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THE BIOLOGY AND GEOMORPHOLOGY OF TROPICAL ISLANDS

Student Research Papers, Fall 1996

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

Above: The 1996 Moorea Class, on the front lawn of the Gump Research Station, with Cook's Bay and fringing reef in the background. Standing, from left: Jennifer Conners, Morgan Hannaford (Graduate Student Instructor), Sandra Trujillo, Solomon Dobrowski, Brent Mishler (Professor, IB), Ylva Carosone, Stephanie Yelenik, Joanna Canepa, Kendra Bergstrom, Peter Weber (Graduate Student Instructor), Julianne Ludwig, Larry Rabin, Damien Filiatrault, Steve Strand (Executive Director, Gump Research Station), and Carole Hickman (Professor, IB). Reclining or seated, from left: Xavier Mayali, Chris Feldman, Sapna Khandwala, Isa Woo, Tracy Benning (Professor, ESPM), Patricia Sánchez Baracaldo (Graduate Student Instructor), and Michael Emmett.

Below: The beach and lagoon at Tetiaroa, site of a class field trip, with Tahiti (left) and Moorea (right) in the background.

1996 Student Research papers

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University of California, Berkeley

Biology and Geomorphology of Tropical Islands

Introductory Remarks

This is a rare course in the modern age of college education, an interdisciplinary course open only by application and interview, that occupies one whole semester (13 units), with a student : teacher ratio of about 2:1, featuring all-inclusive research experience and full immersion in the life of science and a foreign culture. The 15 students spend a month in Berkeley for lectures and labs five days a week, then go to the Richard B. Gump South Pacific Biological Research Station on Moorea in French Polynesia for two months to carry out an intensive research project as well as some general educational field trips and group projects, finally returning to Berkeley for two weeks of non-stop data analysis, library research, and writing. Following a round of peer reviews, the students prepare camera-ready copies for their papers and give an oral presentation in a professional-style symposium.

The 1996 class, whose papers follow in this book, set new standards of achievement and formed bonds with each other and the teaching staff that will last a long time. The professors (who spent 1-3 week periods each on Moorea) and the Graduate Student Instructors (who spent the whole two months on Moorea) had a unique opportunity to help each student design their project, go with them in the field, observe their data-gathering and work habits, and assist them in the analysis and write-up phase. This close living and working situation allows the transfer of fundamental methods, theories, and even attitudes about science, in addition to the expected transfer of basic information about islands and their biology. It is extremely rewarding for us to see students transform into research scientists in front of our eyes!

Such a course is an expensive and time consuming effort that would not be possible without the help of many people. As lead instructor, I had the privilege of working with several other faculty members, all experts in tropical studies but with a wide spectrum of specialties. In addition to myself, field teaching was done by professors Tracy Benning, Roy Caldwell, Carole Hickman, and David Stoddart, all of whom gave lectures at Berkeley as well. Additional faculty who gave lectures on campus include Carla D'Antonio and Vince Resh. Dr. Cherie Semans gave presentations on campus and visited Moorea to help students with cartography; the results of her efforts are evident in this volume.

The three intrepid Graduate Student Instructors, Morgan Hannaford, Patricia Sánchez, and Peter Weber deserve special mention. They were responsible for the day-to-day running of the course on Moorea, helping the students in many ways ranging from mundane logistical matters to sophisticated scientific techniques. We literally couldn't have done without them!

We thank the Director of the Gump Research Station, Dr. Vince Resh, for facilitating the course's stay at the Station. The Executive Director, Dr. Steven Strand, who resides at the station, helped in all aspects of the course, kept everything working, and was generous with scientific assistance and advice. His wife, Pat Strand, also shared her hospitality and biological expertise and was extremely helpful to all. Thanks also to Frank Murphy for organizing the welcoming tamara'a, Hinano Murphy for her helpful advice, and Marimari Kellum for opening her wonderful garden to the students. We also are grateful to Gordon and Betty Moore (and the Moore Family Foundation) for their continuing support of laboratory and computation facilities at the Station.

The three departments involved (Environmental Science, Policy and Management, Geography, and Integrative Biology) committed financial support, personnel, equipment, and facilities. In particular we would like to thank Julie Meyers in Integrative Biology for dealing with finances and accounting, Dorothy Tabron in Integrative Biology for help with supplies and equipment, and Don Bain in Geography for help with computation.

Brent D. Mishler
Department of Integrative Biology
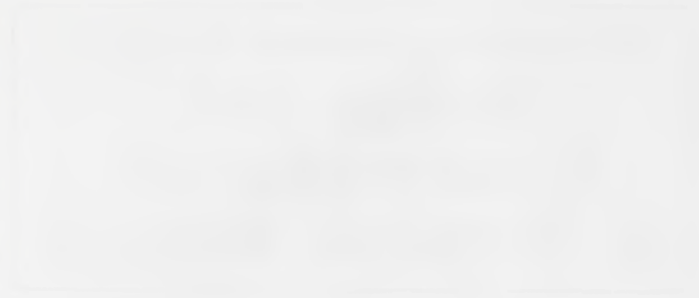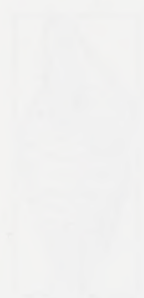
The Distribution and Morphology of Seagrass *(Halophila decipiens)* in Moorea, French Polynesia

Michael Alan Emmett

Environmental Sciences Department, College of Letters and Science
University of California, Berkeley 94720

ABSTRACT. A survey of the seagrass resources in Opunohu and Paupau Bays on the island of Moorea, French Polynesia was conducted between October and November, 1996. A single species, *Halophila decipiens* Ostenfeld. was located in both bays. Each of the bays contained beds in the shallow estuarine backbay areas and the deeper lagoon area of the backreef slope. These seagrass meadows ranged from 3 - 15 hectares in area. Biomass samples and ecological data were taken at two study areas in each bay, one in each of the two habitat types. Leaf surface area, internode length, biomass, percent seagrass cover, and the internodal growth rate data were collected and reported for each study site. The plant morphology within the bed structures was found have statistically significant variations, depending on habitat type and the location within the bed. The plants in the bed margins had a larger internodal length than those in the interior portions of the bed structure ($p=0.0091$). The leaf-blade surface areas were smaller in the bed margins than in the interior ($p=0.0336$). The internodal lengths were shorter in the lagoon habitats ($p=0.0140$). The leaf-blade surface areas were larger in lagoon habitats than in the estuarine areas of the two bays ($p<0.0001$). Leaf surface area was also found to be greater in Opunohu Bay than in Paupau Bay ($p<0.0001$). These morphological differences suggest that *H. decipiens* is a colonizing species adapted to a low light habitat and that it is able to adjust its morphology to accommodate environmental variables.

Introduction

Seagrasses are vascular marine macrophytes that inhabit estuarine and nearshore continental margins in temperate and tropical regions. Seagrass communities provide valuable ecological functions in these environments. They are highly productive ecosystems and are a primary component of the detritus-based food web. Seagrass beds contribute other ecological benefits by providing shelter, habitat, and organic nutrients to these marine communities (Helfferich and McRoy 1980; Phillips 1984; Thayer et al. 1984).

Seagrasses differ from other marine macrophytes, such as algae, because they maintain much of the physiology and morphology of terrestrial plants. It is believed that they evolved from related terrestrial grasses during the Cretaceous Period (den Hartog, 1970). They have leaves (blades) that can extract nutrients from the water column, but unlike other marine plant species, they also have a rhizome and root system which obtain nutrients from the substrate (Short and McRoy 1984; Erftemeijer and Middelburg 1995). This root system anchors the plant to the substrate and provides a secondary ecosystem function of stabilizing bottom sediments (Phillips 1984). As angiosperms, they reproduce sexually utilizing flowers and fruits, but also colonize an area through the extension of the rhizome structures.

Tropical seagrasses inhabit intertidal marine and estuarine habitats where water temperatures average above 20° C (Larkum and den Hartog 1989). They are found in lagoon and bay environments often behind protecting coral reef formations. Seagrasses can grow in a wide range of substrate types from coral sands to muddy clay sediments. The most widely accepted theory on the distribution of tropical seagrasses in the Western Pacific is that they dispersed eastward from a center of origin near Malaysia, where seagrass species diversity is highest (Larkum and den Hartog 1989; Mukai 1993). In a similar pattern to that observed with many other tropical marine species, seagrass diversity declines with the distance east from this center of origin. The limit of this distribution in the Northern hemisphere is the Hawaiian Islands and in the Southern hemisphere it is the Society Islands. In each of these locations, only a single species of seagrass

exists. *Halophila decipiens* is that singular species at the location of this study.

Halophila decipiens, is the only pantropic seagrass species. It is widely distributed in the tropical regions of the Atlantic, Pacific, and Indian Oceans (den Hartog 1970). *H. decipiens* is adapted to low light conditions of turbid estuarine and deep marine environments. In deeper waters (below 30m) it typically forms open monospecific communities (den Hartog 1970). It has been reported up to depths of 85 meters in clear waters. *H. decipiens* tolerates habitat disturbance and is considered to be a colonizer species (Birch and Birch 1984). Because of its ability to colonize these depths, it can be a major source of organic material to these regions which can otherwise have only barren substrates (Josselyn et al. 1986).

Halophila decipiens grows along the marine substrate on thin horizontal rhizomes which can be exposed or below the sediment surface (den Hartog 1970; Phillips and Meñez 1988). The rhizomes have nodes spaced from 10 - 40 mm on which a single root is attached. Secondary branching may occur from these nodes forming rhizome shoots that can be indistinguishable from the main shoot. Single leaf pairs, 10 - 30 mm in length and 3 - 7 mm in width, form on a short 1 - 10 mm lateral shoot from these nodes. The leaf-blades are roughly elliptical and have small unicellular hairs on the surfaces. *H. decipiens* is monoecious with male and female flowers forming between the leaf pairs. The male flower is ephemeral. An elliptical fruit forms from the female flower and is approximately 1.5 mm along the minor axis and 2.5 mm along the major axis.

The occurrence of *H. decipiens,* in French Polynesia was first recorded in 1875 in Papeete Harbor, on the island of Tahiti, at a depth of 18m (den Hartog 1970). A shallow water *Halophila* bed with a patchy distribution was reported in Opunohu Bay on the island of Moorea (Galzin and Pointier 1985). The existence of *H. decipiens* on Moorea was noted in a recent survey of the biogeography of tropical seagrasses (Mukai 1993). Until this study, however, no details of the ecology or distribution patterns of *H. decipiens* on Moorea have been described. This study reports the distribution and morphology of *Halophila decipiens* Ostenfeld in the estuarine and marine

environments of the two deep water bays on the island of Moorea, French Polynesia.

H. decipiens occurs in two distinct environments. Each is characterized by low and variable light conditions. The first is the shallow waters of near shore and estuarine where light is limited by water turbidity. The second area is in the deeper clear water of lagoons, where light is limited by the greater depth. The first objective of this study was to examine *H. decipiens* within these two areas to determine whether there are differences in the plant morphologies associated with differences in the environments. Because *Halophila* is a colonizer species, it may also exhibit differential morphologies when expanding into new or recently disturbed habitat, as compared to when it is growing in an already established matrix. In order to examine this second hypothesis, the study compares the morphologies between the plants at the margins of the distribution and in established areas of the beds. Finally, the study examines the seagrass in each of the two bays to determine if there are morphology differences between the plants between these locations. The plant morphology characteristics measured for this research project were leaf size, internode length, number of fruiting bodies on the plant sections, and above ground and below ground biomass. The ecological data collected were location, water depth, percent substrate cover of seagrass, and rhizome growth rate.

Materials And Methods

Study site
A survey of the seagrass resources in Paupau and Opunohu Bays, on the island of Moorea in French Polynesia, was conducted during the months of October and November of 1996 (Figures 1 and 2). Laboratory and field equipment, logistical support, and living accommodations were provided by the Richard Gump Biological Research Station of the University of California, Berkeley. The island of Moorea is located at 17°32' S latitude, 149°50' W longitude in the Society Archipelago. It is classified as a high oceanic island with its volcanic origins approximately 1.5 - 2.2 million years ago (Nunn 1994). The Island is surrounded by both fringing and barrier reef systems. There are natural and artificial channels through the reefs, leading to estuarine
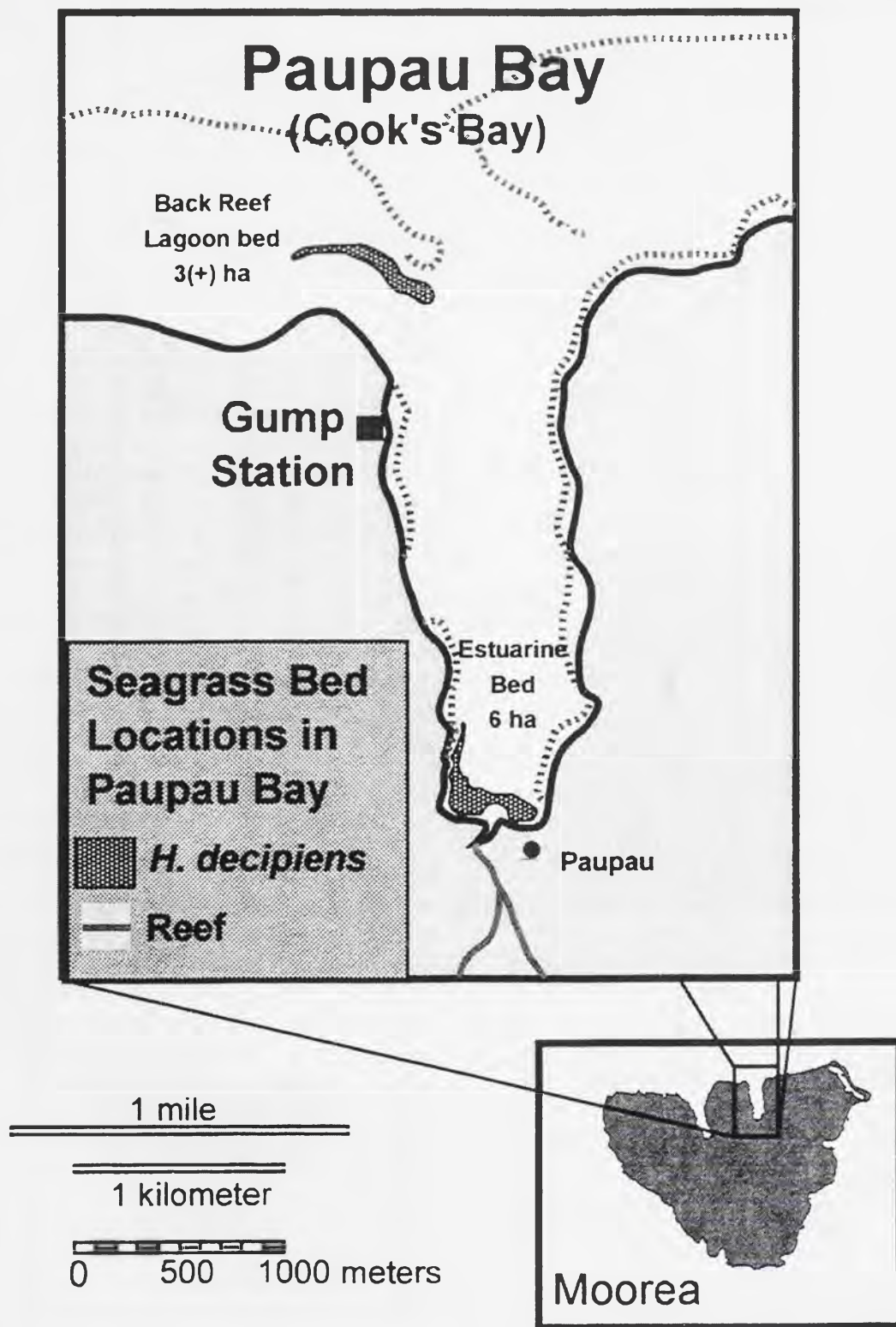
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Figure 1. Map of study area in Paupau Bay and the location of *Halophila decipiens*.
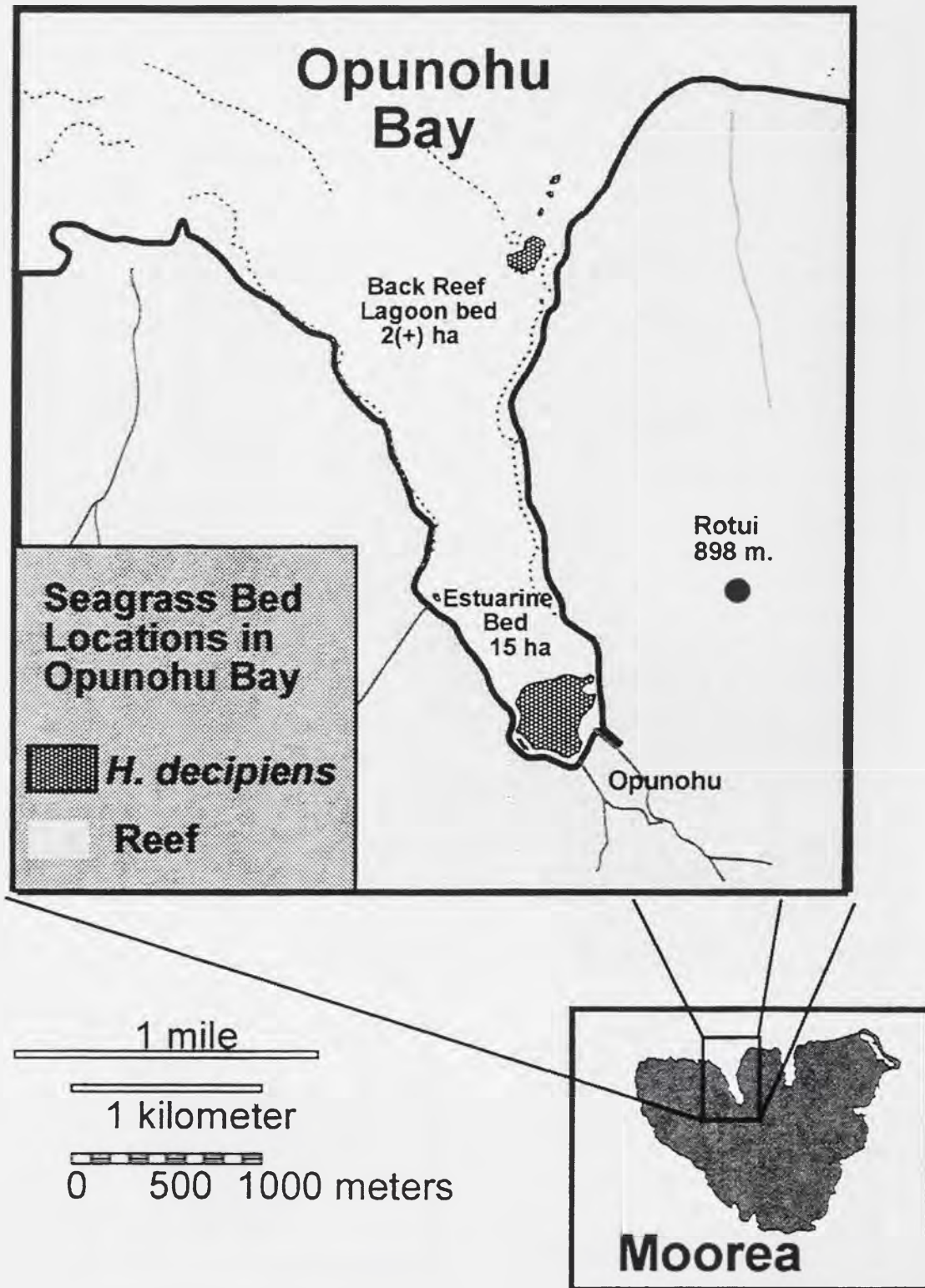
Figure 2. Map of Study area in Opunohu Bay and the location of *Halophila decipiens*.

bays and lagoons which have formed between the two reef systems. The mountainous regions are highly eroded with steep water drainage channels flowing into these bays.

Opunohu and Paupau Bays are the two largest bays on the island. Both are large, north facing, deep water bays with roughly similar areas and shape (Galzin and Pointier 1985). Major rivers, draining large catchment areas, flow into the back of these two bays creating shallow areas of alluvial deposits at the southern ends. These deposits are made up of basalt sand and gravel, silt, and other organic sediments deposited by the river. Otherwise, the bays have narrow fringing reef shelves near shore which drop off steeply to depths of up to 55 meters. The lagoon systems in these bays form behind the algal ridge of the barrier reef, on either side of the entrance channel. The area between the two reef systems has a coral sand substrate which slopes downward to depths up to 45 meters.

Seagrass survey

I surveyed the two bays using standard snorkeling equipment. Access to the bays was either by small boat or from shore. The areas surveyed were limited to those that could be safely reached by free diving or where water clarity allowed a clear view of the bottom below these depths. During the preliminary surveys of the lagoon areas, where water clarity was high, I was towed at low speed behind a boat in order to cover more area in a short period of time. On two occasions, members of the University of California Diving Board made dives in Opunohu Bay using SCUBA in order to confirm the existence of, and take samples in, the deep water beds at this location.

I determined the locations and bed boundaries of four large seagrass meadows by using estimates of distances to shore and bay navigational markers. I also used compass triangulation to 3 and 4 fixed landmarks and GPS measurements, however, the spatial resolution of these techniques proved to be no more accurate than the above method. The locations of the seagrass bed boundaries and my study sites where plotted onto a navigational chart of the bays (SHOM 1989). I made depth measurements at the study sites and at the bed margins with a diver's depth gauge. These measurements were compared with the bathymetric chart of the bays for additional

accuracy in mapping the beds. A video tape record was made of the SCUBA dives in Opunohu Bay. Depth and percent cover (see below) were recorded on the video record as well as a view of the seagrass bed structures at these depths. Voucher samples of the *Halophila decipiens* collected in each bay and in each habitat type were sent to the Jepson Herbarium at the University of California, Berkeley.

