita, Tafano, Taporo, Auti, To, Uru, Haari, Tiairi, Aito
4	12	Avaro, Taporo, Tiatiamoua, Tahinu, Miro, Tiare Tahiti, Haari, Aute, Tou, Nono, Tianina, Fara
5	9	Fara, Uru, Meia, Nono, Aito, Haari, Auti, Patoa Purahi, Aute
6	21	Tiatiamoua, Metuapuaa, Haari, To, Patoa Purahi, Patoa Avaava, Vi Tahiti, Nono, Uru, Taporo, Vi Popoaa, Fei, Tou, Aute, Auti, Tiare Tahiti, Mou'upoo, Taporo, Avota, Piripiri, Moemoe
7	14	Metuapuaa, Tiairi, Tiare Tahiti, Aute, Tahinu, Tou, Iita, Haari, Fara, Meia, Nono, Patoa Purahi, Tafano, Niu
8	11	Metuapuaa, To, Nono, Hutu, Tafano, Tahinu, Vaihinu, Tianina, Fara, Aute, Haari
9	9	Tiare Tahiti, Haari, Nono, Avaro, Meia, Taporo, Uru, Fara, Miri
10	7	Tahinu, Tuava, Taporo, Metuapuaa, Tiare Tahiti, Haari, Tapotapo
Total	114	

Table 8: Frequency and Types of Plants in Ten Temae Gardens

Plants Found in Gardens of Temae	Botanical Name	Frequency (%) (% gardens with the plant in it)
Avota	*Persea americana*	10
Corossol	*Annona reticulata*	10
Fei	*Musa troglodytarum*	10
Miri	*Ocimum basilicum*	10
Moemoe	*Phylanthus amarus?*	10
Mou upoo	*Kyllinga nemoralis*	10
Niu	*Leucas decemdentata*	10
Patoa Avaava	*Oxalis corniculata*	10
Piripiri	*Cenchrus echinatus*	10
Tamore	*Polygonum dichotomum*	10
Tapotapo	*Annona squamosa*	10
Tiapito	*Ophioglossum reticulatum*	10
Tuava	*Psidium guajava*	10
Vaianu	*Adenostemma viscosum*	10
Vi Popoaa	*Mangifera indica*	10
Vi Tahiti	*Spondias dulcis*	10
Hutu	*Barringtonia asiatica*	20
Iita	*Carica papaye*	20
Miro	*Thespesia Populnea*	20
Tiairi	*Aleurites moluccana*	20
Tianina	*Hernandia nympahaeifolia*	20
Tiatiamoua	*Davallia solida*	20
Aito	*Casuarina equisetifolia*	30
Avaro	*Premna obtusifolia*	30
Patoa Purahi	*Rorippa sarmentosa*	30
Tafano	*Guettarda speciosa*	30
To	*Saccharum officinarum*	30
Tou	*Cordia subcordata*	30
Auti	*Cordyline fructosa*	40
Meia	*Musa spp.*	40
Tahinu	*Tournefolia argentea*	40
Fara	*Pandanus tectorius*	50
Uru	*Artocarpus altilis*	50

Aute	*Hibiscus rosa-sinensis*	60
Metuapuaa	*Phyatosorus sp.*	60
Taporo	*Citrus aurantifolia*	60
Nono	*Morinda citrifolia*	80
Tiare Tahiti	*Gardenia taitensis*	80
Haari	*Cocos Nucifera*	90

Table 9: Frequency and Types of Plants in Ten Paopao Gardens

Plants Found in Gardens of Paopao	Botanical Name	Frequency (%) (% gardens with the plant in it)
Te Tumu Anani Popaa	Citrus Grandis	10
Tiapito	Ophioglossum reticulatum	10
Ofeofe	Centosteca lappacea	10
Piripiri	Cenchrus echinatus	10
Ahia	Eugenia malaccensis	10
Avota	Persea americana	10
Purau	Hibiscus Tiliaceus	10
Kava	Piper methysticum	10
Pistas	Eugenia cumini	10
Taofe	Coffea arabica	10
Opuhi	Amonum cevuga	10
Litchi	Litchi Chinensis	10
Croton	?	10
Pohue	Mimosa pudica	10
Teriveti	?	10
Tamiomao	?	10
Miri	Ocimum basilicum	10
Hutu	Barringtonia asiatica	10
Oporo	solanum uporo	10
Maa pape	Commelina diffusa	10
Tou	Cordia subcordata	10
Amae	Thespesia populnea	10
Ati	Calophyllum inophyllum	10
Nahe	Angiopteris evecta	10
Fouka	Momordica charantia	10
Fara	Pandanus tectorius	10
Mati	Ficus tintoria	10
Toroura	Cyathula prostrata	10
Amoa	Nephrolepis spp.	10
Evi	Spondias dulcis	10
Nono	Morinda citrifolia	10
Meia	Musa spp.	20
Taataahiara	Dicrocephala integrifolia	20
Taporo	Citrus aurantifolia	20

Ora	*Ficus prolixa*	20
Hehaa	*Lindernea crustacea*	20
Corossol	*Annona muricata*	20
Tiatiamoua	*Davallia solida*	20
Miro	*Thespesia populnea*	20
Moemoe	*Phylanthis amarus*	20
Rea	*Curcuma longa*	20
Otime	*Menthe arvensis*	20
Iita	*Carica papaya*	20
Uru	*Artocarpus altilis*	30
Patoa Avaava	*Oxalis corniculata*	30
Tuava	*Psidium guajava*	30
Aute	*Hibiscu rosa-sinensis*	30
Vi Tahiti	*Spondias dulcis*	40
Mou upoo	*Kyllinga nemoralis*	40
Tiare Tahiti	*Garendia taitensis*	40
Patoa Purahi	*Rorippa sarmentosa*	50
Haari	*Cocos Nucifera*	50
Auti	*Cordyline fructosa*	60
Metuapuaa	*Phymatosorus sp.*	60

1-MONTH-MONOGRAPH

M