Morphology Sampling

I selected two study areas in each bay representing the two different habitat types found in the survey. I will refer to these in this study as *lagoon*: for the deep water sites behind the barrier reef, and *estuarine*: for the sites in the shallow back-bay near the river inflows. Within these four areas, I selected three sites on the bed margins and three sites in the bed interiors in order to study differences between these two bed locations. These sites were marked with stakes and floatation markers so that they could be located later. To measure rhizome growth rates, I placed marker tags behind the terminal leaf pairs on three plants at each site (Dennison 1990a). These tags were reexamined after a period of 10 to 15 days and the number of new nodes was recorded. I collected density, biomass, and depth data at three random samples around each of these six sites. A total of 72 sample sets were collected.

To measure seagrass density, I placed a 0.25 m^2 PVC quadrat with a 5 x 5 wire grid into the sediment at the random sample location (Dennison 1990b). The percent cover was estimated as a the number of grid line intersections that overlaid seagrass out of a total of 25 intersections. I measured and recorded water depth at each sample site with a diving depth gauge. I collected biomass samples as sub-set of this quadrat using a second 100 cm^2 sampling quadrat (Ott 1990). The quadrat was constructed as a modified corer with a 10cm x 10 cm bottom and a 5 cm high rim enclosing three sides. The quadrat was inserted under the substrate inside the perimeter of the larger PVC quadrat and lifted upwards, thereby capturing both above-ground and below-ground biomass samples. These samples were placed in plastic bags and transported back to the lab. I adopted this biomass sample technique after several attempts using standard square frames and corer devices proved too difficult to use or unsafe

within the limits of the free diving research protocols.

In the lab, I separated the seagrass from the substrate collected with the samples. The seagrass was rinsed in saltwater and the epiphytes that could be separated without damaging the plants were removed and discarded. Three intact shoots were removed from each sample bag for plant morphology measurements. Internode length was measured as the distance between two consecutive roots. Leaf length and leaf width were measured at their respective maximums. I differentiated leaves on the main rhizome and those on secondary branches when recording the data. Leaf surface area was estimated as an ellipse with the major and minor axis being length and width respectively. This calculation includes top and bottom surfaces of the leaf. All morphometric measurements were made to the nearest millimeter. I recorded the number of secondary branches as a ratio of branches to nodes on the main rhizome of each plant section. I recorded the number of fruiting bodies as a ratio of fruits to total leaf pairs on the plant section.

All of the plants within each sample were separated into above-ground and below-ground fractions. The above-ground parts were the leaves, petioles, leaf sheaths, fruiting bodies and leaf buds. The below-ground parts were the rhizomes and roots. The samples were treated in a 5 percent solution of acetic acid for 4 hours to remove encrusting calcareous algae and epiphytes (Ott, 1990). They were then rinsed in fresh water and dried at 48° C for 48 hours. I weighed the dried samples on a laboratory scale. The mean of three separate measurements was recorded for each sample.

Results

Seagrass survey

Halophila decipiens Ostenfeld was found in Paupau Bay (Figure 1) and Opunohu Bay (Figure 2). Both bays had seagrass beds in the shallow estuarine and deeper lagoon areas. The range in the bed size was from 2-15 hectares (Table 1). There is uncertainty in the size of the beds in the lagoon habitats because the depths of these beds prevented mapping with the methods available for this study. The video records made with SCUBA at the Opunohu Bay

lagoon site show that this bed is certainly larger than the surface survey estimates. Anecdotal evidence provided by other divers indicate that the lagoon bed in Paupau extends to at least a depth of 20 m. The areas given in Table 1 for the lagoon sites should, therefore, be considered lower limits for the size of these beds. The depth distribution varied between the beds. Bed depths in the estuarine regions of the bays ranged from 0.5-8 m whereas the depth in the lagoons was between 4.5- 38.7 m (Table 1). As with the bed areas, there is some uncertainty in the maximum depth in the deep beds at the lagoon sites.

H. decipiens was also found in Vairae Bay, on the east side of the island. The distribution was in small discreet patches ranging in size from two to five meters in diameter in the shallow estuarine portion of the bay. The limited time available for this research project precluded a more detailed examination of these beds. This distribution is noted only for possible future study as no morphology data was collected for these sites.

Morphology sampling

Two hundred sixteen *H. decipiens* shoots were examined from 72 field samples to determine if morphological differences paralleled the variations in the habitats seen in the distribution survey. The following results are expressed as the mean ± the standard deviation of these measurements. The overall mean internode length for this study was 22.1±6.91 mm (Table 2). The mean leaf length and leaf width in this study were 17.6±4.12 mm and 5.5±1.01mm respectively. Estimating top and bottom leaf surfaces area as ellipses, the mean leaf surface area for all sample sites was 157.4±63.85 mm².

Table 1. Seagrass Bed size and depth distribution in Opunohu and Paupau Bays.

	OPUNOHU		PAUPAU	
	estuarine	lagoon	estuarine	lagoon
Bed Area	15 ha	2 (+) ha	6 ha	3 (+) ha
Depth Range	0.5-12 meters	6.5- 39 meters.	0.5-4.0 meters	4.5-20 meters

Table 2. Mean sample measurements of *H. decipiens* morphology by habitat type and bed location.

| | OPUNOHO BAY | | | | PAUPAU BAY | | | | |
| | Estuarine | | Lagoon | | Estuarine | | Lagoon | | Mean |
	margin	center	margin	center	margin	center	margin	center	
Internode Length (mm)	21 (6.0)	23 (6.4)	25 (7.7)	21 (6.0)	26 (8.8)	22 (7.3)	20 (5.7)	21 (6.2)	22.1 (6.91)
Leaf Length (mm)	18 (3.3)	20 (3.9)	15 (2.5)	16 (2.3)	22 (4.4)	22 (3.8)	16 (2.1)	14 (2.1)	17.6 (4.12)
Leaf Width (mm)	5.4 (0.83)	5.8 (0.97)	5.3 (1.02)	5.5 (0.78)	6.2 (1.19)	6.2 (1.02)	5.2 (0.69)	4.7 (0.69)	5.5 (1.01)
Surface Area (mm^2)	156 (49.9)	192 (60.7)	127 (42.3)	144 (37.2)	220 (85.2)	219 (67.7)	133 (32.4)	107 (29.1)	157.4 (63.85)
Branch Ratio	0.37 (0.17)	0.26 (0.84)	0.44 (0.17)	0.33 (0.09)	0.31 (0.25)	0.35 (0.20)	0.33 (0.22)	0.24 (0.28)	0.33 (0.194)
Bud Ratio	0.41 (0.15)	0.25 (0.12)	0.47 (0.18)	0.34 (0.09)	0.22 (0.16)	0.37 (0.19)	0.33 (0.26)	0.28 (0.25)	0.33 (0.190)
Fruit Ratio	0.14 (0.13)	0.27 (0.25)	0.19 (0.26)	0.48 (0.28)	0.11 (0.13)	0.05 (0.09)	0.15 (0.26)	0.15 (0.16)	0.20 (0.236)

The above data is expressed as the mean ± (standard deviation).
Internode length, leaf length, and leaf width are in mm. Leaf surface area is in mm^2.

The mean leaf surface area was larger on leaves located on the main rhizome as compared to those on the secondary branching shoots. The mean surface area of the leaves on the primary rhizome was 171.5±62.7 mm^2 verses a mean surface area of 124.9±53.8 mm^2 for leaves on the secondary shoots. The ratio of branches to the number of nodes on a shoot is an indicator of the degree of secondary branching occurring in these *Halophila* beds. The mean branch to node ratio was 0.33±0.19 (Table 2). Similarly, the ratio of fruits to the number of leaf pairs indicates the amount of these reproductive structures in the beds. The mean fruit to leaf pair ratio was 0.20±0.24. Table 2 shows additional morphology data organized by site, bed location, and habitat.

Ecological measurements were taken at the sample level. A total of sixty-two biomass samples, separated into above-ground and below-ground fractions, were collected and processed. This did not include the samples collected in the SCUBA dives in Opunohu Bay, as some of that material was used for voucher samples. Samples from one site in the estuarine area of Paupau Bay were lost in the lab and one sample was removed from the data base because it was coded incorrectly. The mean biomass for this study sample was 29.7±20.9 g m^{-2}. Of this total the mean above-ground fraction was 15.5±11.9 g m^{-2} and the below-ground fraction was 14.2±11.8 g m^{-2} (Table 3). The mean above-ground to below-ground ratio for this study was 1.4±0.98. Density measurements, as percent cover estimates, were recorded for each sample site. The overall mean percent cover by *H. decipiens* was 49±28% (Table 3).

The density and biomass measurements were used primarily to document and aid in the selection of sample sites on the bed margins. The mean biomass of the samples on the bed margins was less than that for samples in the bed interiors. The mean biomass on the bed margins was 14.6±7.2 g m^{-2} compared to a mean biomass of 42.1±20.4 g m^{-2} in the bed interiors. Density estimates followed a similar pattern with percent cover at bed margins and bed interiors of 0.27±0.13 and 0.69±0.21 respectively.

Table 3. Mean sample measurements of *H. decipiens* ecological characteristics by habitat and location.

	OPUNOHO BAY				PAUPAU BAY				
	Estuarine		Lagoon		Estuarine		Lagoon		Mean
	margin	center	margin	center	margin	center	margin	center	
above-ground Biomass (g m^{-2})	11.7 (3.93)	27.8 (17.3)	7.3 (4.74)	24.4 (10.9)	10.6 (6.48)	18.6 (9.00)	4.5 (2.43)	14.0 (7.29)	15.5 (11.9)
below-ground Biomass (g m^{-2})	6.5 (4.23)	14.1 (5.40)	5.9 (3.98)	20.7 (12.5)	6.3 (2.69)	22.6 (14.3)	6.2 (1.94)	29.5 (13.8)	14.2 (11.8)
Total Biomass (g m^{-2})	18.2 (5.56)	41.9 (21.3)	13.2 (7.46)	45.1 (21.9)	16.9 (8.31)	41.1 (20.7)	10.7 (2.34)	43.5 (20.6)	29.7 (20.9)
Biomass Ratio	4.2 (6.31)	2.1 (1.38)	1.6 (0.89)	1.4 (0.62)	1.7 (1.23)	1.0 (0.58)	0.8 (0.53)	0.5 (0.13)	1.40 (0.98)
Percent Cover	0.24 (0.12)	0.56 (0.15)	0.36 (0.14)	0.84 (0.10)	0.22 (0.11)	0.73 (0.20)	0.24 (0.12)	0.70 (0.22)	0.49 (0.28)
Internode Growth Rate (internode day^{-1})	0.35 (0.0)	0.33 (0.10)	0.68 (0.15)	0.48 (0.11)	0.40 (0.14)	0.40 (0.11)	0.47 (0.06)	0.60 (0.26)	0.43 (0.16)

The above data is expressed as the mean ± (standard deviation).
Biomass data is in grams per m^2. Rhizome growth rate is in internodes per day.

Marker tags were placed on terminal leaf pairs of three shoots at each study site and the growth of the rhizome was measured as the number of new nodes after 10-17 days. Of the sixty-six tags set, only thirty-seven were recovered with usable growth data. High surf due to storm surge condition disturbed several of the site markers in the lagoon areas of both bays towards the end of the study period. The mean daily growth rate was calculated, adjusted by the measurement period. The mean internode growth rate for this study was 0.43±0.16 internode day^{-1} (Table 3). The reciprocal of this rate is the plastochrone interval of the rhizomes (PIR). PIR is a measure of the time interval between the formation of successive internodes. The mean PIR for this study was 2.6±0.86 days. Table 3 shows additional ecological data organized by site, bed location, and habitat.

The following variations in the morphologies of *H. decipiens* were found at the different study sites. The mean leaf surface area in the lagoon habitats was greater than in the estuarine (Table 4). Leaf measurements in the estuarine sites resulted in a calculated mean surface area of 195.0±70.9 mm^2. The mean surface area of the leaves in the lagoon sites of the two bays was 129.0±38.6 mm^2. The mean internode length was shorter in the lagoon than in the estuarine sites. The mean internodal lengths in the estuarine and lagoon environments were 22.7±7.2 mm and 21.6±6.7 mm respectively (Table 4). The mean internodal growth rate was higher in the lagoon sites than in the estuarine sites. The lagoon sites mean growth rate was 0.55±0.17 internode day^{-1} and the estuarine mean growth rate was 0.37±0.11 internode day^{-1}.

Differences in the mean leaf surface area and internode lengths were found within the bed structures between plants in the interior sections and those on the bed margins (Table 5). Internode lengths were longer on rhizomes in the bed margins, with a mean of 22.8±7.4 mm compared to a mean of 21.6±6.5 mm in the bed interiors. The leaves from the bed margins were smaller than those in the central portions of the beds. The mean surface area in the bed margins was 154.5±64.3 mm^2. The mean surface area of the leaves in the bed interiors was 159.8±63.4 mm2. margins. The central portions of the beds have a mean ratio of 0.25±0.26 fruits per leaf pair.

Table 4. Morphology differences between *H. decipiens* in estuarine and lagoon environments.

	Estuarine (mean±s.d.)	Lagoon (mean±s.d.)	Difference (mean±s.e.)	t	p	n
Internode Length (mm)	21.6 (6.67)	22.7 (7.16)	1.2 (0.47)	2.46	0.0140	856
Leaf surface Area (mm^2)	195.0 (70.9)	129.0 (38.6)	66.0 (2.17)	30.38	<0.0001	2603
Internode Growth Rate (internode day^{-1})	0.37 (0.111)	0.55 (0.174)	0.17 (0.047)	3.72	0.0007	37

Table 5. Morphology differences between *H. decipiens* in bed margins and bed interiors.

	Bed Margin (mean±s.d.)	Bed Interior (mean±s.d.)	Difference (mean±s.e.)	t	p	n
Internode Length (mm)	22.8 (7.42)	21.6 (6.46)	1.2 (0.48)	2.62	0.0091	856
Leaf Area (mm^2)	154.5 (64.27)	159.8 (63.40)	5.3 (2.51)	2.13	0.0336	2603
Fruit to Leaf Ratio	0.13 (0.189)	0.25 (0.262)	0.11 (0.054)	2.11	0.0381	72

Above measurements are expressed as means ± standard deviation. Differences between the means is expressed as mean ± (standard error).
A one-way ANOVA with a t-test of the group means was used to calculate the statistical values.

The ratio of fruiting bodies to leaves is higher in the interior of the bed than on the bed The bed margins have a mean ratio of 0.13±0.19 fruits per leaf pair (Table 5). The mean leaf surface area for *Halophila* plants in Opunohu Bay was 165.2±76.3 mm^2 which was greater than the mean surface area of 151.5±51.9 measured in Paupau Bay.

Discussion

Halophila decipiens is the most widely distributed tropical seagrass species. It was the only seagrass species found in this survey. These beds on Moorea are possibly the most eastward extension of its range in the Indo-Pacific (den Hartog 1970; Mukai 1993). The maps produced as part of this study show the distribution of *H. decipiens* in Opunohu and Paupau Bays. The bed area estimates show that the total area of seagrass resources is greater in Opunohu Bay,

specifically in the estuarine habitat. There were no significant results from the morphological or environment data that account for this difference, although mean leaf surface area was found to be greater in Opunohu Bay by 13.7±2.5 mm^2 (mean±s.e., t=5.44, p<0.0001, n=2603). The geomorphology of these two bays is similar, but Paupau Bay is more commercially developed than Opunohu Bay and has more recreational boat traffic (Galzin and Pointier 1985). Anthropogenic causes may be a factor in these differences, however, this is an area for future research. Because *H. decipiens* was located in the two distinct habitat types of the shallow estuarine bay and deeper backreef lagoon, there was an opportunity to examine morphological differences occurring between these different habitats.

The mean leaf surface area for all samples was 157.4±63.9 (mean±s.d.). This is comparable to other studies on *H. decipiens*.

There was differential leaf morphology found between the leaves on the rhizome main axis and those on the secondary branches. The difference in the means was 46.5 ± 2.57 mm^2 (mean±s.e.) and was statistically significant (t=18.1, p<0.0001), n=2603).The mean internode growth rate for all study sites was 0.43 ± 0.16 internode day^{-1} (mean±s.d.). This rate is equivalent to a plastochone interval (PIR) of 2.6 ± 0.86 days (mean±s.d.) and similar to internode growth rates reported for other species of *Halophila* (Brouns 1987; Herbert 1986; Josselyn et al. 1986).

The mean biomass for all of the sample sites was 29.7 ± 20.9 g m^2 (mean±s.d.). This is over twice the dry biomass reported for *H. decipiens* beds in the U.S. Virgin Islands (Josselyn et al. 1986). Resource limitations at the field station did not permit the processing of the samples according to the recommended methods. With the available equipment, the samples could only be dried at a maximum temperature of 48°C. Desiccation tests on the available dryer indicated that after 48 hours, no additional moisture was removed from the samples (Dobrowski, in press). The remaining moisture in the plant tissues, as a result of the methods used, may account for much of this difference in biomass measurements. Because the sample sites were selected based on habitat type and bed structure, the mean biomass measurement cannot be used as an accurate estimate of bed structure. However, as this study represents the first survey of the seagrass resources on Moorea, I include these results as preliminary findings. The ratio of above-ground to below-ground biomass is an indicator of how seagrass partitions its energy into photosynthetic and non-photosynthetic tissues. The mean above-ground to below-ground biomass ratio measured in Moorea was 1.40 ± 0.98 (mean±s.d.). This is approximately 25 percent higher than reported in the above study. The Virgin Islands study only sampled deep water *Halophila* beds in 15-27 m depths (Josselyn et al. 1986). This study sampled both deep water beds and shallow water beds. The shallow estuarine sites had a higher ratio of above-ground to below-ground biomass, but this difference of 0.48 ± 0.24 (mean±s.e.) was just below the level of significance (t=1.97, p=0.054, n=62). This difference in biomass ratio is consistent with the finding that the mean leaf surface area is larger in the estuarine sites (see below). These differences in the study conditions may account for the higher ratio of above-ground to below-ground biomass in found in this study.

Morphology differences, within the bed structure, between plants growing on the margins and plants growing in the interior were statistically significant (ANOVA). The mean leaf surface area on plants in the bed margins was less than bed interior plants. The difference between the means was 5.33 ± 2.51 mm^2 (mean±s.e., t=2.13, p=0.034, n=2603). The mean internode length was longer in the bed margins than in the interior of the beds with the difference between the means of 1.23 ± 0.48 mm (mean±s.e., t=2.62, p=0.0091, n=856). These morphological differences suggest that *H. decipiens* puts more of its energy into growing laterally across the substrate and less into leaf production when growing in the bed margins compared to the bed interior. This combination of less leaf surface area and longer internode lengths is indicative of colonizing seagrass species (Birch and Birch 1984; Brouns 1987). Further support for this conclusion is that the ratio of fruits to leaf pairs also declines in the bed margins, making more of the plant's energy available for rhizome extension. The difference between the mean fruit to leaf ratio in the bed margins and the bed interior was 0.11 ± 0.054 (mean±s.e., t=2.11, p=0.0381, n=72).

Statistically significant differences in plant morphology were found between the *H. decipiens* in the lagoon and estuarine habitats using ANOVA and a t-test of the difference between the means. The pattern of these variations suggest adaptations to the lower intensity and/or altered light spectrum of the deeper waters on the backreef slope. The mean leaf surface area in the lagoon sites was 66.0 ± 30.4mm^2 (mean±s.e.) less than the mean for the estuarine sites. This difference in the means was statistically significant (t=30.38, p<0.0001, n=2603). Smaller leaf size has been suggested as a mechanism in *H. decipiens* to reduce self shading in low and variable light environments (Josselyn et al. 1986).
The mean internode lengths were shorter in the lagoon than in the estuarine habitats with a difference in the means of 1.2 ± 0.47 mm (mean±s.e., t=2.46, p=0.014, n=856). This may be a natural consequence of the smaller leaf

sizes, but also results in effectively reducing the non-photosynthetic tissues that the plant would produce compared to the estuarine plants. No statistically significant differences in biomass were seen between the two environments, but the mean above-ground to below-ground biomass ratio reported above is a further indication that *H. decipiens* is maximizing photosynthetic tissues in this environment. The mean internodal growth rate is higher in the *H. decipiens* sites in the lagoon than in the estuarine sites. The difference between the means was 0.17 ± 0.05 internode day^{-1} (mean$\pm$s.e, t=3.72, p=0.0007, n=37). This high growth rate gives *H. decipiens* the ability to colonize new habitat where suitable light conditions exist.

Conclusions

Halophila decipiens is distributed in two distinct habitat types in Opunohu and Paupau Bays on the island of Moorea. Both Bays have a similar distribution pattern with a beds in the shallow estuarine backbay and beds in the lagoon behind the barrier reef. *H. decipiens* was also found in Vaiare Bay. Prior to this study, the reported distribution of seagrass was only as small patches in Opunohu Bay (Galzin and Pointier 1985). These results add to the knowledge of the distribution patterns of this seagrass on the island. In light of the broader distribution patterns found, it would be useful to look at the possibility of faunal relationships within these larger bed structures.

Greater leaf surface area and shorter internode lengths were found in the *Halophila* plants in the lagoon areas of both bays, compared to the plants in the estuarine environments. These results support the first research hypothesis of differential plant morphologies occurring between bay habitats. These morphological differences combined with the high ratio of above-ground to below-ground biomass and higher rhizome growth rates in the lagoon sites are consistent with other research that suggests that *H. decipiens* is adapted to the low and variable light conditions in deep water

environments. The smaller leaf surface area and longer internode lengths found on the bed margins as compared to the denser bed interiors support the second research hypothesis of differential morphology between these two locations. This combination of reduced leaf area and increased shoot length is consistent with determination of other researchers that Halophila is a colonizing species. What is interesting, from the above results, is that these ecological and morphological characteristics would seem to be plastic depending on environmental conditions. In the case of the estuarine and lagoon habitats, additional research is needed to determine if these morphological differences are genetic or are purely adaptive in nature. Transplant studies at these sites would be informative.

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Zonation of lagoon algae in Moorea, French Polynesia

Xavier Mayali
Department of Environmental Sciences
College of Letters and Science
University of California Berkeley 94720

ABSTRACT. In order to quantify the horizontal zonation of algae along a coral reef habitat on Moorea, French Polynesia, percent cover of all species found along a transect was examined. Three zones identified in previous studies were sampled: algal ridge, back-reef, and fringing reef. To improve qualitative analysis, the densities of all species found were compared between zones. Various species were found present in distinct zones whereas others did not. In addition, individuals of *Padina boergesenii* were transplanted from the fringing reef to the barrier reef under different treatments, caged, uncaged, and half-caged, to determine the factors responsible for its distribution.. It was concluded that water stress on the back-reef near the algal ridge during strong surge events is too high for the large frondose *P. boergesenii* individuals to survive, therefore only smaller individuals are present there.

Introduction

The ecological role of algae in benthic coral environments is multifold: protection of corals, primary production, structure for microfaunal habitat, and a sink for calcium carbonate (Belsher et a l 1990). The majority of intertidal environments show zonation of sessile organisms, including algae (Lalli and Parsons 1993). Various studies in temperate areas have described vertical zonation in rocky intertidal zones, which is controlled by tidal flux. However, many tropical coral reef intertidal zones are less strongly affected by tides due to geomorphology. In addition, tides in many central Pacific tropical islands are low because they are located in the center of the ocean basin. The tides become less ecologically important in comparison to other factors such as wave action, herbivory, tolerance to desiccation, and light availability.

The controlling factors for the zonation of algae are both biotic and abiotic. Although biotic factors include all interactions with other organisms, including competition with other species of algae, the most important factor is herbivory (Steinberg and Paul 1990). Both vertebrate (reef fish) and macroinvertebrate (sea urchins) herbivores graze on algae (Morrison 1988). Micrograzers have also been shown to be important herbivores on tropical algae (Brawley and Adey 1981).

Abiotic factors include tolerance to desiccation, high light intensity, nutrient levels, and water stress. For example, periodic effects of storm waves may be the most influential environmental factor regulating the size of frondose marine algal crops from a Hawaiian reef flat (Doty 1971). In addition, the density of *Sargassum* species on Hawaiian coral reefs have been shown to be highly correlated with water temperature (Glenn et al. 1990) suggesting that environmental factors are important.

Tropical shallow-water marine algae can be divided into two categories: calcareous, including both frondose and encrusting, and non-calcareous, including macroalgae and small filamentous species. Frondose non-calcareous forms are normally reduced by herbivores (Littler and Littler 1988) unless they are defended by secondary metabolites (Steinberg and Paul 1990). Calcareous forms are often resistant to herbivores both due to the calcium carbonate and their tough, hard surface. Other advantages to calcification include protection against epiphytes, mechanical support, resistance to sand

scour, and protection against photoinhibition (Littler and Littler 1988). Microfilamentous algae often dominate habitats with low nutrient levels and low levels of herbivory. Corals dominate in high herbivory and low nutrient levels. Coralline algae dominate high herbivory and high nutrient levels, and frondose non-calcareous macroalgae dominate low herbivory and high nutrient level habitats (Littler and Littler 1988).

Various studies have examined algal species on coral reef habitats. Fagoonee (1990) concluded that the coral ecosystems of Mauritius island are similar to Hawaii's coral ecosystems. Doty (1966) described many species present in Hawaii that are similar to those on Moorea, French Polynesia (Payri 1987). Although a number of studies have examined variations in spatial distribution of algae along tropical reef habitats (Payri and Naim 1982; Belsher et al. 1990; Fagonee 1990; Morrison 1988. Atlas de Polynesie Francaise 1993), only one recent study, on the north face of Moorea, quantified algal zonation based on the presence of the seven most common species (Payri 1987). The purpose of this study is to test Payri's results with replicated transects at a similar site and to examine species not previously quantified.

Materials and Methods:

Study site

Moorea (17° 31' S 149° 50' W) is a volcanic island located 11 km west of Tahiti, French Polynesia. Sampling took place just outside Cook's bay, on the north shore of Moorea (figure 1). The coral reef complex on the north shore of Moorea follows the typical barrier reef island geomorphology of Darwin's theory of atoll formation. The fore-reef zone is located on the ocean side and ends at the low tide line, where the algal ridge zone begins. The substrate of both of these zones is a combination of basalt rocks, hard corals, and crustose algae. The algal ridge is exposed at low tide. The next zone is the lagoon or back-reef.

Its substrate is a mixture of coral patches and sand continuing 200 to 300 meters. A deep channel divides the back-reef from the fringing reef, and was not sampled because of its depth. The fringing reef is adjacent to the shore and its substrate closely resembles the back-reef slope. Because the ocean waves go through the barrier reef on the opposite side of the bay (figure 1), the surge is not as strong, making the reef flat a much easier and safer area to sample.
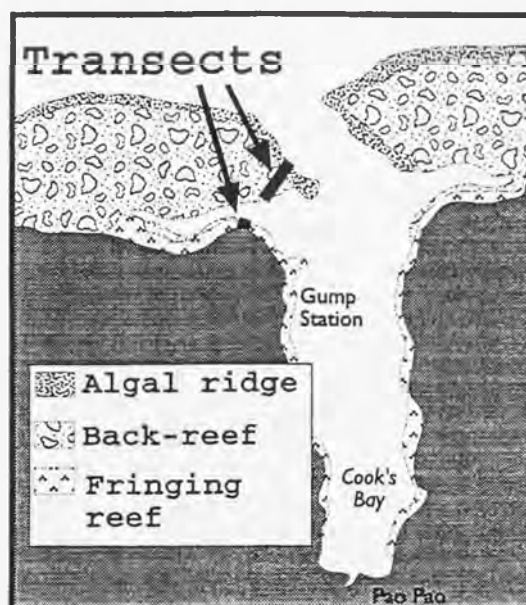
Figure 1. Location of transects spanning the three zones sampled.

Before sampling the transects, I collected as many species of macroalgae as I could find and dried the specimens in a plant press. I used various field guides (Macgruder and Hunt, 1987; Littler et al 1989) to identify the genera. The vouchers were sent to UC Berkeley to be deposited and identified to the species level (Richard Moe pers. com. 1996). The appendix includes a list of all the algae collected on Moorea in October and November 1996.

Zonation

I used a one square meter quadrat separated into one hundred squares to measure percent cover of each species of algae at each station along the transect. I counted one percent for each species present in one square. Therefore, the

total percent cover of one quadrat can add up to more than one hundred percent. The transect begins at the low tide line on the algal ridge of the barrier reef (distance = 0 meters) and ends on the shore (distance = 450 meters, not including the channel). Quadrats were sampled every six meters for the first 24 meters (the algal ridge and the transition into the back-reef) and more highly spaced thereafter. This was because of the distinct zonation existing within the algal ridge zone. The remainder of the barrier reef was sampled over 11, 25, and 50 meter intervals because of the similarity of the habitat throughout the back reef slope. The fringing reef was sampled over 25 meter intervals. Each of the 21 stations along the transect was replicated 3 times for a total of 63 samples.

The quadrat sampling took place between October 14 and October 28, 1996. The percent cover data was transformed (by the inverse sine of the square root function) to normalize the data. The algal species found in all three zones (algal ridge, back-reef, and fringing reef) were analyzed using a one way ANOVA (alpha = 0.01) and a Tukey-Kramer test (alpha = 0.05) to determine if the distributions were different between the three zones. A Principle Component Analysis was also performed for the 5 most common genera found along the transect.

Transplants

In order to determine if herbivory is a factor in the distribution of *Padina boergesenii*, I decided to do a transplant experiment. Although the species is present throughout the reef complex, individuals on the fringing reef are much larger in size. I collected large *P. boergesenii* fronds on the fringing reef and transplanted them to the barrier reef (distance = 25 m along the transect) where sandy substrate is present. The plants were first harvested from the fringing reef adjacent to the station and kept in an outdoor saltwater tank. Each large *Padina* frond grows from one set of rhizoids attached to a rock or piece of coral rubble; the individuals growing on

a small piece of rubble were cemented to larger rocks using underwater patching cement so they could be placed into the sand at the transplant sites. I measured each of the 30 individual fronds for length to the nearest centimeter and for volume to the nearest 5 centiliters by measuring the volume of water displaced. Mass was not measured because of the difficulty of handling the plants in air.

Five replicates were placed in 0.5 cm wire mesh cages with dimensions 30 x 30 x 17 cm to inhibit potential macrograzing. Five other replicates were placed in half-cages of similar dimensions with two open sides (figure 2).
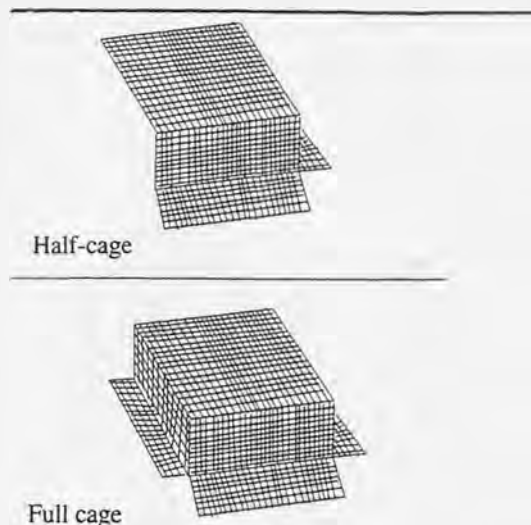
Figure 2. caged and half-caged treatments

The half-cages control for caging effects while still allowing herbivory. Five other replicates were placed uncaged. All three treatments were repeated for the control groups on the fringing reef for a total of 30 transplants. Each rock onto which the plants were attached was placed in the sand at both control and experimental sites. The rocks were tied to a piece of string and the cages were placed on the substrate. The string was also attached to a large piece of coral rubble so the transplants could be found again. The sides of the cages were

covered with pieces of coral rubble to keep them from moving. The transplants were left in their two respective habitats for 6 days instead of the planned 10 due to an unusually strong surge created by Hawaiian storms which dislodged several cages. The lengths and volumes of the plants were again measured after harvest. A two-way ANOVA was performed which compared lengths and volumes before and after the harvest in order to determine if biomass loss was statistically significant. Alpha value was set at $p=0.01$.

Results

Zonation

A Principle Component Analysis was performed with the 5 most common genera of algae found along the transect. The biplot (figure 4) is found at the end of this section.

species	zones	Rsquare	Pvalue	significant?
Turbinaria ornata	1 > 2,3	.43	p < .0001	yes
Sargasum sociale	1 > 2,3	.56	p < .0001	yes
Colpomenia sinuosa	1 > 2,3	.46	p < .0001	yes
Boodlea composita	1 > 2,3	.49	p < .0001	yes
Dictyota friabilis	no	..058	p = .16	no
Dictyota bartayresiana	no	.10	p = .04	no
Halimeda opuntia	1 < 2,3	.23	p = .0005	no
Padina boergesenii	no	.09	p = .06	no
Rosenvingia intricata	1 > 2,3	.23	p = .0005	yes
Caulerpa serrulata	no	.056	p = .18	no
Hydroclathrus clathrus	2 > 3	.18	p = .003	yes
Chnoospora implexa	2 > 3	.13	.015	yes
Neomeris annulata	3 > 1,2	.12	p = .019	yes
total *Halimeda* spp.	no	.069	p = .12	no

Table 1. Results of one-way ANOVA (R square and p-value) and Tukey-Kramer significance (alpha = 0.05) of most common species of algae sampled. A "yes" in the last column indicates that the distribution of the species is statistically different between the zones indicated.

Turbinaria and *Sargassum* are correlated, and *Dictyota*, *Padina*, and *Halimeda* are correlated, based on transformed percent cover values. In addition, the zones show clusters which indicates differences between them.

Table 1 summarizes R square and p-values of the one-way ANOVA and the significance of the Tukey-Kramer tests performed on species distribution between the three zones.

The distribution of *Dictyota friabilis*, *Padina boergesenii*, *Caulerpa serrulata*, and *Halimeda opuntia* over the three assigned zones is not statistically different. However, *Turbinaria ornata*, *Sargassum sociale*, *Colpomenia sinuosa*, *Boodlea composita*, *Rosenvingia intricata*, *Hydroclathrus clathrus*, *Chnoospora implexa*, and *Neomeris annulata* show significantly different densities in different zones.

The remainder of the results are qualitative, based on observations in the field and graphing percent cover values over distance along the transect (figure 3).

Turbinaria ornata (Phaeophyta, Fucales) was found in all zones but in highest density on the algal ridge, where it is exposed at low tide and surf is strong. The next highest densities were

on the edges of the fringing reef and back-reef areas closest to the channel. This species was found on top of coral heads the majority of the time.

Sargassum sociale (Phaeophyta, Fucales) was found only on the barrier reef, in highest density on the algal ridge. The fringing reef has been shown to have higher temperatures at low tide and lower salinity during rains.

Colpomenia sinuosa (Phaeophyta, Scytosiphonales) was found only on the algal ridge.

Boodlea composita (Chlorophyta) was found only on the barrier reef (algal ridge and back-reef).

Amphiroa fragilissima (Rhodophyta, Corallinales) was found only on the first 6 meters of the algal ridge, with one exception at 200 meters from the ridge, and often found under a *Sargassum* turf.

Cheilosporum acutilobum (Rhodophyta) was also found only on the first 6 meters of the algal ridge.

Ulva sp. was not sampled in any quadrat but was only observed on the top of large rocks on the algal ridge.

Rosenvingia intricata (Phaeophyta, Scytosiphonales) was found only on the barrier reef with highest densities on both edges.

Hydroclathrus clathrus (Phaeophyta, Scytosiphonales) is an ephemeral species and was found only on the barrier reef.

Chnoospora implexa (Phaeophyta, Scytosiphonales) was found only on the barrier reef with highest densities on the channel edge. It is another ephemeral species.

Dictyota friabilis (Phaeophyta, Dictyotales) was found throughout the transect in high densities. *Dictyota bartayresiana* was also found throughout the transect, with highest densities on the edge of the barrier reef near the channel.

Padina boergesenii (Phaeophyta, Dictyotales) is a slightly calcified algae. This species was found throughout the transect except on the seaward edge of the algal ridge and the

edge of the fringing reef close to the channel.

Figure 3a-c. Percent cover of each species over distance; 0-18m is the algal ridge, 24-250m is the back-reef, and 300-450m is the fringing reef

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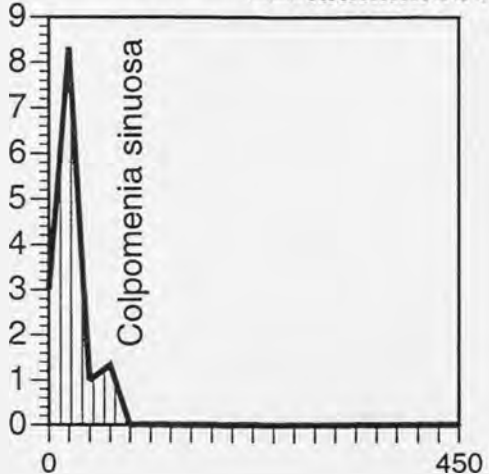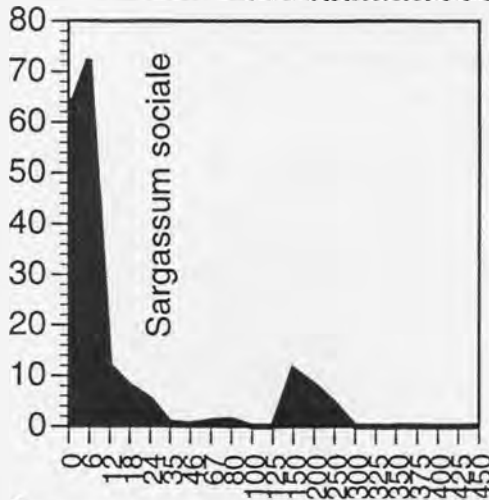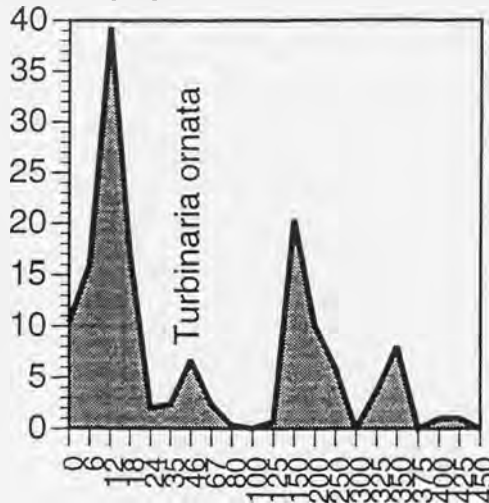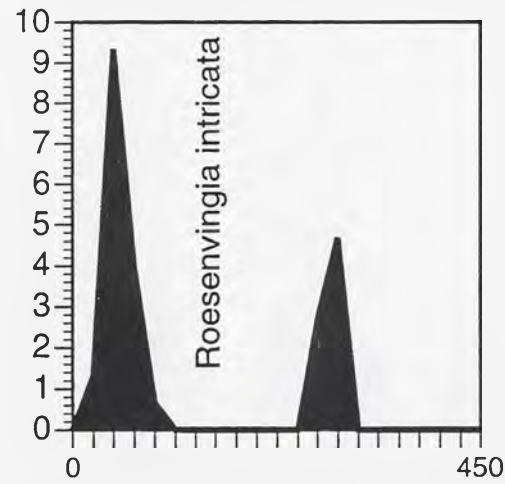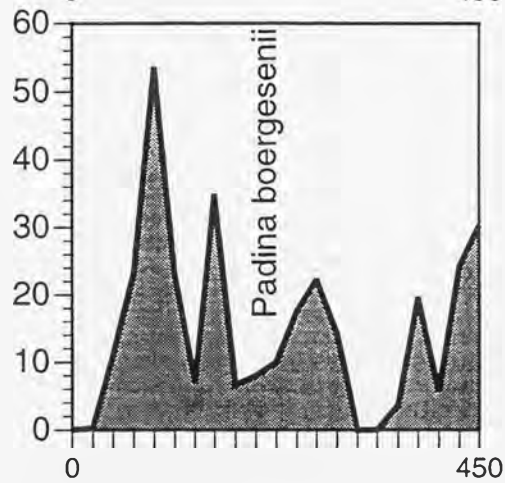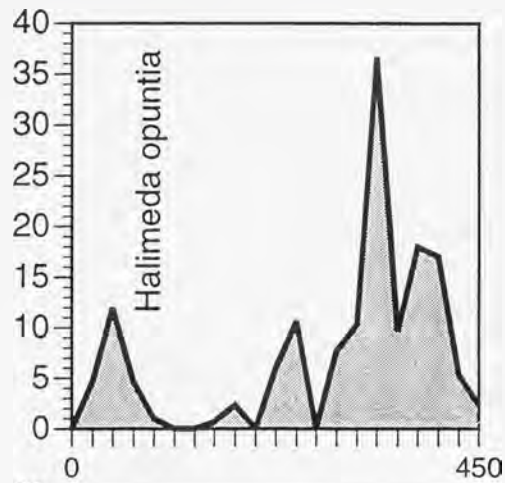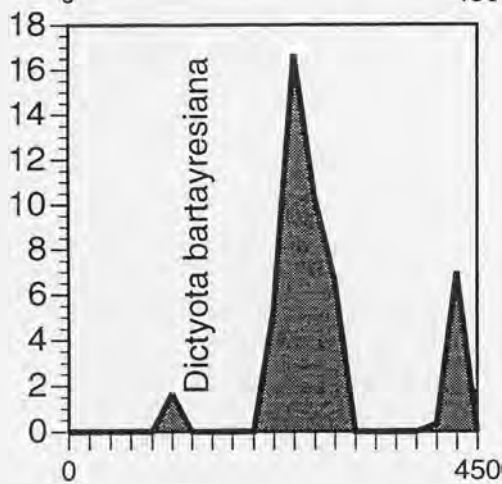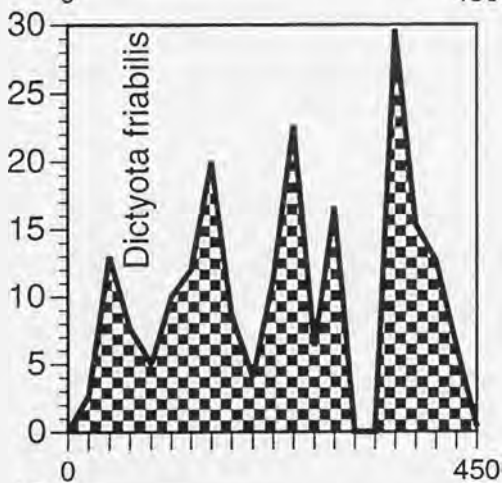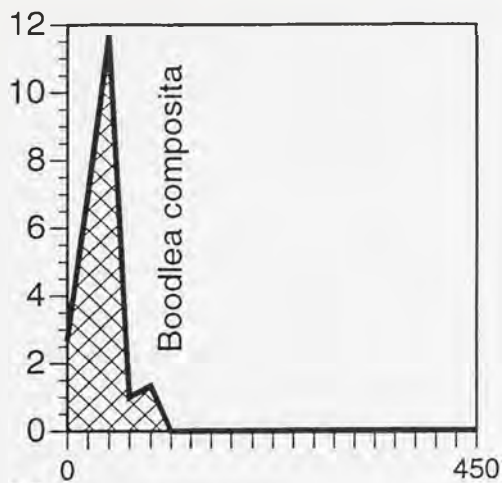
Figure 3d-f. Percent cover of species over distance; 0-18m is the algal ridge, 24-250m is the back-reef, and 300-450m is the fringing reef

Figure 3g-i. Percent cover of species over distance; 0-18m is the algal ridge, 24-250m is the back-reef, and 300-450m is the fringing reef
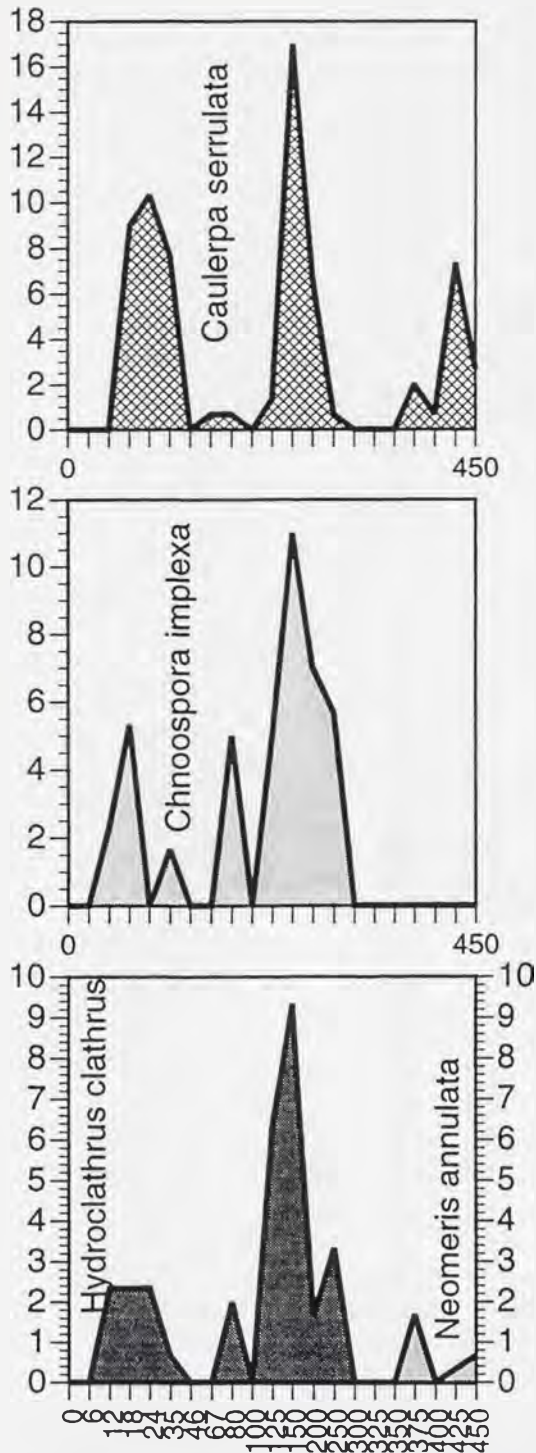
Figure 3j-1. Percent cover of each species over distance; 0-18m is the algal ridge, 24-250m is the back-reef, and 300-450m is the fringing reefthe seaward edge of the algal ridge.

Neomeris *annulata* (Chlorophyta, Dasycladales) was found only on the fringing reef.

Caulerpa *racemosa*, *Hypnea* *pannosa* (Rhodophyta, Gigartinales), and *Dictyota* *hamifera* were also sampled on the transect but were present in insignificant numbers.

Padina transplants
    The strong surge created by storms dislodged 2 cages on the barrier reef, exposing the plants. The two treatments were therefore changed from caged to uncaged. No differences in volume or length lost between the plants recovered were found to be significant(p > 0.05). However, 3 of 7 uncaged barrier reef transplants were ripped off their substrate, as opposed to none ripped off in the other 5 treatments.

Discussion
    Cheilosporum, *Sargassum*, *Turbinaria,* *Colpomenia*, *Amphiroa*, *Boodlea,* and *Ulva* are found on the seaward edge of the algal ridge, where herbivory is low and water stress is high. *Cheilosporum* and *Amphiroa* are short calcareous species. Advantages to being calcareous include mechanical support, resistance to sand scour, wave shock, and grazing, and protection against epiphytes and photoinhibition (Littler and Littler 1988).
    The *Sargassum* distribution is more extensive than that found by Payri (1987), who found it strictly on the algal ridge. *Sargassum* has been shown to be grazed by sea urchins (Vaziri 1995), so herbivory appears to be the strongest factor limiting its distribution. However, the density of other species of this genus have been shown to be highly correlated with antecedent water temperatures (Glenn et al. 1990), suggesting that environmental factors are also important.
    The distribution of *Turbinaria ornata* is similar to that found by Payri (1987), and is possibly related to water temperatures: it seems to prefer areas of stronger flow. Another possible hypothesis is that it needs desiccation to survive. Many temperate species use desiccation as a defense against fungal attacks (John Zupan pers. com. 1996). Yet

Figure 4. Principle Component biplot of transformed percent cover values of *Turbinaria*, *Sargassum*, *Padina*, *Dictyota*, and *Halimeda*. Points 1-12 are algal ridge values, 13-42 are back-reef values, and 43-63 fringing reef values. *Turbinaria* and *Sargassum* are correlated while *Dictyota* and *Padina* (to a lesser extent) are correlated.

another hypothesis is that the wide distribution of *Turbinaria ornata* could be explained by an increased amount of available substratum for algal attachment after a coral destruction (Payri 1987). This is corroborated by the observation that smaller, younger plants are present where strong water turbulence occurs. *Colpomenia* and *Ulva* appear to be dessication tolerant, and their exclusive presence on the algal ridge is a probable results of herbivory in other zones. *Boodlea*, on the other hand, has been documented in other zones (Payri 1987) and its unique presence on the ridge is likely due to seasonal variations in abiotic conditions such as salinity.

Chnoospora intricata and *Hydroclathrus clathrus* are ephemeral species (Payri and Naim 1982) and disappear after the rainy season begins. Their distribution is controlled by lowered salinity due to rains (Payri 1987). Although I only found these two species on the barrier reef, they have been documented on the fringing reef at other times of the year (Payri 1987). The

presence of *Rosenvingia intricata* is highly correlated with *Chnoospora* and *Hydroclathrus*, so it could also be an ephemeral species and also affected by salinity.

Halimeda simulans was only found on the landward side of the fringing reef, on the sandy substrate. This is similar to the distribution of Halimeda incrassata found by Payri (1987), and the two species are likely the same. The presence of many *Halimeda* spp. is characterized by calm soft-bottom habitats (Littler and Littler 1988). This species seems to be resistant to fish grazing, low salinities, and is one of the few algal species in this habitat that does not need a rock to attach to. The distribution of *Neomeris annulata* is likely also affected by lower salinity levels

Halimeda opuntia was found everywhere but on the seaward edge of the algal ridge. This is likely due to the strong surge prevalent in this habitat. This species is found everywhere else because it is resistant to herbivory, as

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many *Halimeda* species are. This is because of their strong calcification (Lewis 1985). In addition, this species is most often found on the side of corals and in cracks. Corals protect plants from herbivores (Payri 1987). The *Caulerpa serrulata* distribution is similar but there are too many factors to consider in this species.

Many species of *Dictyota* have been found highly resistant to herbivory. Steinberg (1990) found that extracts of *Dictyota spiralis* and a *Padina* sp deterred herbivorous fishes from feeding. This explains the wide distribution of both *Dictyota* species and *Padina boergesenii* found in this study. Their distributions are limited by abiotic factors. Although Payri (1987) found a *Padina* species (*Padina tenuis*) strictly on the fringing reef, the dissimilarity with the findings of this study can be due to microhabitat differences between the two areas sampled. It has not been determined whether the two species are indeed the same or why Payri did not find any *Padina* on the barrier reef. Perhaps the proximity of this site to the channel and Pao Pao Bay affect the salinity which allows *Padina* to grow on this section of the barrier reef. The transplant experiment shows that large fronds of fruiting *Padina boergesenii* cannot survive close to the algal ridge through a strong surge event. Such events take place a few times every season and have been thought to affect algal distribution (Doty 1971).

In conclusion, the wide distribution of *Padina boergeseniii* and *Dictyota friabilis* compliments the Steinberg (1990) study of herbivore deterrence by species of the same genera. The distribution of the ephemeral species *Chnoospora implexa, Hydroclathrus clathrus, Colpomenia sinuosa,* and possibly *Rosenvingia intricata* are controlled mainly by abiotic factors that change seasonally, such as salinity. The zonation of *Padina boergesenii* and *Halimeda simulans* is opposite to that of *Turbinaria ornata* and *Sargassum sociale* because of different substrate requirements and water flow resistance: sand and calm water on the land side of the fringing reef, and rock and strong surge on the algal ridge of the barrier reef.

The distributions of *Turbinaria, Boodlea, Halimeda simulans, Hydroclathrus,* and *Chnoospora* correspond to those found by Payri (1987). Both *Padina* and *Sargassum* were found more widely distributed in this study in comparison with Payri 1987. The remaining species were not sampled by Payri.

The zonation of some species of algae on a horizontal gradient is evident from this study. However, microhabitat changes are also important. This means that certain species exist on top of rocks, on the sides, or on the sand adjacent to the rocks. Although depth was not a zonational factor along the transect, a microhabitat study is needed to test if depth is a factor on a smaller scale.

In addition to spatial distribution, the algae on the north face of Moorea have been shown to exhibit temporal variations. Not only are some species ephemeral (*Chnoospora implexa, Hydroclathrus clathrus, Colpomenia sinuosa*) but algal densities of perennial species seem to differ from year to year as well. (Payri and Naim 1982). For example, *Turbinaria* and *Sargassum* were not found on the north face of Moorea before 1971 (Payri and Naim 1982).

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Appendix

The following species of algae were collected on Moorea throughout October and November, 1996, by myself and Michael Emmett. The species were identified by Richard Moe at the University of California at Berkeley Herbarium. All voucher samples are deposited at the U. C. Berkeley Herbarium.

Acanthophora spicifera (Vahl) Borgesen, found on the algal ridge.

Amphiroa fragilissima (Linnaeus) Lamouroux, found on the algal ridge.

Avrainvillea obscura (C. Agardh) J. Agardh, found in Vaiare bay.

Boodlea composita (Harvey) Brand, found on the algal ridge.

Caulerpa racemosa (Forsskal) J. Agardh, found on the barrier reef.

Caulerpa serrulata (Forsskal) J. Agardh, found throughout the reef complex.

Caulerpa sertularioides (S. Gmelin) Howe, found in Vaiare bay.

Ceramium spp., found in Cook's bay.

Cheilosporum acutilobum (Decaisne) Piccone, found on the algal ridge.

Chnoospora implexa (Hering and Martens) J. Agardh, found on the barrier reef.

Codium geppiorum Schmidt, found on the barrier reef.

Colpomenia sinuosa (Mertens ex Roth) Derbes and Solier, found on the algal ridge.

Dictyota bartayresiana Lamouroux, found throughout the reef complex.

Dictyota friabilis Setchell?, found throughout the reef complex.

Dictyota hamifera Setchell, found on the barrier reef.

Enteromorpha flexuosa (Wulfen) J. Agardh subsp. flexuosa, found in Vaiare bay.

Grateloupia filicina (Lamouroux) C. Agardh, found in Vaiare bay.

Halimeda opuntia (Linnaeus) Lamouroux?, found throughout the reef complex.

Halimeda simulans Howe?, found between the fringing reef and the shore.

Hydroclathrus clathrus (Bory) Howe, found on the barrier reef.

Hypnea pannosa J. Agardh, found on the algal ridge.

Hypnea spinella (C. Agardh) Kutzing, found on the fringing reef.

Padina boergesenii Allender and Kraft, found throughout the reef complex.

Rosenvingia intricata (J. Agardh Borgesen), found on the barrier reef.

Sargassum sociale (Grunow) Setchell, found on the algal ridge.

Spyridia filamentosa (Wulfen) Harvey, found in Opunohu bay.

Ulva fasciata Delile, found in Cook's bay.

Ulva sp. unknown, found on the algal ridge.

Distributional patterns of mobile epifauna associated with two species of brown algae (Phaeophyta) in a tropical reef ecosystem

Kendra G. Bergstrom
Department of Integrative Biology
University of California, Berkeley, CA 94720

ABSTRACT. Microinvertebrates are a major trophic link between primary producers, such as phytoplankton or algae, and fish in marine ecosystems. Algae provide one habitat for a diverse group of epifaunal microinvertebrates. Algal morphology was investigated as a factor in determining epifaunal distribution. Invertebrate abundance was correlated with morphological complexity between two algal species and within one alga. Invertebrates showed a higher abundance on *D. friabilis* than *T. ornata* and on the holdfast of *T. ornata* as compared with the blade. Invertebrate diversity was correlated with the presence of multiple microhabitats within one algal species, with *T. ornata* showing a higher species diversity than *D. friabilis*.

Introduction

Microinvertebrates constitute a major trophic link between primary producers and fishes (Edgar 1987). Primary producers such as phytoplankton, epiphytic algae, and macroalgae are consumed by epifauna, which are in turn heavily predated by fish.

The abundance and distribution of algal epifauna commonly follows distinct patterns. Algal epifaunal distributions have been found to be influenced by gross morphology (Sarma, Ganapati 1972), salinity (Norton 1971; Fenwick 1976), depth (Dahl 1948), water movement and wave exposure (Norton 1971; Fenwick 1976), and epiphyte load (Edgar 1991). Distribution has been shown in Japan to fluctuate biannually, in both winter and summer (Mukai 1971), and in Tasmania to fluctuate seasonally with highest abundance from February through May (Edgar 1993).

Extensive study has characterized the epifaunal communities associated with seagrasses (e.g.. Nelson 1979; Stoner 1980; Bell, Hall 1988) but less work has been done to characterize the fauna associated with algae. A similarity exists in the function of seagrasses and macroalgae as a substrate for epiphytic algal growth and the epifauna associated with those epiphytes.

Invertebrate fauna associates with algae as a food source and as a refuge. Epifaunal use algae as a platform for filter feeding, as a point of detrital accumulation, as a substrate for grazing on epiphytic algae, and as a direct food source. As a refuge, macroalgae provide retreat from omnivorous fishes (Nelson 1979; Dethier 1980; Stoner 1980; Edgar 1983; Could, Wells 1983) and against current extremes (Norton 1971; Fenwick 1976; Moore 1978).

Algae benefit from its epifauna. Copepods, shrimp, andisopods consume the superficial film of organic matter coating the thallus, improving photosynthesis (Peres 1961). Detritus feeders such as Amphinomidae, Eucinidae, and Nereidae polychaetes restrict the amount of sediment trapped by the thallus (Vittor, Johnson 1977). Opistobranch snails consume various sessile animal epiphytes (Naim 1988), decreasing mechanical drag on the thallus and increasing light availability.

The gross morphology of a macroalga plays an important role in its function as a substrate and refuge from predation for an epifaunal assemblage. Invertebrate species diversity and abundance on a species of algae has been correlated with morphological complexity.

Figure 1. Site Map
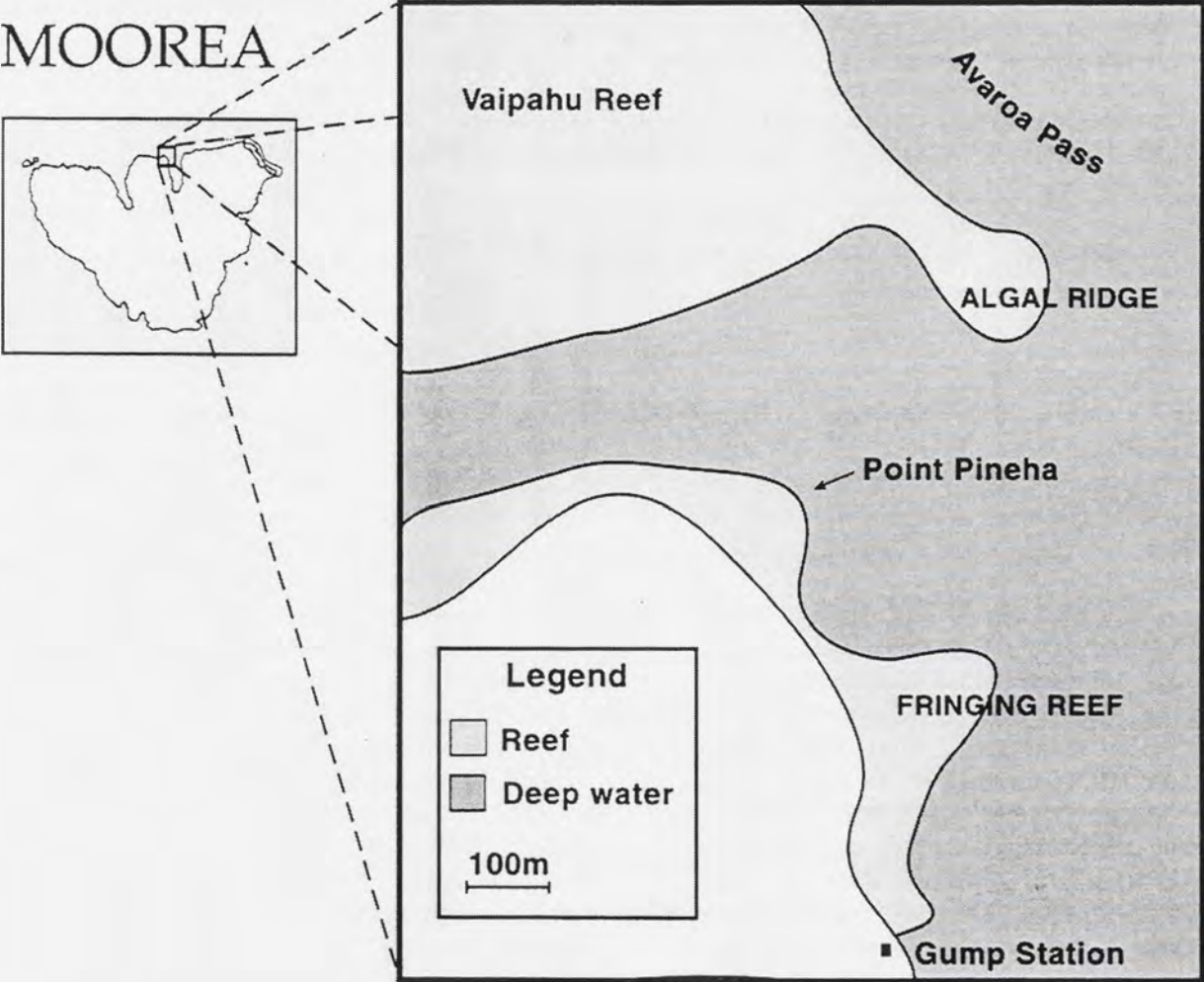
Narrower, more finely branched algae constitute a substrate for a larger number of microinvertebrates than algae with wide blades and a low degree of branching. Predation has been shown to increase significantly if an invertebrate's body shape does not match algal morphology (Duffy, Hay 1991).

The brown algae (Phaeophyta) of Moorea differ greatly in gross morphology between species. Two species, *Dictyota friabilis* (Dictyotalae) and *Turbinaria ornata* (Sargassae), with distinctly differing morphologies, were surveyed in order to characterize the epifaunal communities they host.

The two species were sampled for invertebrate distribution and abundance between and within an algal species. Both algae grow in a lithophytic littoral to sublittoral environment. Both species produce chemicals that act as a deterrent to herbivores that ingest the algae. *T. ornata* produces Turbanic acid (Sawai 1994) while *D. friabilis* produces Dictyol-E and Pachydictyol-A (Fenical et al 1988) to prevent herbivory by fishes.

T. ornata has a thick primary stipe that supports secondary stipes and thick, air filled blades. A well developed holdfast allows *T. ornata* to inhabit environments impacted by high wave energy.

D. friabilis is a low growing, turfy brown alga that anchors on rocks or as an epiphyte on algae such as *Turbinaria* and *Halimeda*. Its flattened thallus shows similar morphology throughout the organism.

Materials and Methods

A survey of epifaunal invertebrate communities was conducted from October 15 to November 21, during austral spring.

Site Description

The study site is located on Moorea, French Polynesia, near Avaroa Pass in the Cook's Bay reef system. This site was selected because of the accessibility of the wave impacted algal ridge at this location. Algae was sampled from the fringing reef and algal ridge on the west side of Cook's Bay and Avaroa Pass (Figure 1).

The fringing reef site is located at Gump Reef, adjacent to Gump Biological Research Station on the west side of Cook's Bay. This site extends 500 m north from the north edge of Gump Station. The reef extends 30 m from shore at a depth of 0.5-1.0 m. The substrate is coral sand with scattered live and dead coral formations. Samples were collected from dead coral heads at 0.2 to 0.5 m depth.

The algal ridge site is located at Vaipahu Reef on the west side of Avaroa Pass outside Cook's Bay. The reef at this site is bordered on one side by a large black buoy which marks the west boundary of the pass and extended 100 m west. Samples were collected from the coral rubble substrate in water of 0.1 - 0.3 m depth at a distance of 5-10 m from the ridge crest.

Samples of both algal species were collected from each site. Eight organisms of each species were sampled from each site. To separate invertebrates from the algae, samples were first agitated in sea water for two minutes. The algae was then removed from the sea water and discarded. Excess sea water was decanted. Invertebrates found in each sample were counted using a dissecting microscope at 20X magnification.

Invertebrate species were identified to taxonomic family level. Families which occurred in less than 10 percent of the samples were grouped into higher taxa in order to analyze differences in distribution different algal species, reef location, and portion of an alga. Voucher specimens are deposited at the UC Berkeley Museum of Paleontology.

Figure 2. *Dictyota friabilis*

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Comparison of Algal Species

Two species of brown algae were studied to compare the effects of morphological variation on epifaunal distribution. Although their chemical composition is similar, *D. friabilis* (Figure 2) and *T. ornata* (Figure 3) were selected in order to contrast two distinctly differing morphologies.

Figure 3. *Turbinaria ornata*, with arrow indicating seperation point.
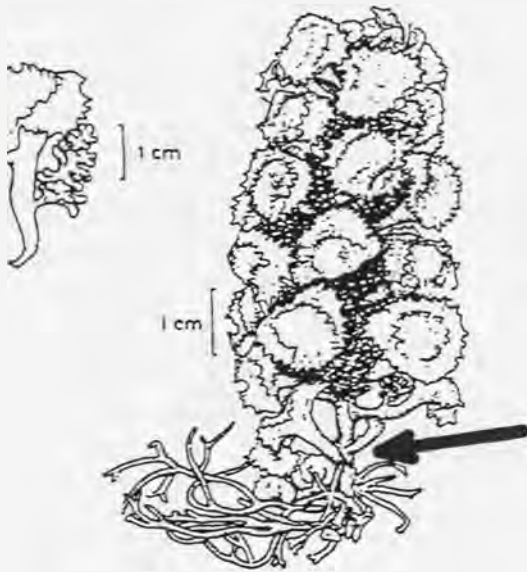
Comparison of Algal Blade and Holdfast

The holdfast of *T. ornata* is composed of finely branched secondary stipes, while the blade consists of many large extensions from the primary stipe spaced at wide, even intervals (Figure 2). In order to separate the two morphologies, the blades and holdfasts of the algae were cut with scissors at the point where the blade begins to grow extensions from the main stipe (Figure 3, arrow). The blades and holdfasts were removed and collected separately from the coral substrate.

Blades and holdfasts were separately washed in fresh water for two minutes. The alga was discarded, and the total number of invertebrates dislodged from the alga was counted from the fresh water. Five blades and holdfasts, collected from five plants, were sampled.

Statistical Analysis

Data was log transformed using $\ln(x+1)$ in order to prevent significant heteroscedasticity. A one-way ANOVA was used to compare the data from invertebrate abundance, two algal species and two sections of *T. ornata*. Invertebrate diversity was evaluated using the Shannon-Weaver Diversity Index. Statistical tests were conducted using Microsoft Excel and Jmp In software.

Figure 4. Average number of organisms per sample, comparison of two species

Organism	*T. ornata* (average)	*D. friabilis* (average)	$p<$
Tanaidacea	1.0	74.3	0.0001
Gastropoda	42.3	84.5	0.02
Platyhelminthes	10.5	9.2	0.08
Ostracoda	7.3	6.1	NS
Acarina	1.5	5.9	0.01
Isopoda	13.6	21.9	0.08
Mysidacea	4.0	4.6	NS
Euryalae	3.1	0.9	0.02
Ophsocomidae	0.4	1.9	NS
Amphipoda	10.5	15.1	0.09
Copepoda	29.3	30.8	NS

Figure 5. Invertebrate distribution by algal species.
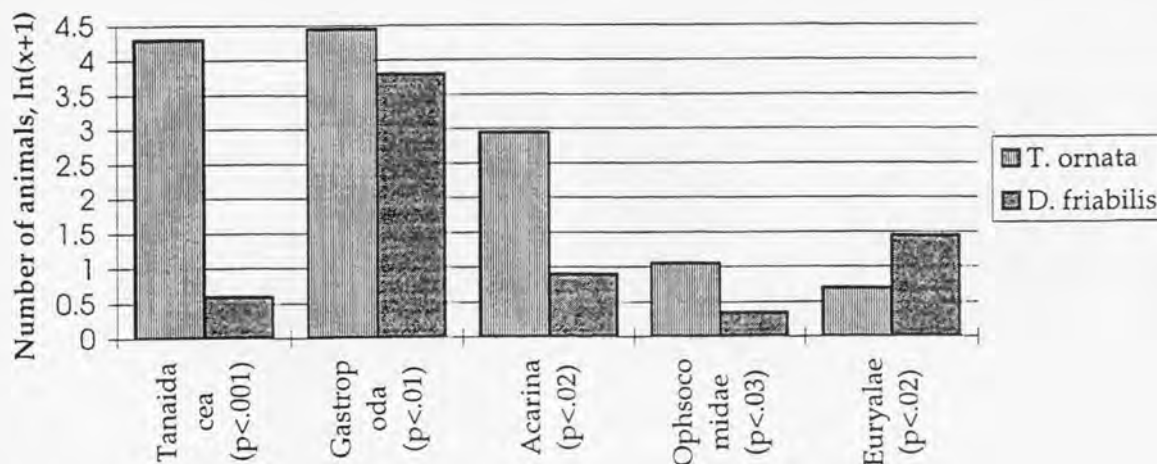
Results

Comparison of Algal Species

The average number of epiphytic invertebrates per *D. friabilis* sample was significantly higher than the organisms in a *T. ornata* sample of equal volume (x=268 on *D. friabilis*, x=133 on *T. ornata*. p<0.001). Species diversity, evaluated by the Shannon-Weaver Diversity Index, was greater in the invertebrates living on *T. ornata* (H'= 3.649) than on *D. friabilis* (H'=2.840).

On *D. friabilis*, Tanaids occurred with high frequency relative to *T. ornata* (p<0.0001). Gastropods (p<0.02) and Acarina (p<0.01) also showed significantly higher distributions in *D. friabilis*. Euryalae basket stars were found mainly in *T. ornata* (p<0.02).

Comparison of *T. ornata* Blade and Holdfast

The holdfast of *T. ornata* created a habitat for a significantly higher number of invertebrates than the algal blade. Species richness was higher in the holdfast than the blade of *T. ornata*..

Of 11 taxa evaluated, numbers of Gastropoda (p<0.002), Acarina (p<0.006), and Platyhelminthes (p<0.001) were significantly higher in the holdfast than the blade of *T. ornata*. Amphipod abundance varied with the blade and holdfast, but the results were not significant (p<0.06) due to the small number of replicates. In contrast, Isopod abundance was significantly higher on the blade than the holdfast (p<.03).

Figure 6. Comparison of Algal Blades and Bases, average number of organisms

Organism type	Holdfast	Blade	p<
Gastropoda	14.6	3.6	0.0001
Nudibranchia	1.6	0.6	NS
Ostracoda	2.0	1.6	NS
Acarina	4.4	0.4	0.003
Isopoda	13.8	23.4	0.03
Copepoda	20.6	33.0	NS
Amphipoda	12.6	7.2	.06
Polychaeta	7.6	0.6	0.0001
Platyhelminthes	7.4	1.2	0.0001

Figure 7. Invertebrate distribution by portion of an alga.
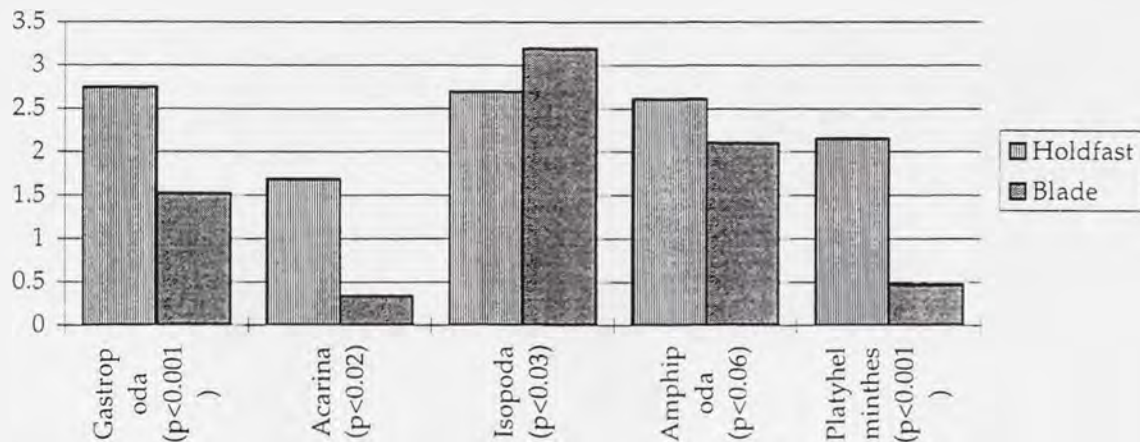
Discussion

The total number of invertebrate species found from all algal samples was 123. Past studies have found species richness to vary from 73 on *Macrocystis* kelp in Tasmania (Edgar, 1983c) to 340 on species of the genus *Halimeda* at the Tiahura transect, Moorea (Naim 1988).

Species diversity, as evaluated by the Shannon-Weaver Diversity Index, was positively correlated with habitat complexity. Between *D. friabilis* and *T. ornata*, *T. ornata* had a higher level of diversity (H'=3.4) than *D. friabilis* (H'=2.6). The separate blade and base morphologies of *T. ornata* create two distinct microenvironments for different assemblages of epifauna The single, homogeneous morphology of *D. friabilis* creates only one mircoenvironment. On *T. ornata* alone, the holdfast showed a higher level of diversity (H'=1.8) than the blade (H'=1.4).

The significant variation of Tanaid distribution between the two algal species may be an example of incompatible morphology. Tanaids may be unable to successfully habit *T. ornata* because its large gross morphology acts as an impediment to the Tanaid's ability to cling to the substrate. Tanaids build structures on empty shells of Rissoelid and Trochid snails. These shell structures are usually 2-3 times as long as the width of the animal itself, adding to the animal's size and wave resistance. Tanaids may not be able to use *T. ornata* as a substrate because they are not able to successfully cling to the algae in the face of wave action.

Gastropods may be incompatible with *T. ornata*'s morphology because of their large shell sizes in relation to their body size. Gastropods are found in significantly higher numbers on *D. friabilis* than *T. ornata*, and on *T. ornata*'s holdfast compared to its blade. The foot strength of many gastropods may not be strong enough to withstand wave action that impacts *T. ornata* over the surface of their large shells, especially on the algal blade. Acarina, sea mites, were present in significantly higher numbers in *D. friabilis* than *T. ornata* (p<0.02). These mites are very small in comparison to the gross morphological structure of *T. ornata*. Each mite is <0.1 mm in length. Each *T. ornata* stipe ranges from 0.25-1.0 cm in diameter. Acari mites may be particularly susceptible to the influence of wave energy because their size is not appropriate for clinging effectively to the large blade of *T. ornata*.

Another reason why Acarina distribution may vary between different algal species and morphologies is that Acari mites show site retention as adults to their host alga. Sommerfield and Jeal (1995) have shown that this algal fidelity is constant through seasonal fluctuations of temperature, salinity, and sedimentation.

Basket stars (Euryalae) were the only group found to have a significantly higher (p<0.02) distribution on *T. ornata* than on *D. friabilis*. The higher abundance on *T. ornata* is consistent with the basket star's role as a predatory suspension feeder. The microhabitat created by the *T. ornata* blade experiences a high rate of flow relative to the low, turfy *D. friabilis* blade because the long *T. ornata* blade is buoyant, extending up into the water column. In past research, basket stars have been found by Emerson (1991) to be adapted for life in strong currents and to concentrate in regions on medium to strong flow. Basket stars were not found to have significant variation between the blade and holdfast of *T. ornata*, most likely because of their low abundance over the sample size used (0-1 individual per sample).

Isopods with a wide, fat body shape were found in significantly higher abundance in the blade than the holdfast of *T. ornata* (p<0.03). This trend is consistent with findings by Edgar (1987) that the blade and holdfast of *Macrocystis* kelp from New Zealand shows a similar isopod distribution.

Amphipods were found most often on the base of *T. ornata*. This finding was not statistically significant (p<0.06) due to low sample size. The trend is consistent with earlier findings by Taylor (1991) that amphipods are numerically dominant in finely branched morphology but poorly represented in thick morphologies such as those found in Laminarian algae. The density of amphipods and total animals has showed a strong inverse exponential relationship with mean algal thallus width (Williams 1996). Unlike narrow blades which tend to be branched and densely packed, wide blades create a poor habitat for amphipods. Wide blades do not create hiding places to avoid being eaten by predatory fish. As visual predators, fish are able to locate and capture amphipods on wide algal blades (Edgar 1983b). Amphipods and other small invertebrates on wide algal blades are additionally exposed to predation by larger invertebrates such as crabs (Taylor 1991). In contrast, densely packed algae hinders size-selective predation by fish (Edgar 1983b).

The distribution of invertebrates such as copepods and polychaetes is even, with no significant differences between their distribution on *D. friabilis* or the blade or the base of *T. ornata*. The even distribution suggests movement of organisms among different algae. Both of these species nocturnally enter the water column to become demersal zooplankters (Robertson, Howard 1978; Macguard-Moulin 1984). Research indicates that some species of amphipods (Edgar 1983b) and isopods (Hobson, Chess 1976) also participate in nocturnal migration. Resettlement after migration is random, accounting for the even distributions found for polychaetes and copepods among the different variables.

Invertebrate abundance was positively correlated with algal complexity in the comparison of algal blade and holdfast in *T. ornata*. The thin, more finely branched, more densely packed holdfast supported a more diverse epifauna than the thick, widely spaced secondary stipes of the blade. These results are consistent with findings by Edgar (1987) regarding invertebrate diversity associated with the holdfasts of *Macrocystis* kelp in New Zealand.

Species diversity was positively correlated with morphological variation. *T. ornata*, with its significantly differing morphologies on its blade and base, hosted a higher number of species and higher species diversity than *D. friabilis*. This result is inconsistent with the significantly higher invertebrate abundance on *D. friabilis*. Varying diversity between the two species suggests that the homogeneous morphology of *D. friabilis* supports one group of fauna in its microhabitat while *T. ornata* creates more than one with its diverse morphology within the individual organism.

Observations suggest a nursery role for tropical algae similar to that of sea grass, as a refuge for juvenile invertebrates as well as fish. Cephalospidaeans and other nudibranchs were observed in epifaunal assemblages as very small sizes, 0.5-1.0 mm in length, which are characterized in their adult form as 2-3 cm long.

In northeast New Zealand, epifaunal crustaceans are major dietary

components for juvenile reef fish (Williams 1996).

Algae can provide a refuge from predation by fish and decapods. Predation was deterred most effectively in situations where invertebrate body shape matches algal morphology. Its function as a refuge is most effective when the morphology of the alga is similar to that of the invertebrate. The Gammarian amphipods, which use finely branched algae as a refuge, have significantly higher survival rates on that alga than on other algae or outside of algae. The decreased foraging efficiency of predators within densely vegetated areas allows a high population of invertebrates to exist inside finely branched algae (Stoner 1979, 1982; Heck, Orth 1980).

Epifauna associated with macroalgae use a variety of mechanisms to feed. Different invertebrates have been characterized filter feeding (Caine 1977), grazing on epiphytic algae (Brawley, Fei 1981), eating detritus (Zimmerman et. al. 1979), grazing from the host plant itself (Duffy 1990; Taylor 1994), and preying on other epifauna (Roland 1978). Edgar (1991a) used artificial habitats to show that the main determinant for invertebrate habitation on synthetic algae is epiphyte growth for the 35 most common species found on both natural and artificial substrates in Japan.

Differing morphologies, between different algal species and within one alga, support different epifaunal assemblages (Colman 1940; Sarma, Ganapati 1972; Warwick 1977). The narrow, finely branched holdfasts of algae create a favorable habitat for caprellid amphipods. Amphipods are more abundant in the base of *T. ornata* than the blade. Statistical significance was not seen due to low sample size. A similar amphipod distribution has been observed on *Macrocystis* kelp in New Zealand (Edgar 1987).

Some of the variability in invertebrate species distribution between identical replicates may be attributed to incomplete invertebrate removal by physical displacement in sea water. Large standard deviations were observed in invertebrate counts after displacement in saltwater. Invertebrate count variability decreased with the use of a freshwater displacement technique for the blade and base comparison. Lower variability found with freshwater washing suggests that it removes a more consistent percentage of the total invertebrate fauna.

Conclusion

This study investigated the effect of algal gross morphology on the distribution of algal epifauna. Algal morphology affects epifaunal distribution on different algal species and within one alga. Further studies involving the distribution of epifauna are needed to further understand the complex interactions between these invertebrates and the algae they inhabit. Research characterizing the seasonal fluctuation of epifauna should be done in order to improve understanding of the role epifauna plays as a food source for fish and macroinvertebrates. Studies into the role competition between organisms might contribute to the definition of forces driving epifaunal distribution.

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Appendix 1. Abundance and number of species of major animal groups.

Animal Group	Number of Species	Total Abundance
Gastropoda	16	2175
Tanaidacea	1	1279
Copepoda	19	1232
Isopoda	21	763
Amphipoda	12	515
Platyhelminthes	15	356
Ostracoda	2	231
Polychaeta	11	205
Acarina	2	147
Mysidacea	18	139
Euryalae	1	62
Ophiuroidea	1	38
Pugettia	1	5
Brachyura	1	3
Diogeniidae	1	3
Pycnogonida	1	2
Anomura	1	2
Holothuria	1	2

Neuston Composition and the Effect of Freshwater Sediment Plumes in Paopao and Opunohu Bays (Moorea, French Polynesia)

Joanna L. Canepa
Department of Environmental Science, Policy, and Management
University of California, Berkeley 94720

ABSTRACT. The composition and abundance of surface zooplankton (neuston) was examined in Paopao and Opunohu Bays (Moorea, French Polynesia) at three sites in October and November 1996. The zooplankton composition was compared between the bays, which are physically and geographically similar, with distinct levels of disturbance in their catchments. Samples were also taken in freshwater sediment plume waters, to note the effect of these plumes on neuston populations. Both bays had similar zooplankton compositions, being largely dominated by gastropod veligers and copepods. There was not a significant difference in total zooplankton abundance found between the bays (p > .05), however there were significant differences observed between small copepods, foraminifera, and polychaete larvae, which were all found in greater abundance in Opunohu Bay, the one least disturbed by anthropogenic influences. It is unknown whether the observed differences are indicators of varying disturbance between the bays, physical characteristics of the bays, or other factors. Freshwater sediment plumes had a highly significant effect on neuston populations (p < .0001) causing their abundance to decline sharply. This decline in zooplankton abundance in plume waters is distinct from results found in other plume studies, and may be attributed to the high flow pulse event plumes that characterize the plumes in Moorea. The freshwater plumes may cause surface zooplankton to flush out of the bay toward the ocean, or vertically migrate to avoid low salinity waters. The role of freshwater sediment plumes is important for zooplankton transport and distribution and deserves further research attention.

Introduction

Marine zooplankton has a predominant role in the transfer of energy to higher trophic levels (Lafontaine 1994; Omari et al. 1992). Because of their role as secondary producers, any factor affecting zooplankton could have major influences in the functioning of marine food webs. (Lefevre 1985). The spatial organization of zooplankton communities is determined by the physical, chemical, and biological properties of water masses (Villate 1994). The current scientific consensus holds that spatial variability in the species composition and abundance of zooplankton may translate into spatial differences in secondary production. (Omori et al. 1982; Lafontaine 1994). Because of the close association of zooplankton with higher trophic levels, detailed investigations of zooplankton communities in relation to environmental variability are necessary to understand the ecological processes in marine systems, and the way in which they are affected by anthropogenic influences. (Villate 1994; Lafontaine 1994).

One environmental variable that may affect zooplankton populations is storm driven freshwater sediment plumes. In all parts of the world where there are rivers, turbid low density plumes extend into coastal waters (Grimes et al. 1996). These plumes are easily detectable by the presence of a distinct color change between turbid plume water and clearer coastal water (McKinnon et al, 1995). Because of their delectability and frequency, freshwater riverine plumes provide an opportunity to study an important phenomenon that may have a significant influence on numerous physical and biological properties of the upper layer, including zooplankton transport and ultimately reef fishes (Kaartvedt et al. 1990) It has been suggested that these plumes play an important role in determining the distribution and abundance of zooplankton communities, but they have seldom been the focus of scientific investigation (Kaartvedt et al. 1990). In tropical waters, there have been no studies of the effect of storm driven freshwater sediment plumes on surface zooplankton (neuston).

The role of zooplankton communities in Pacific island coral reef ecosystems has been a subject of research

interest for many years (Sale et al. 1976; Renon 1978). Because most of the tropical zooplankton research has been concentrated on reef and lagoon zooplankton assemblages (Auchtancutty 1989; Sale 1976), little is known about the zooplankton composition in large bays on tropical islands.

This study looks at the neuston composition and abundance in two high island tropical bays in Moorea, French Polynesia (17° 30' South, 149° 50' West). Previous zooplankton studies in Moorea have looked at the composition of zooplankton in the lagoons of Moorea (Renon 1978), the species richness of zooplankton in the lagoons of Moorea and Opunohu Bay (Lefevre 1985), the spatial and temporal variability of one copepod species in Paopao Bay (Houston 1995), but no research has been conducted which looks at the composition of zooplankton comparatively in Paopao and Opunohu Bays. The similar physical characteristics and proximity of these bays coupled with the distinct level of anthropogenic disturbance in each bay present a good opportunity to identify characteristics of zooplankton composition in high island bays and to conduct comparisons between the two bays related to environmental disturbance variability.

In addition, this study investigates the effect of storm-driven freshwater sediment plumes on surface zooplankton populations in Paopao Bay. Given the importance of zooplankton populations in coral reef environments, like those which are found in Moorea, it is necessary to discern what factors control their distribution and abundance.

The purpose of this study three fold. The first aim is to characterize the composition of neuston in Paopao and Opunohu Bays, then to test two hypotheses about zooplankton communities in relation to environmental variability: 1) Different zooplankton abundances be observed in Paopao and Opunohu Bay, reflecting the distinct patterns of environmental disturbance in the catchments and littoral planes of the two bays; 2) The presence of freshwater sediment plumes after rain events affects neuston populations and community structure.
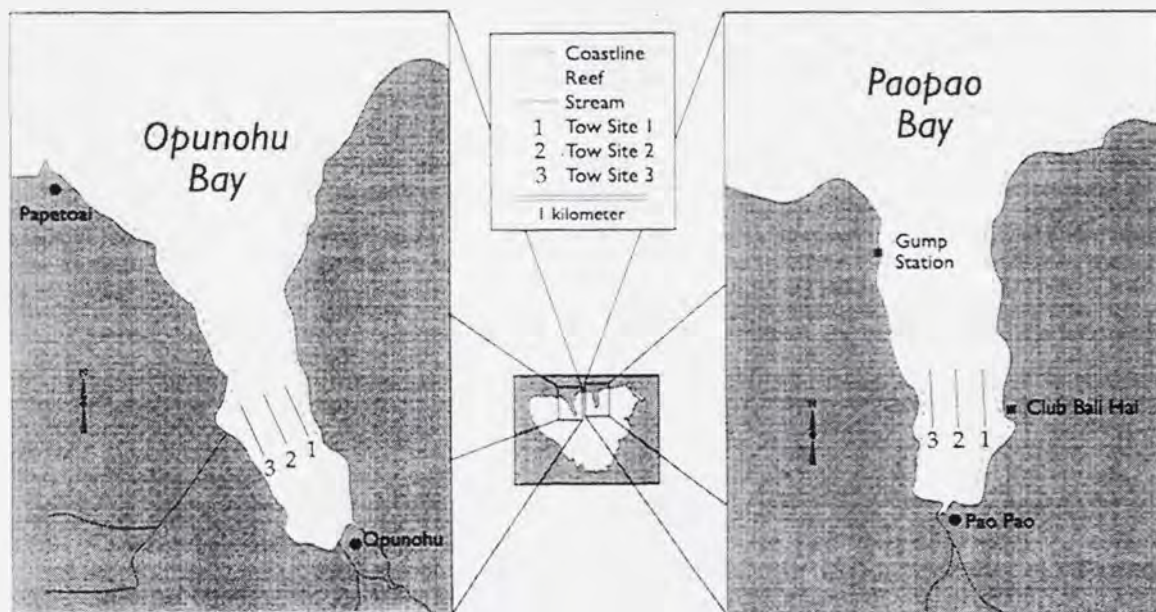

Table 1: Opunohu Bay and Paopao Bay in relation to the northern coast of Moorea, French Polynesia. Plankton tow sites in each bay are denoted as 1, 2, and 3.

Materials and Methods

Study Sites

The northern side of the island of Moorea, French Polynesia is indented by two large narrow bays: Paopao and Opunohu Bays (Figure 1) These bays are physically and geographically similar, both being approximately 3.5 km long and 600 m mean width with the same wind and wave conditions (Moraney 1994). The two bays are separated by a 3 km wide mountainous ridge, and are situated in a valley surrounded by highly erosive steep slopes. Paopao Valley is 16.8 km² and Opunohu Valley is 28.5 km² (Moraney 1994).

The anthropogenic disturbance and land use in Paopao and Opunohu Valley is very different, with Paopao Valley being developed and Opunohu Valley remaining more pristine. Paopao Bay is surrounded by a constructed littoral plain composed of tourist hotels, housing developments, the town of Pao Pao, and the majority of the pineapple plantations in Moorea. Opunohu Bay remains largely undeveloped, with few housing developments and no town. The catchment of Opunohu Bay is farmed for pineapple and other crops, although the agriculture use is not as intensive as the use in the Paopao drainage (Moraney 1994).

The mean rainfall in Pao Pao valley is 184.3 mm/year in October and 313.0 mm/year in November. The rainfall in Opunohu Valley averages 235.5mm/year in October and 318.4 mm/year in November. (Service meteorologique de Polynesie 1992) This rainfall when paired with the erosive steep slopes surrounding each bay, combines to produce visible freshwater sediment plumes in the bays after large storm events. The amount of solid material supplement in the bays during rainy days is approximately 240 T/year (Moraney 1994).

The prevailing wind and waves are generated by steady NE winds that dominate from mid-morning to sunset with an average windspeed of 14 km/hr (Gabrie et al. 1985). High tides occur from 11:00 AM to 2:00 PM and from 11:00 PM to 2:00 AM. Low tides occur from 5:00 AM to 8:00 AM, and from 5:00 PM to 8:00 PM (Gabrie et al. 1985).

Sampling Methods

The composition of zooplankton in samples depends on the method, place, and time of their collection. (Sorokin 1990). In order to obtain representative samples of neuston populations during the two month span of the study (October and November, 1996), all sampling was conducted between 10:00 AM and 3:00 PM at specific sites. Each sample was collected using a 350 um neuston net with a 255 cm² trapezoidal opening , and a 250 ml cod end. Neuston tows were conducted by submerging the net 10 cm into the water alongside a small skiff traveling at approximately 4.5 km/hr for 5 minutes. Each tow was approximately 0.375 km long and sampled approximately 9.56 m³ of water (not taking into account surface current variability). Every sample was stored and refrigerated until being counted. The neuston net was thoroughly rinsed clean between tows. The samples were transferred into a 250 ml graduated cylinder and thoroughly mixed for counting. Both 5 ml and 10 ml sub-samples were extracted from the sample and viewed under a dissecting scope. All organisms in the sub-samples were counted and recorded in class groups including: gastropods (Mollusca: Gastropoda), copepod "A" (Arthropoda: Crustacea: Copepoda, small copepods with carapace length <1.25 mm), copepod "B" (large copepods with carapace length >1.25 mm), bivalves (Mollusca: Gastropoda: Pelecypoda), shrimp (Arthropoda, Crustacea: Malacostraca: Decapoda: Natantia), brachyuran larvae (Arthropoda: Crustacea: Malacostraca, Decapoda: Reptantia), foraminifera (Protozoa: Sarcondinea: Foraminifera), echinoderms (Echinodermata), fish larvae, chaetnogaths (Chaetognatha: Sagittoidea), ostracods (Crustacea: Ostracoda), mysidacea (Arthopoda: Crustacea: Malacostraca: Mysidacea), and polycheate larvae (Annelida: Polychaeta). Voucher specimens of the zooplankton found are stored at the University of California Berkeley Museum of Palentology.

Non-Plume Days

Sampling was conducted in both Pao Pao and Opunohu Bays on days with no visible freshwater sediment plume present to determine the composition of the neuston in these bays. Samples were collected at three parallel sites approximately .5 km from the inlet streams at the foot of each bay on a total of 16 non-consecutive days for a total of 54 plankton tows. Site 1 in Paopao Bay (17° 30. 132' South, 49° 49.156' West) was located on the eastern side of the bay, Site 2 (17° 30.135' South, 149° 49.225' West) was located in the center of the bay, and Site 3 (17° 30. 187' South, 149° 49.379' West) was located on the eastern side of the bay. The three towing sites in Opunohu Bay were in comparable locations to the sites in Pao Pao Bay. (Site 1: 17°30.346 South, 149°49.299' West, Site 2: 17°30.755' South, 149°51.055' West, and Site 3: 17° 30.772' South, 149°51.170' West) MAP Samples were only collected on days when the wind was coming from the north east because variable surface currents driven by winds are known to produce different zooplankton concentrations (Hobson et al. 1978). On each sample day, the conductivity, water temperature, wave height, and wind direction were recorded. Conductivity readings were measured as an indirect measure of salinity, for which there was no meter available for the study.

Plume Days

Zooplankton tows were done in Paopao Bay on days when a visible freshwater sediment plume was present after rain storms in order to note the effect of freshwater sediment plumes on neuston populations. The plumes in the bay were of varied sizes and durations, with samples being taken on days when the plume fronts reached approximately .5 km from the inlet stream in Pao Pao, toward the mouth of the bay (Figure 1). Plume waters were identified visually by a distinct color change between brown sedimented plume water and the clearer, unsedimented non plume water and empirically by conductivity readings taken inside and outside of plume waters. The plumes were characterized by a 2-15 cm freshwater lens of turbid water lying atop more dense, less turbid, saline bay water depending on the influx of fresh water coming through the bay. A total of eleven plume tows were taken in four different plume events. At each tow site, the conductivity, water temperature, wave height, and wind direction were recorded. A 2 liter freshwater sediment plume sample was taken from each tow site and filtered through a weighed and dried coffee filter. The filter was oven dried and re-weighed to obtain an estimate of the sediment load in the freshwater sediment plumes at each site.

Data Analysis

Because zooplankton populations are highly variable (Omari et al. 1984), tow counts from Paopao and Opunohu Bays were subjected to a Welch ANOVA allowing standard deviations not equal to see if there was any significant difference ($p < .05$) in the quantity of neuston in the two bays. A Welch ANOVA was also used to note differences in the quantity of individual taxonomic groups between the two bays and in plume and non-plume days in Paopao Bay.

Results

During the study period the surface water temperature ranged from 26° C to 28° C in both bays. The surface water temperature did not change significantly with the presence or absence of a freshwater sediment plume. Conductivity measurements varied significantly between the presence and absence of a freshwater sediment plume ($p < .0001$), with the mean plume and non plume conductivities at 9.33 ms and 13.84 ms, respectively.

There was not a significant difference found between the zooplankton counts at site 1, 2, and 3 within each bay ($p < .70$ in Paopao non plume tows, $p < .25$ in Opunohu tows, and $p < .31$ in Paopao plume tows), so the data from the three tow sites taken each day were combined for statistical analysis.

Zooplankton Composition

The zooplankton tows from both bays were dominated by two main

taxonomic groups: gastropod veligers and copepods (Table 1). Gastropod veligers comprised > 80% of Paopao tows and > 57% of Opunohu tows, followed by copepods which accounted for > 16% of Paopao tows and > 41% of Opunohu tows. The small copepods (copepod "A") made up a substantial percentage of Paopao Bay (> 14%), with large copepod "B" plankters being less abundant at > 2% of the total zooplankton population. In Opunohu Bay, copepod "A" plankters consisted of a large percentage (> 40%) of the total zooplankton composition, with large copepod "B" plankters consisting of a very small percentage (< .3%) of the plankton.

In Paopao Bay, bivalves made up > 1% of the zooplankton composition, but the abundance of all other taxa found in either bay comprised < 1% of the total zooplankton composition, including chaetognaths, ostracods, foraminifera, mysidacea, echinoderm larvae, polychaete larvae, fish larvae, brachyuran larvae, and shrimp larvae (Table 1).

Besides these taxa, few specimens of isopods, amphipods, stomatopod larvae, cladocerans, and siphonophora were also encountered in the samples. These plankters constituted < .01% of the plankton population at both sites so they were not included in the statistical analysis.

There was a substantially greater abundance in meroplankton (transitory or temporary plankton in the egg or larval stages) observed than holoplankton (permanent plankton) in both bays, with the meroplankton comprising > 17% and > 41% of the sample in Paopao and Opunohu bay, respectively, and holoplankton comprising > 84% in Paopao and > 58% in Opunohu Bay (Table 1).

Two-Bay Comparison
There was not a significant difference in the total quantity of zooplankters found in Paopao Bay and Opunohu Bay tows (p > .0633)(Table 1).

Table 1. Percentage composition of various taxonomical groups of holo- and meroplankton to total zooplankton in Paopao and Opunohu Bays. (For Paopao Bay, n = 23 and for Opunohu Bay n = 21)

	Paopao	Opunohu	Difference
Total Zooplankton	63.46	228.69	not significant
Holoplankton (%)			
Copepod "A"	14.56	41.20	p < .01
Copepod "B"	2.10	0.23	p < .0001
Total Copepods	16.66	41.43	
Chaetognaths	0.16	0.14	not significant
Ostracods	0.01	0.03	not significant
Foraminifera	0.04	0.30	p < .01
Mysidacea	0.39	0.06	not significant
Total holoplankton	17.26	41.96	
Meroplankton (%)			
Gastropod veligers	80.89	57.28	not significant
Echinoderm larvae	0.86	0.11	not significant
Polychaete larvae	0.28	0.49	p < .01
Bivalve larvae	1.80	0.88	not significant
Fish Larvae	0.12	0.01	not significant
Brachyuran Larvae	0.04	0.00	not significant
Shrimp Larvae	0.34	0.13	not significant
	84.33	51.90	

	Plume	No Plume	Difference
Total Zooplankton Per ml.. of Sample	4.93	47.9	$p < .0001$
Holoplankton (%)			
Copepod "A"	17.36	14.56	$p < .0001$
Copepod "B"	5.49	2.10	$p < .0001$
Total Copepods	22.85	16.66	$p < .0001$
Chaetognaths	0.00	0.16	not significant
Ostracods	0.28	0.01	not significant
Foraminifera	0.72	0.04	not significant
Mysidacea	2.74	0.39	not significant
Total holoplankton (%)	26.59	17.26	
Meroplankton (%)			
Gastropod veligers	59.91	80.89	$p < .0001$
Echinoderm larvae	2.46	0.86	not significant
Polychaete larvae	1.59	0.28	not significant
Bivalve larvae	8.97	1.80	$p < .05$
Fish Larvae	0.72	0.12	not significant
Brachyuran Larvae	1.01	0.04	not significant
Shrimp Larvae	4.19	0.34	not significant
Total Meroplankton (%)	7885	84.33	

Table 2. Percentage composition of various taxonomical groups of holo - and meroplankton in Paopao Bay in plume and non-plume waters in October and November, 1996. For plume data n = 11 and for non plume data n = 23.

However, there are some interesting differences in the occurrence of certain taxonomic groups. Opunohu Bay is host to significantly more small copepods (copepod "A," p<.0152), planktic foraminifera (p<.0076), and polychaete larvae (p<.0123) than Pao Pao Bay (Table 1). In Paopao Bay, there is a larger population of large copepods (copepod "B," p<.0001) than in Opunohu Bay (Table 1).

Plume vs. Non Plume Neuston

The total zooplankton abundances declined sharply in response to the presence of a freshwater sediment plume (p < .001, Figure 3). Greater zooplankton abundance was observed in higher concentrations in non-plume waters for all taxa sampled, with the exception of brachyuran larvae. The taxa for which the observed difference in zooplankton abundance is statistically significant include gastropod veligers (p <.001), small and large copepods "A" and "B" (p < .0002 and p < .0001, respectively), and bivalves (p < .0265). The total percentage of holoplankton (26.59%) and meroplankton (78.85%) for the plume tows are very similar to the percentages found in non-plume conditions.
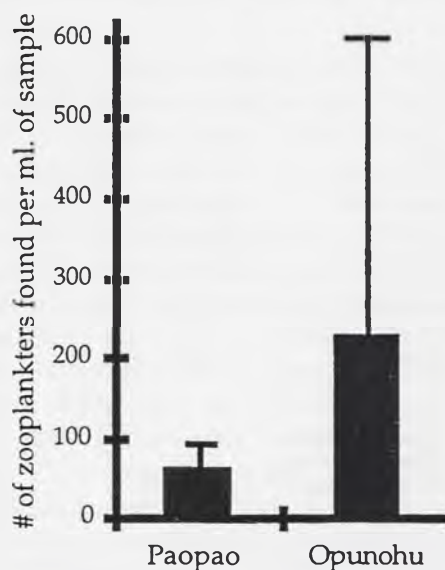
Figure 2. A comparison of zooplankton found per ml. of sample in Paopao and Opunohu Bays (p > .05, error bars = 1 s.d.)
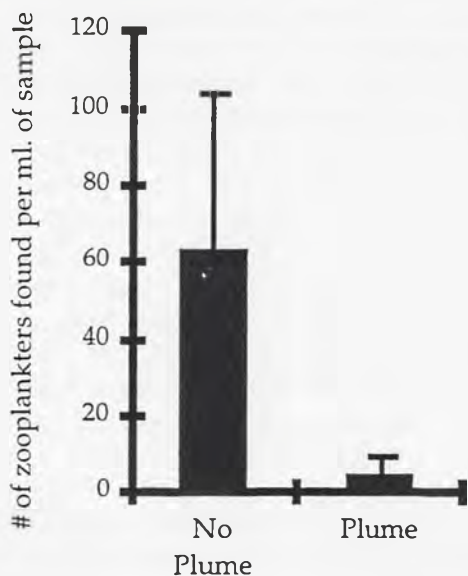
Figure 3. A comparison of zooplankton found per ml. of sample in Paopao Bay in plume waters and non-plume waters (p < .001, error bars = 1 s.d.)

The experiment using filtered and weighed samples of plume water to get an estimate of sediment loads was inconclusive due to equipment problems with the scales.

Discussion

Composition of Zooplankton in Both Bays

Zooplankton assemblages in tropical estuaries are largely dominated by a few species (Achuthankutty 1989). Although individual species were not compared in this study, it was found that the zooplankton population is clearly dominated by two taxa: gastropod veligers and copepods, comprising > 97% of the total zooplankton composition in both bays (Table 1). In most tropical bays, copepods largely predominate, followed by gastropod veligers, brachyuran larvae, and chaetognaths (Longhurst et al. 1987). Interestingly, this study found gastropod veligers rather than copepods as the dominant taxon in both bays, with gastropods comprising > 80% of the Paopao tows and >57% of the Opunohu tows. Copepods constituted >16% and > 41%,

respectively (Table 1). Brachyuran larvae and chaetognaths were not observed in substantial abundance, comprising < .15% of the total zooplankton found in both bays (Table 1).

This unusual dominance of gastropods may be due to several factors, including the timing of sampling and the life cycle of gastropods on Moorea. First, some copepods are demersal plankters, meaning that they appear in the water column mostly at night, when they emerge from the benthic biotopes (Sorokin 1990). The abundance of one species of copepod in Paopao Bay has been shown to be greatest between 9pm and 12 midnight (Houston 1996). Gastropod veligers do not exhibit this demersal migration, so the mid-day timing of all tows in both bays could account for why gastropods were found in greater abundance than copepods, which during the day may have been in the benthos. Second, the fact that all freshwater gastropods on Moorea are diadromous (meaning that they rely on marine water to complete their life cycle) could account for this gastropod dominance (Haynes 1988). These diadromous species spend their veliger stage in marine water, possibly causing an increased concentration of them in Moorea's bays that would not be a factor in other tropical bays without the presence of these species.

Conspicuously absent from the tows in both bays is one major group of zooplankton: appendicularia. This taxa has been present in the lagoons of Moorea (Lefevre 1985) and the fact that it was not found in either bay is surprising. It is possible that the sampling method employed was destructive to the more delicate plankters, including appendicularia. They might have gotten destroyed by the mesh of the net or during the transport of samples. Notably, the plankters which constituted the majority of the samples in both bays (copepods, gastropods, and bivalves) are the same taxa with calcified shells or exoskeletons which would make them less vulnerable to destructive sampling methods, suggesting that the destruction of delicate plankters may have had some influence on the results (Table 1).

The species found in any zooplankton sampling program is strongly influenced by the type of methods used to collect samples. Quite a different qualitative composition of zooplankton is found with net tows, traps, light traps, and air lift methods (Sorokin 1990), so more research using different methods should be conducted to compare with the findings of this study.

Comparison of Zooplankton Between Bays

A comparative analysis between Paopao and Opunohu Bays suggests that both bays are very similar not only in their physical properties, but also in their zooplankton composition. The lack of a strong statistically significant difference between the total number of zooplankters found per sample in each bay suggests that there is no difference between the bays at the sampling scale used in the present study (p > . 0633)(Figure 2). However, the close p-value to the level of significance (p < .05), the high variability of the samples, and the personally observed differences between the total zooplankton composition in each bay indicate that in future studies a significant difference may be reached if the time scale of the study is expanded and more replicate tows are taken.

Significant differences in certain taxa abundances between the two bays were observed for four taxa: small copepod "A" (p < .05), foraminifera (p < .01), polychaete larvae (p < .05), and large copepod "B " (p < .0001)(Table 2), with the former three taxa being more abundant in Opunohu Bay and the latter taxon being more abundant in Paopao Bay. Not much is known regarding the disturbance tolerances of these taxa. Moreover, it is difficult to establish whether or not these differences in number are due to the differential levels of disturbance in the catchments of both bays or other untested factors that influence zooplankton distribution such as predation and patchy distribution.

Not enough the other taxa were present to make an analysis of the varied zooplankton communities in each bay meaningful (> 3% of the total counts from both bays were taxa other than gastropods and copepods). For future studies, increasing the volume of water towed and counting larger sub samples would make comparisons of these less abundant taxa more appropriate.

The three taxa found in greater abundance in Opunohu Bay, small copepods, foraminifera, and polychaete larvae, have all been used in previous studies as bioindicators of environmental stress. (Ragosta et al. 1995; Van Bulogh 1988) Plankton species are useful for general monitoring of certain aspects of the environment, such as hydrographic events, eutrophication, pollution, warming trends, and long-term changes symptomatic of environmental disturbances (Omori et al. 1984). Recent work has shown that differences in zooplankton species composition could indicate stress before modifications in environmental parameters are detectable (Ragosta 1995). By establishing a record of the surface zooplankton abundances in both Opunohu and Paopao Bays, this study is important because it makes it possible for future studies to monitor the zooplankton communities as indicators of environmental stress. Small copepods, foraminifera, and polychaetes could feasibly be the environmentally sensitive species needed for such a project to be successful.

The fact that the bays have similar zooplankton concentrations lends itself well to comparative monitoring. There is continuous housing and agricultural development pressure on land in Paopao Valley, so the anthropogenic disturbance of land use change and the associated increase in pollution runoff with development could increase substantially in the foreseeable future in Paopao Bay. Alternatively, development in Opunohu Valley is tightly restricted, so it does not face the same development pressures and will likely remain in an undisturbed condition. Because the land use pressures are different for each bay catchment, a future study could periodically monitor zooplankton abundance and species composition in both bays as indicators of long-term changes in environmental disturbance. A knowledge of the pollution levels in each bay and of the pollution

tolerance of specific species may show some interesting results in future studies.

Effect of Freshwater Sediment Plumes on Neuston Populations

The recent explosion in frontal plume research has not reached consensus regarding the effect of sediment plumes on zooplankton distribution and abundance. It is well established that sediment plumes in estuarine environments result in a net increase in phytoplankton biomass (Gaudy et al. 1990), however results for the effects on zooplankton populations are not as clear. Riverine plume research has overwhelmingly concluded that zooplankton populations are conspicuously elevated in riverine plumes (Gundy et al. 1990; McKinnon et al. 1995; Grimes et al. 1996). However, a few studies have challenged that conclusion by demonstrating that zooplankton abundance is either unaffected by sediment plumes or is lower than the abundance outside of plumes. (Grimes et al. 1991; Cadee 1975, Pagano, 1993) The results of plume tows in Paopao Bay show that the abundance of zooplankton observed was over 10 times less in plume waters than in non-plume waters, with an average of 4.9 organisms per ml. of sample in plume tows and 49.9 per ml in non-plume tows (p < .0001). Such a drastic absence of zooplankton abundance in freshwater sediment plume tows has not been observed in any previous research.

All freshwater plumes are buoyancy-driven flow structures that propagate away from the generation region as plume fronts (O'Donnell 1993). The size and shape of plumes and their associated fronts is variable, depending upon the nature of tidally induced turbulent mixing, the dimensions and shape of the estuary and adjacent shelf area, and the rate of freshwater discharge (Grimes et al 1996). The freshwater sediment plumes discussed in this study are generated by pulse events of high flow that characterize the Paopao watershed after a rainstorm. This freshwater runoff drains through a narrow outlet river into Paopao Bay, resulting in an episodic turbid freshwater lens situated atop clear, saline bay water, forming within hours after rainfall and lasting

anywhere from 2 hours to 1 day. In contrast, most plume research concluding that zooplankton abundances are higher in plume water has not been conducted on this type of storm-driven plume, but on the everyday plume fronts of large continental rivers in temperate zones like the Mississippi (Grimes et al. 1991) and Rhone River (Gaudy et al. 1990), which have a longer residence time in the estuary (Grimes et al. 1996). Also, the majority of these studies focus on the convergence zone at the very front of a forward-moving sediment plume (McKinnon et al. 1995), whereas the focus of this study is the middle of the sediment plume.

Because the plumes observed in this study are so distinct from that of other plume research in both their physical properties and zooplankton abundance suggests that the different characteristics of Paopao Bay plumes may be critical factors in determining the fate of zooplankton in a freshwater sediment plume. These major areas of distinction include: the episodicity of plumes (is it a ephemeral or perennial plume?), the narrowness of the river (if it is narrow, the plume will be a thinner buoyant layer that will not mix well with marine waters), the part of the plume sampled (is it the plume front or mid-plume?), the residence time of the plume, and the type of system it is in (is it a continental river plume or an island plume?). These factors are untested by this study, however they warrant future research to establish if they are determining factors for whether or not zooplankton thrives in or is absent from sediment plume waters.

It has been suggested that the temperature of the plume region also plays an important factor in the role of plumes in relation to secondary production. Grimes (1996) recently put forth two hypotheses to explain why lower rather than higher secondary production in tropical plumes may be observed. First, the discharge of low density plume water into highly thermally stratified tropical waters may intensify stratification and retard the mixing of nutrient-rich plume waters below the plume, so that the turbid plume water remains on the surface and has little effect

on productivity. Second, the year-round high temperatures in the tropics may promote the stripping of nutrients in the soil before they ever reach an estuary, delivering nutrient poor but turbid water to the marine system that would have no positive effect on either primary or secondary productivity. However, Grimes put forth these ideas without much data supporting them, so a continuation of this study looking at the nutrient composition of sediment plumes and the vertical temperature stratification in a plume could be an interesting test of these hypotheses.

There are two widely discussed factors that the current literature suggests may be causing the observed lack of zooplankton in surface freshwater sediment plume tows. First, the change in water chemistry with the presence of a plume may be too harsh an environment for the plankters. Second, the physical flushing effect of a large volume of water draining into the bay could be flushing the neuston out of the bay toward the ocean along the front of the plume. Due to the limited time frame of this study and two extended droughts during the study period, these factors were untested by this work but the indications of other works suggest that both factors may play an important role.

The water chemistry effect has been the focus of recent studies which conclude that it is a minor factor, but not a major one in causing the lack of zooplankton abundance in plume waters. Pagano (1993) found that a high salinity gradient is not a barrier for zooplankton movement, so that plankters are physically able to enter plume waters if they can withstand the low salinity. The question then becomes what the salinity tolerance is for different taxa, a topic on which little research has been done. Other studies have concluded that the distribution of zooplankton biomass is independent of the distribution of surface water salinity, but further investigation into this subject is needed before conclusive statements can be proclaimed (Lafontaine 1994).

The physical flushing effect of a sediment plume carrying zooplankton out to sea has been shown in several studies to be an important factor determining the zooplankton composition in plume waters. Several studies have found that the densest aggregation of zooplankton in plume waters is where the low salinity lens expands southward from the mouth of the river over saline surface water. They have shown that a plume front aggregates zooplankton and retains them at or near the frontal margin of a plume, where converging water masses move downward owing to gravity. Surface seeking organisms (like neuston) accumulate at the surface as they resist the downward movement, which can deplete larval fish and zooplankton numbers in mid-plume waters and concentrate larval fish and zooplankton in plume fronts (Mackas et al. 1988; McKinnon et al. 1995; Grimes et al. 1996).

It is not clear whether the cause of the lack of zooplankton in Paopao Bay plume tows is due to the water chemistry effect resulting from freshwater inundation from a sediment plume, the physical flushing effect of a large volume of water draining into the bays, or an number of other untested factors. Whatever the main causal factors are, the results of this study strongly indicate that the observed sharp dropoff in zooplankton abundance in plume waters is tightly linked to factors associated with sediment plumes.

However, because there is often a considerable time lag in the response of biological populations to physiochemical variables, even if a particular species appears or disappears from certain waters it is difficult to make a determination as to whether or not the change is a result of the variable of interest (Omori et al. 1984). Therefore, additional research is needed to test which factors are important for causing a decline in zooplankton populations in mid-plume waters.

Suggestions for future research
I would encourage follow up research to the present study on the effect of sediment plumes on zooplankton distributions in Moorea. More specifically, a follow up study involving plankton tows at different depths during plume events to test whether or not surface plankters vertically migrate to avoid the low

salinity waters of a plume would be interesting. Also, looking at the nutrient composition of the sediment plumes and their effect on phytoplankton abundance would be important to note the effect of the plumes on primary productivity. In addition, recent studies are beginning to use zooplankton species as environmental indicators (Ragosta 1995). A useful project would be the long term monitoring of the zooplankton composition in both Paopao and Opunohu Bays to look for any changes that might signal an environmental disturbance.

Conclusion

Being secondary producers, marine zooplankton play a vital role in marine food webs upon which island communities rely. The role of zooplankton in tropical bay ecosystems is poorly understood, especially in the context of environmental variables such as human disturbance and freshwater sediment plumes. Through a comparison of the zooplankton composition in Paopao and Opunohu Bay, this study has reached several conclusions. First, the zooplankton taxa in both Opunohu and Paopao Bay are similar, being largely dominated by gastropod veligers and copepods. Second, copepods, foraminifera, and polychaete larvae are significantly less abundant in Paopao Bay, which may indicate that they are sensitive to the anthropogenic disturbance in Paopao Bay.

Armed with knowledge of the neuston composition in Paopao and Opunohu Bays, future studies can monitor any changes in their composition as possible indicators of environmental disturbance.

What this research has established regarding the effect of freshwater sediment plumes on zooplankton populations is unprecedented. The overwhelming decline of plankters in sediment plume water demonstrates that sediment plumes, or factors associated with sediment plumes, have a highly significant effect on neuston, causing populations to decline sharply. The implications for this result are far reaching and important for island communities, as these plumes are frequent events that effect secondary producers in a complex reef ecosystem.

Acknowledgements

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Habitat and Cavity Preference
in the Stomatopod *Gonodactylus childi*

Larry Rabin
Department of Integrative Biology
University of California, Berkeley 94720

ABSTRACT. A two part study of habitat and cavity entrance preference was conducted on the stomatopod *Gonodactylus childi* on the island of Moorea, French Polynesia. In Part 1, Density, porosity, and faunal diversity within coral rubble that contained *G. childi* were recorded as factors of habitat. *G. childi* was found to be negatively correlated with density and positively correlated with Synalpheidae present in rubble. All other correlations were not significant. The negative correlation with density is believed to be a consequence of difficulty in modifying cavities with large densities. Causes for the positive correlation with synaplpheids is unknown. In part 2, *G. childi* was exposed to three different cavity entrance sizes (one approximately equal to, one 55% wider, and one 55% smaller than body width) and allowed to choose a cavity. *G. childi* chose the large cavity (55% wider) significantly more often than any other cavity size. This is likely to be caused by the need for *G. childi* to bring large prey back to the cavity for processing as well as to provide *G. childi* with adequate water circulation for respiration.

Introduction

Stomatopods, also known as mantis shrimp, are living members of a clade that diverged more than 400 million years ago from Malacostracan stock (Reaka 1980). Species are recognized by the presence of enlarged second thoracopods called raptorial appendages which, in modern stomatopods, are used to capture prey, construct or modify shelters, and are also used in inter- and con- specific interactions (Caldwell and Childress 1990). Stomatopods can be divided into two functional groups, "Spearers" and "Smashers," based on morphological differences of the raptorial appendages between the two groups. The families Squillidae, Pseudosquillidae, Lysiosquillidae, Bathysquillidae and some members of the family Gonodactylidae make up the spearers while the remaining members of the gonodactylids comprise the smashers (Caldwell and Dingle, 1975). Differences in the morphology of the raptorial appendages, in turn, dictate differences in behavior between the two groups (Caldwell and Dingle 1976).

Spearers have long, thin, flat raptorial appendages used to impale soft-bodied prey. These prey are ambushed by the stomatopod from the stomatopod's burrow which is dug in mud or sand (Caldwell and Dingle 1976). In contrast to spearers, the smashers' (*Gonodactylus sp.*) raptorial appendage is well armored, contains no barbs, and is used to smash hard-shelled prey such as snails and crabs (Caldwell and Dingle 1976). These prey are stalked and captured away from *Gonodactylus* cavities typically located in coral rock or rubble. The stomatopods then return to their cavities to process food items (Caldwell 1988).

Although *Gonodactylus* generally do prefer cavities as opposed to burrows in mud or sand, variations in cavity preference are present between species (Caldwell 1988). Species may occupy cavities in coral rubble, live coral or shale. Some species create their own cavities by breaking off pieces of branching coral and taking shelter inside the branches, while other species prefer cavities that are excavated by boring sponges, sipunculids, bivalves, and polychaete worms (Reaka and Manning 1981). *Gonodactylus* may prefer different types of cavities, but in all species acquisition and maintenance of a cavity is necessary for avoidance of predatory fish, and is also important in allowing individuals a place to molt, mate, and brood eggs (Reaka 1980).

Because the cavity itself plays such an important role in the survival of *Gonodactylus*, it is reasonable to assume that animals are not randomly choosing

cavities in which to live. Therefore, we should not see an even distribution of *Gonodactylus* in a habitat. Rubble with a greater number of cavities (greater porosity) should contain greater numbers of stomatopods because rubble of this type allows for greater variety of cavity choices. Because individuals often modify their cavities by striking cavity entrances and chipping off small rubble (Caldwell 1988), more modifiable cavities should be preferable over less modifiable ones. Therefore, as density of rock and difficulty in modification increases, we should find fewer stomatopods present. The characteristics of the cavity itself are important in choosing a cavity in which to live. Shape, volume, location, orientation and cavity entrance size should all influence cavity preference. Finally, we would expect to find *Gonodactylus* preference for rubble containing a particular faunal diversity. Specifically, cavities in rubble containing prey should be preferable over cavities in rubble without prey because this would afford individuals an opportunity to hunt closer to home and better avoid predators. Rubble containing predators is likely to be unfavorable as is rubble containing species that compete with stomatopods.

The purpose of this study is to examine several aspects of habitat preference in one species of gonodactylid, *Gonodactylus childi*, present in the central Pacific. Specifically, I addressed the following questions: (1) With what types of fauna does *G. childi* live? and (2) How do the abiotic factors of density, porosity, and cavity entrance size affect *G. childi's* preference of cavity?

Methods

Study Site

Gonodactylus childi was studied and collected at three sites in Cook's Bay, Moorea, French Polynesia (Figure 1). Site 1 was located along the backreef of the barrier reef bordering Cook's Bay while Sites 2 and 3 were located on the fringing reef along the west coast of the bay. All sites were located on the reef flat and were
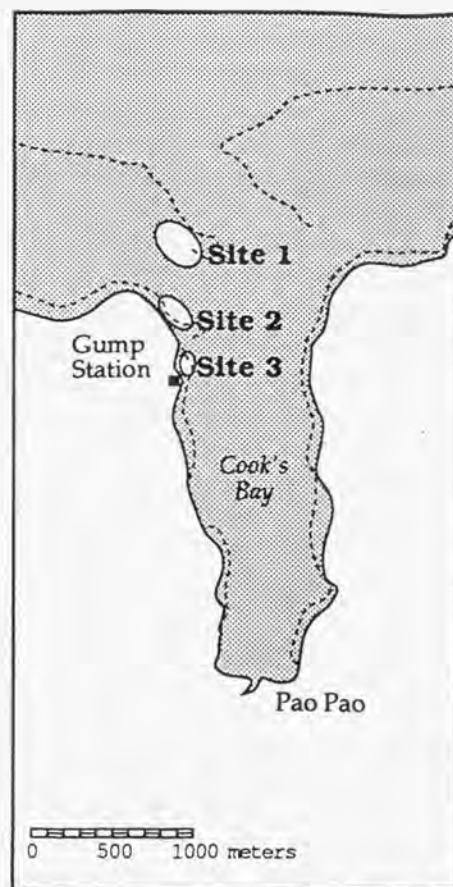
Figure 1: Map of Study Sites, Cook's Bay

submerged in 2-4 feet of water with living coral and coral rubble resting on a substrate of sand. Due to location in the bay and on the back reef, these sites seldom experienced high water velocity. Macro-algae at all 3 sites consisted of *Padina sp.* and *Halimeda sp.*. The main industry in Cook's Bay is tourism and large cruise ships entered the bay at least once a week creating possible disturbances for marine wildlife. In addition, because of erosion on the island of Moorea, a large plume of sediment often fills the bay after heavy rains. No formal study has been conducted which examines the effects of these disturbances on wildlife but a possible effect should be considered. Coral rubble typical of *G. childi* was collected from each study site and processed as described below.

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Collection of Coral Rubble

Collection and processing of rock for studies of habitat preference occurred from September 30 to October 20, 1996. Collection for laboratory experiments continued until November 4, 1996. Rubble collected was usually flat, partially submerged in sand and contained visible surface cavities. This type of rubble is typical of *G. childi* habitat (Caldwell R, personal communication). Pieces of rubble were lifted from the sand and immediately put in large plastic bags while still under water, in order to ensure that no fauna escaped from the rocks. Rubble removed from the bay was transported to the Gump Biological Research Station and kept in a large saltwater holding tank until processing began. A total of 38 rocks were collected and processed.

Characterization of Density, Porosity, and Faunal Diversity in Rubble Collected

After the removal of any macroalgae, volume of each piece of rubble was determined by displacement of water in a tank. Porosity of each rock, was determined based on the appearance of holes and cavities in the rock and rated on a scale of 1-5 with 5 being the most porous and 1 being the least porous. Each piece of rubble was then broken into smaller fragments in order to find any animals present within each rock. All rubble fragments were processed to a size less than 1 cubic inch. Rubble fragments were then dried, mass was measured, and density was calculated.

Species of invertebrates, as well as abundance of each species encountered during rock processing were recorded. In many cases, fauna could not be identified down to genus or species level. This will be noted where appropriate. The fauna recorded are given in Table 1.

Voucher specimens of each species were collected and are housed at the University of California Museum of Paleontology, Berkeley. *G. childi* individuals with a width of 3-4 mm at the posterior of the head were collected live and housed as described below.

Data Analysis: A linear correlation was performed which compared density, porosity, and animals observed with *G. childi*. Alpha value was set at p=0.05.

Table 1. Faunal Diversity in Coral Rubble

Gonodactylidae-Stomatopod
      Gonodactylus childi
Pseudosquillidae-Stomatopod
      Raoulserenea sp.
Crabs-size classes
      small (3-5mm)
      medium (6-8mm)
      large (>8mm)
Paguridae-Hermit Crab
      Pagurus sp.
Galatheidae
      (genus and species unknown)
Synalpheidae -Snapping Shrimp
      (genus and spcies unknown)
Alpheidae-Snapping Shrimp
      (genus and species unknown)
Sipunculid
      (2 unknown species)
Annelid
      (unknown)
Amphinomidae-Bristle Worm
      (maybe *Eurythoe sp.*)
Sigalionidae-Scale Worm
      (genus and species unknown)
Serpulidae-Christmas Tree Worm
      Spirobranchus giganteus
Echinometridae-Sea Urchin
      Echinometra sp.
Ophiuroidea -Brittle Star
      (genus and species unknown)
Arcidae
      Arca sp.
Isognomidae
      Isognomon nucleus
Mytilidae- Boring Bivalve
      Lithophaga sp.
Cypraeidae-Cowry
      Cypraea annulus
Marginellidae
      Marginella pacifica

Cavity Entrance Preferences

Housing, and Maintenance of *Gonodactylus childi*: *G. childi* with widths of 3-4mm at the posterior of the head were collected from the above study and transferred to one of two types of enclosures: 1) Rectangular enclosure with dimensions 320 x 170-mm, with water to a depth of

60mm and constant water flow, or 2) 330-ml specimen containers with water changes daily. Eight animals were housed in enclosures of Type 1 and 10 individuals were housed in Type 2 enclosures (utilized due to space limitations). All animals were maintained under natural light conditions. Once each week, individuals were fed live crabs of sizes 3-5mm which were collected during rock processing and housed in a saltwater tank.

Experimental apparatus: Animals were tested for cavity preference in an experimental arena of dimensions 170 x 130-mm with a constant flow of water to a depth of 60mm (Figure 2).
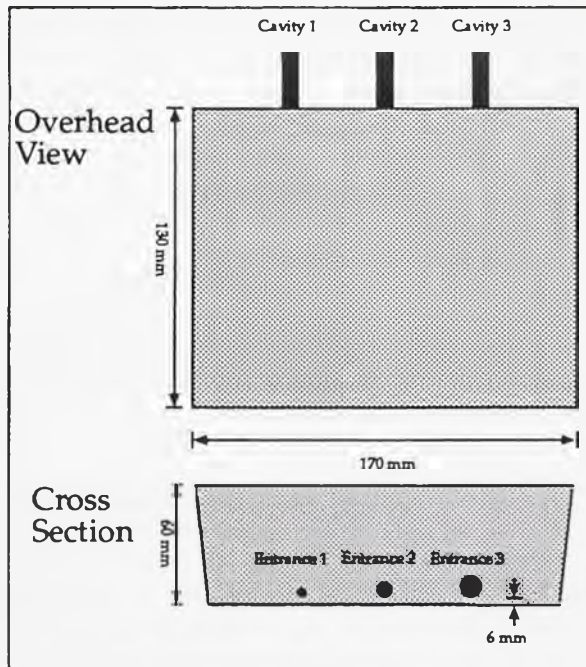
Figure 2: Experimental Arena

The floor was covered with a thin layer of sand. One 170-mm side of the arena was made of a removable wall containing three cavity entrances with diameters of 2.5mm (55% smaller than size-class width), 4.5mm, and 7.0mm (55% larger than size-class width). Each entrance was drilled 6mm from the bottom of the removable wall. An artificial cavity (a 3-ml black shell vial) was fitted to the back of each entrance . In order to avoid bias based on hole location, 6 removable walls were made Each wall

contained entrances in a different sequence. All stomatopods were run in 6 trials, once with each wall.

Experimental Procedure: Individuals were removed from their enclosures and transferred to a transparent holding container (inverted plastic cup) in the center of the experimental arena. This container allowed animals visual access to the entire arena as well as to the cavity entrances. Once animals in the transparent container ceased erratic swimming, the container was removed allowing the individual to search the arena and choose a cavity. If the stomatopod immediately flushed to one of the artificial cavities, the animal was removed and the trial was started again. Animals were left in the experimental arena for 30 minutes at which point all three artificial cavities were examined and cavity choice was recorded. In the event that no cavity was chosen, the trial was marked as "no choice". A total of 18 animals were tested. As noted above, each animal was tested once with each artificial wall. Each animal was tested once in a 24 hour period. At the conclusion of each trial, the animal was returned to its enclosure and the artificial cavities were cleaned with running water.

Data Analysis: In order to compare the overall choice preference of each individual as well as the magnitude of difference between choices among each individual, a Wilcoxon Matched-Pairs Signed Ranks Test for small samples (Seigel, 1956) was conducted on data collected from cavity entrance trials. Alpha value was set at p=0.05.

Results

Correlations of Density, Porosity and Fauna with G. childi

The presence of *G. childi* in coral rubble was negatively correlated with density (df=37, r=-0.325, p<0.05). The mean density of rubble where *G. childi* was present was 1.26 kg/L (sd=0.18 kg/L). There was no significant correlation between porosity and *G. childi* (p>0.05). r values of species of fauna living with G. Childi are given in Table 2. The only significant faunal correlation was between

the Synalpheid and *G. childi* (df=37, r= 0.43, p<0.05) which were positively correlated.

Table 2. Faunal Correlations with *G. childi*

Animal	r values
Raoulserenea sp.	0.153
Small Crabs (3-5mm)	0.252
Medium Crabs (6-8mm)	0.083
Large Crabs (>8mm)	0.166
Pagurus sp.	-0.149
Galatheidae (unknown species)	0.206
Synalpheidae(unknown sp)	**0.434**
Alpheidae (unknown species)	-0.191
Sipunculid #1 (unknown species)	0.130
Sipunculid #2 (unknown species)	-0.033
Annelid (unknown species)	0.200
Amphinomidae (unknown sp.)	-0.183
Sigalionidae (unknown species)	-0.159
Spirobranchus giganteus	-0.117
Echinometra sp.	-0.008
Ophiuroidea (unknown species)	-0.142
Arca sp.	0.139
Isognomon nucleus	-0.143
Lithophaga sp.	-0.117
Cypraea annulus	-0.061
Marginella pacifica	0.161

df=37, critical value for p<0.05= 0.316

Cavity Entrance Preference

In all trials conducted, animals never chose the 2.5mm (small) cavity entrance. Therefore, this hole size has been left out of all analyses and graphs. Choices of either the medium (4.5mm) or large (7.0mm) cavity by individual stomatopods are shown in Figure 3. A significant difference was seen between choice of the 4.5 mm (medium) cavity entrance and the 7.0mm (large) cavity entrance (Wilcoxon matched-pairs signed-ranks test, T=9.5, N=18, p<0.05) with *G. childi* individuals choosing the large cavity more often. In fact, only 2 individuals out of 18 chose the medium cavity more often than the large cavity. A singed-ranks test was not conducted for either medium/no-cavity or large/no-cavity pairs because choosing no-cavity does not reveal preferences for entrance size.

Discussion

Density, Porosity and the Need for Cavity Modification

The number of strikes needed to modify cavities should increase as density of rubble increases. Full (1989) reports that the energetic cost per strike will remain relatively constant however

Figure 3. Cavity Entrance Preference
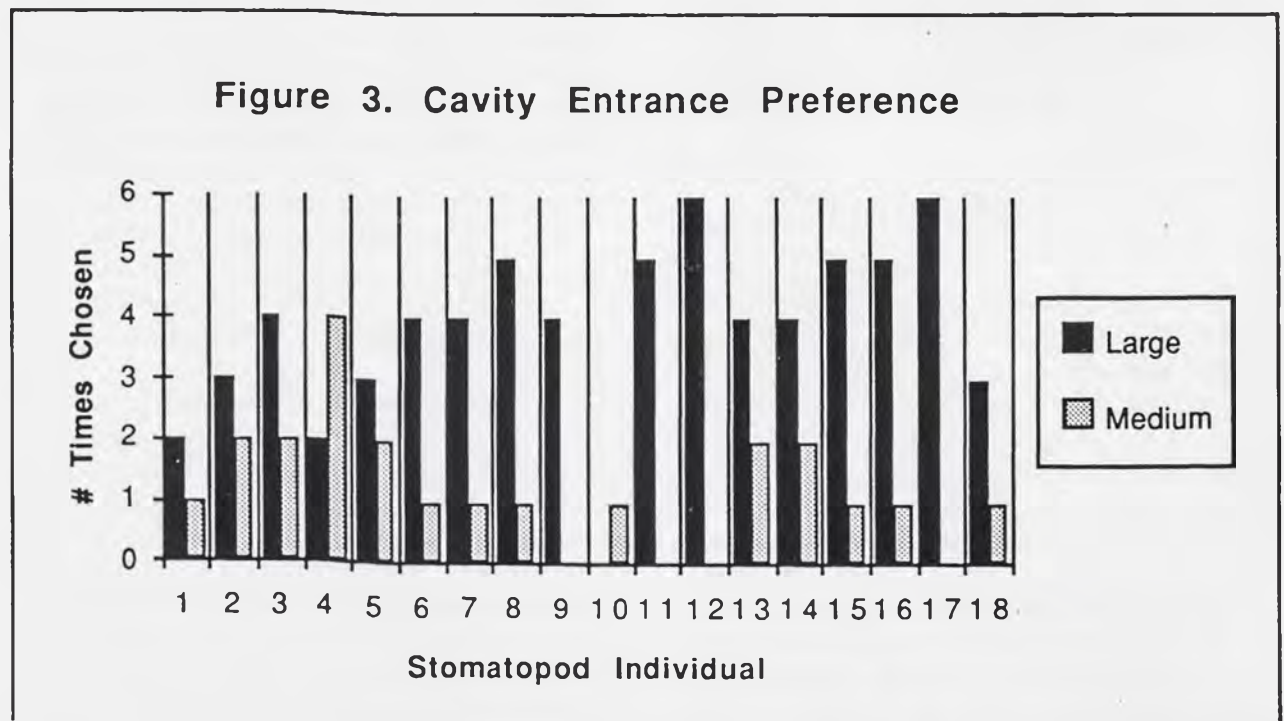
a greater number of strikes will be needed to modify larger, denser items. With an increase in strike number, there is also a resulting increase in energetic cost. Gradually, the energetic cost needed to modify a cavity becomes disadvantageous to the stomatopod. As a result, stomatopods should choose cavities in rubble with high densities less often than they should rubble in cavities with lower densities.

Results did show that as density of coral rubble increases, the presence of *G. childi* decreases. As stated above, this is most likely a consequence of *G.childi* choosing cavities that are more easily modifiable. Although cavity modification has never been documented in *G. childi*, it does play an important part in the behavior of other gonodactylids. For example, *G. bredini* and *G. oerstedii* live in hollow coralline algae nodules that are formed by pounding pebbles or shell fragments in between the branches of the algae (Caldwell 1988). *G. ternatensis* modify branching coral, *Pocillopora spp.*, by using their raptorial appendages to break off branches and take residence in the interior of the branching coral (Caldwell 1988). In order to provide the resident with a positional advantage against other invading gonodactylids, cavity entrances of many species are modified by pounding small pieces of coral into the cavity opening or by chipping material away to enlarge cavity entrances (Caldwell 1988). Therefore, the negative correlation of *G. childi* with density is not surprising.

Porosity however, did not correlate significantly with the presence of *G. childi*. Originally I hypothesized that more stomatopods would be found in more porous rocks because they contained a greater number of cavities. However, because many holes are carved by boring animals, even dense rubble can become quiet porous. *G. childi* does not prefer to inhabit cavities in the denser pieces of rubble even if they contain a large number of cavities. So, it was not the number of cavities present in each piece of rubble but instead the presence of a suitable cavity that dictates

whether or not a stomatopod chose to inhabit it.

Faunal Correlations with G. childi

Both Caldwell et. al. (1989) and Caldwell (1990) report that snails and hermit crab numbers are affected negatively by the presence of *G. bredini*. One would expect that *G. childi* individuals would also deplete the number of prey in their habitat. While this study of *G. childi* did not survey the entire habitat of the species, we expect to see that their presence has a similarly depleting effect on crabs and hermit crabs in coral rubble containing *G. childi*. *Gonodactylus* do prefer to select prey that are closer to their cavity (Caldwell and Childress 1990). Therefore, predation by *G. childi* is likely to occur in rubble in which the stomatopod's own cavity lies. As a result, prey living in rubble should correlate negatively with the presence of *G. childi*.

However, there was no significant correlation between the presence of *G. childi* and other crabs or hermit crabs (Table 2). This is surprising but may be explained by an overabundance of prey in Cook's Bay. If prey are present in exceptionally large numbers, stomatopod predation may not remove enough prey to observe a significant negative correlation between predator (*G. childi*) and prey. It is also possible that no significant negative correlation was seen between *G. childi* and prey items because densities of *G. childi* are low in Cook's Bay and do not have a significant effect on prey populations. While no studies have been conducted which measure normal ranges of *G. childi* abundance, Caldwell (1989) reports that the normal abundance of *G. bredini* ranges between 0.5 animals/m^2 to 20 animals/m^2. Although no formal census of *G. childi* abundance was conducted in this study, based on qualitative observations, the abundance of *G. childi* was lower than 0.5 animals/m^2. This would support the notion that stomatopod abundance was too low to observe any possible correlations between predator and prey.

In addition to negative correlations between gonodactylids as predators and

other fauna, *G. childi* should be absent from any piece of rubble that contains an animal which preys on stomatopods. The absence of gonodactylids in rocks with predators could be caused either by past predation upon stomatopods or by the avoidance of rubble containing any predators. While there were no likely predators (octopus or predatory fish) present in any rubble housing stomatopods, no conclusions can be drawn regarding *G. childi* associations with predators because predators were absent from all rocks. This does not however, indicate that predators are absent from *G. childi* habitat. Instead, lack of data is likely to be a result of highly mobile predators which don't live in rubble or were able to avoid capture during rubble collection by rapid locomotion out of rubble. In order to examine *G. childi* associations with predators, a study would have to be devised that either passively observed *G. childi*/predator interactions in the wild or brought both predators and stomatopods into a controlled laboratory setting so that both types of animals could be confined and kept under constant observation.

The only animal observed that showed a significant correlation with *G. childi* was the synalpheid which correlated positively (Table 2). It is unclear, at this point, why the synalpheid and *G. childi* are positively correlated in rubble collected. It is unlikely that the correlation is based on associations between the two species. It is more plausible that both simply prefer rubble with similar biotic and abiotic characteristics. Still, it is interesting that two invertebrate predators are able to live sympatrically. If both species consume similar prey, competition should exclude one species from each piece of rubble. However, snapping shrimp (synalpheidae) probably prey on soft bodied animals (Pearse et. al. 1987). Because *G. childi* preys on hard shelled animals, the animals may not compete and can thus successfully live sympatrically.

Observations of *G. childi* with fauna recorded in this study produced only one significant correlation. However, a variety of organisms were not present in this study that might also correlate with *G. childi*. Among organisms not recorded were the boring sponges and macro-algae. Future research which looks at these correlations would be worthwhile. It would also be interesting to determine if *G. childi* prefer certain types of coral rubble over others as use for cavities. Correlations of the size class of *G. childi* with fauna, density, porosity, etc. may yield significant correlations in the future as well. It is clear that more research must be conducted in order to determine correlations of *G. childi* with other characteristics in its habitat.

Cavity Entrance Preferences

As mentioned previously, the possession of a cavity is a necessity for gonodactylid survival (Reaka 1980). While occupancy in a cavity of any sort will provide some form of shelter, certain physical characteristics of the cavity may be preferable over others. Cavity entrance size is important in providing the resident with security over other aggressive stomatopods who may try to seize a cavity (Caldwell 1988). Cavities that are too large could be infiltrated easily by other stomatopods or predators and small cavities might be impossible to enter. Therefore, I originally hypothesized that *G. childi* would choose cavities with entrances just large enough to enter.

Data do not support this hypothesis (Figure 3) but instead show *G. childi* choosing cavities with larger entrances (55% larger than the stomatopods' widths) significantly more than cavities with entrances equal to their width. It is important to remember though that the cavity is not used solely for predator avoidance but also in a variety of daily activities. One important function of the cavity is its use as a location to process food. Food items that need to be processed by gonodactylids are rarely eaten in the open but are instead brought to the safety of the cavity where they are pulverized and ingested (Caldwell 1988; Caldwell et. al. 1989; Caldwell and Childress 1990). However, the size of the cavity sets an upper limit on the size of prey that may be brought back to the cavity (Caldwell et. al. 1989). As a benefit for feeding then, a stomatopod should choose cavities as large

in diameter as the width of the largest prey they eat. The need for circulation within the cavity is also important in allowing the resident stomatopod to respire. Circulation is more difficult in cavities with smaller openings. Thus, if circulation were the only concern in choosing a cavity, a stomatopod would also be likely to choose a cavity with a large entrance. But a cavity's use as a site for food processing as well as to provide water circulation have to compete with the needs of the cavity as a place of security. Therefore, cavities with extremely large openings should be unfavorable.

An upper limit on cavity entrance preference was not established because *G. childi* chose the largest of the three cavity choices in experiments. Although this paper established that *G. childi* does prefer cavities with entrances larger than body width, further research must be conducted which will place an upper limit on cavity entrance size as it relates to body width.

Acknowledgements

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Factors affecting the distribution of holothuroids on Vaipahu Reef, Moorea, French Polynesia

Daniel Damien Filiatrault
Department of Geography
University of California, Berkeley 97420

ABSTRACT: A transect survey was conducted to determine the distributions of all holothuroids on the fringing reef and barrier reef on the north shore of Moorea, French Polynesia. Tests on wave action, current velocity, and substrate characteristics were done to explain the distributions that were found. 15 species were encountered, *H. atra* and *B. argus* being the most common. Coral debris on the algal ridge was found to be an important microhabitat for many species. Night snorkels and a light/dark preference experiment were done to confirm that certain holothuroids avoid light by hiding under rubble during the day and come out to forage at night. Substrate was found to affect the distribution of *B. marmorata* because this species must have loose sand to burrow into, but sand particle size was not found to be important in feeding behavior. *A. mauritiana* was the only species that could withstand the force of direct wave energy on the fore-reef slope. Larger species were found at greater depths. The barrier reef was found to have a significantly higher diversity than the fringing reef. This higher diversity and abundance can be attributed to greater habitat diversity and faster current velocity which causes higher nutrient circulation.

Introduction

Holothuroids, commonly referred to as "sea cucumbers", are echinoderms that lie on one side with the mouth and anus at opposite ends of a cylindrical body (Nichols, 1962). Most holothuroids, except the synaptids, have thick, leathery skins and are rather unpalatable to predators. Nonetheless, the Polynesians, who call them "rori", make a soup out of certain varieties. When threatened, many species exude sticky cuverian tubules, which are no more than a nuisance to humans.

The class Holothuroidea is made up of approximately 1400 living species (Smiley and Pawson, 1991). Being deuterosomes, holothuroids are more closely related to humans than most invertebrates. They can be considered a successful group as they are found from the intertidal zone to the ocean trenches and constitute a large proportion of the total marine biomass (Gilliland, 1993). Much of what is known about their evolution comes from the study of tiny bones known as sclerites, ossicles, or spicules that can be found in the fossil record.

Previous work on holothuroids in French Polynesia has been done by Alain Guille and also by John Pearse. Guille, who took a general survey of holothuroids on many islands, found 22 different species.

Pearse, who did a survey of Moorean holothuroids during a month long stay at the Gump Biological Research Station, found 19 species on the island. Still there is confusion and disagreement over the identification of many species because, not only were these surveys published without photographs, but the latest identification keys available today often contradict one another (Guille, 1986)(Allen & Steene, 1994)(Gosliner, Behrens, & Williams, 1994).

The goal of this study was not simply to find which species inhabit the waters surrounding the island of Moorea, but to determine which microhabitats different species prefer, in what numbers they occur, and which factors lead to their distribution.

Preliminary investigation of the study site resulted in the following hypotheses:

1) Substrate affects the distribution of holothuroids.

2) Wave action will prevent certain holothuroids from inhabiting areas with a strong surge.

3) Areas with a higher current velocity will have more holothuroids because faster water flow results in more nutrient turnover.

(figure 1) Study Site

MOOREA

Vaipahu Reef

Avaroa Pass

Point Pihaena

Legend

Reef

Deep water

100m

N

Transect

Gump Station

(Figure 2) Profile of reef complex
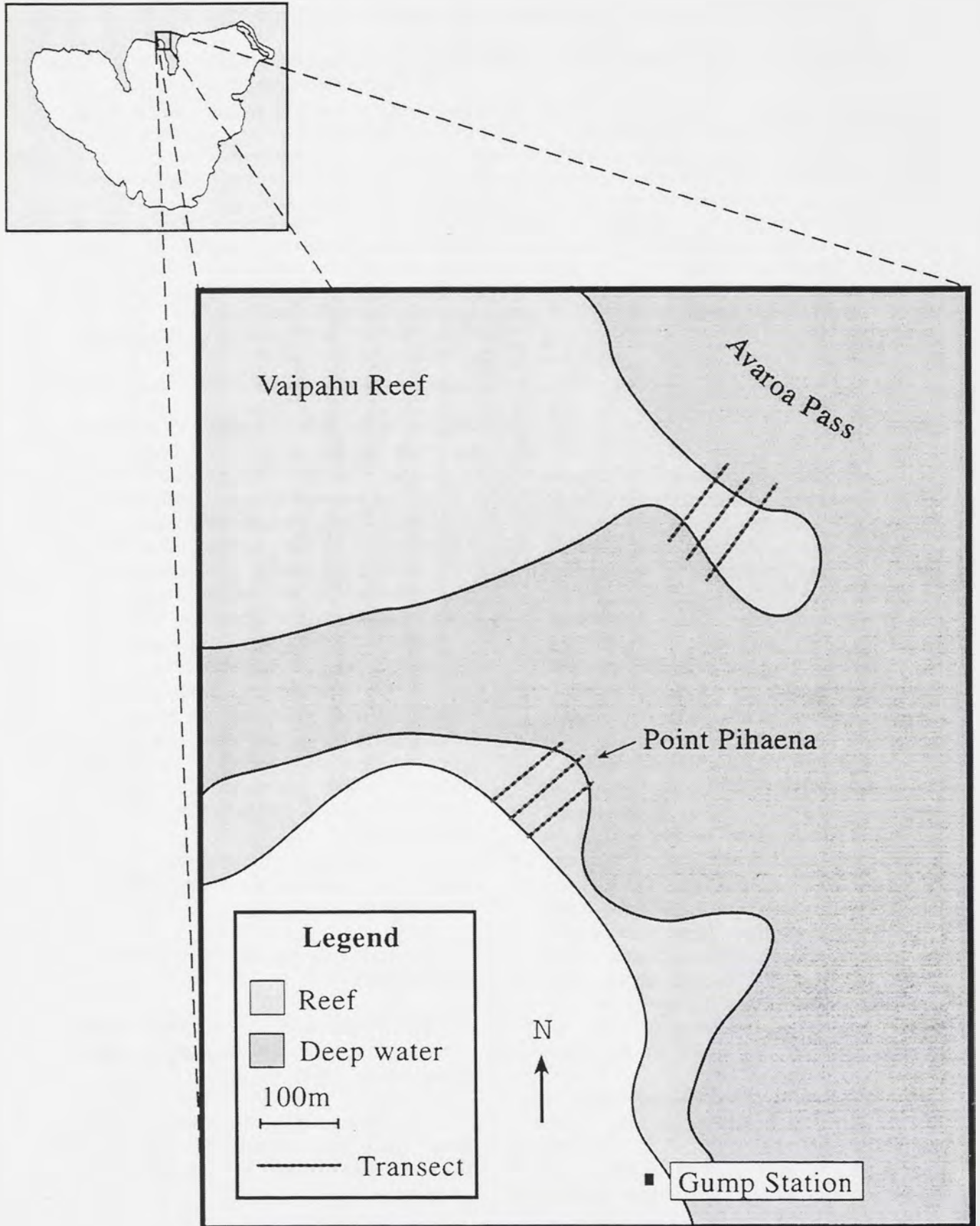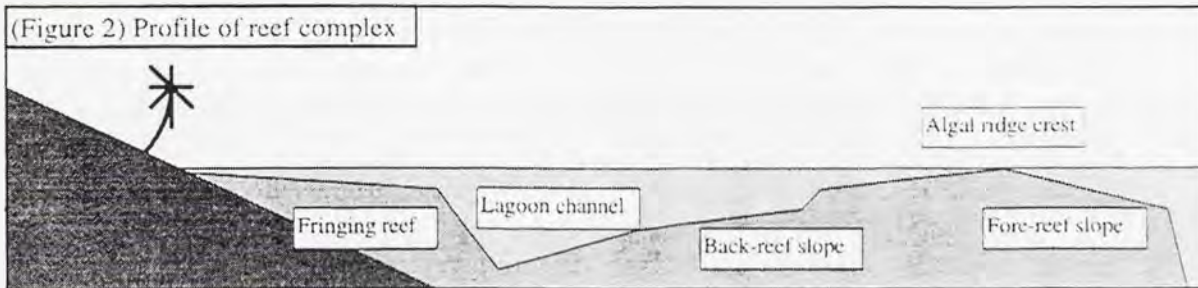
4) Holothuroids are more active at night

5) Species that occur under coral rubble prefer dark to light habitats.

Study site

Research was conducted on the island of Moorea French Polynesia (149°50'W, 17°32'S). Three transects were run from the shore at Point Pihaena to Vaipahu reef (figure 1).

The fringing reef at Point Pihaena consists of a shelf averaging about 80cm in depth that extends approximately 120m toward the lagoon and then drops off steeply into the channel. This shelf is mainly covered in sand, and coral heads become more and more frequent as one approaches the channel. At the reef crest, where the slope begins to descend into the channel, the coral heads become less and less frequent, and the substrate is mainly rock (see figure 2).

As one moves to the back-reef slope, a sandy shelf covered in sea grass is encountered. This shelf rises gently as one approaches the algal ridge until a depth of about 8m where the slope increases sharply and then levels off again at about 80cm. Here on this second shelf, like on the fringing reef, the substrate is sand, but as one approaches the algal ridge, coral heads become more and more frequent. These coral heads grow from the sandy bottom to approximately 40cm below the water surface, and eventually, they become so dense that the tops of the coral heads form the floor of yet another shelf which we call the algal ridge.

On the fore-reef slope, the substrate is mostly rock. The slope descends at about 8° until approximately fifty meters from the

algal ridge crest and then drops steeply into the open ocean.

The eastern end of Vaipahu reef forms the west side of Avaroa Pass and is protected from wave action by the barrier reef on the other side of the pass. This reduced wave action makes it possible to safely sample the algal ridge and fore-reef slope without risking injury from large surges. The fact that the wave action is reduced on this part of the reef has also led to the accumulation of a significant amount of large coral rubble. We find this is true of the pass at Opunahu bay as well, where the algal ridge on the west side of the pass is covered by many more large coral blocks than the rest of the reef. These large coral blocks were most likely deposited by waves during large storm events (Stoddart, 1978).

Materials and Methods

All research was conducted during the months of October and November, 1996. The Gump Biological Research Station was used as a base of operations and for laboratory experiments.

Transect survey

Data was collected from three transect bands. Each band was divided into two parts, fringing reef and barrier reef, separated by a deep lagoon. Sampling was conducted down to a depth of 10m. Scuba divers made superficial observations at lower depths.

The transects were broken into 5m x 5m quadrats. At the corner of each quadrat, a depth measurement was taken to create a topographic profile of the transect. Every species of holothuroid encountered was recorded along with its depth, distance from shore, substrate, and cover. The percent

cover of sand, rock, coral, algae, and large coral rubble was estimated in each quadrat.

On the fringing reef, distance along the transects was measured from the shore. On the barrier reef, distance was measured from the point where waves break on the algal ridge crest (distance toward the back-reef was measured in negative values and distance on the fore-reef was in positive values).

Water flow tests

A 10cm x 10cm square of 1 inch plywood was used to measure the surface velocity at three sites: the algal ridge crest, the back-reef slope, and on the fringing reef. The square of wood was placed in the water and timed as it floated a distance of 2m. This test was replicated five times between 3-5pm on five separate days.

Water velocity was also tested with fluorescent dye on November 18 to compare with the results of the first test. The powder dye was mixed with alcohol and sea water to make a bright orange solution. The dye was released from an eye-dropper in the water column and timed until the center of the resulting cloud had traveled 1m. This test was replicated ten times at each of the three sites.

Wave action

Wave action on the fore-reef slope was measured simply by measuring the height of the waves with a 2m long measuring stick. The greatest trough/crest difference that occurred in a ten minute period was recorded. Measurements were taken on five separate days from 3-5 p.m.

Night observations

On October 5 and November 17, my colleague Larry Rabin and I snorkeled at the fringing reef adjacent to the Gump Station at 11 p.m. Species encountered, along with their location and activity, were recorded.

Shannon/Weaver diversity index

A Shannon/Weaver diversity index was used to compare the fringing reef and the barrier reef (Begon, Harper &

Townsend, 1986). This index, which accounts for inequities in the populations of the different species, is calculated with the following formula:

$$P_i = \frac{\text{number of individuals of species}_i}{\text{total number of individuals of all species}}$$

Diversity, $H = -\text{sum}(P_1 \ln P_1, P_2 \ln P_2,...)$

Light/Dark preference experiment

The species of *Holothuria atra*, *Stichopus horrens*, *Holothuria leucospilota?*), "filter", and "tiger" were tested to determine if they had a preference for a light or dark environment. *H. atra* is a species that is almost never found under rubble in the field, whereas the other four that were tested where found almost exclusively under coral blocks. A 120cm x 50cm aquarium was covered with 1cm wire mesh to prevent the sea cucumbers from escaping and to create a uniform ceiling on both sides. The bottom of the aquarium was covered with layer of sand 3cm deep for the sea cucumbers to feed on. Half of the aquarium was covered with a dark blanket while the other half was illuminated with a common 60 watt light-bulb. Both sides of the aquarium were made identical except for the difference in light received.

Individuals of these five species were placed in the aquarium at 6am and their position was observed for 24 hours at 6 hour intervals. The test was performed 12 times with different individuals each time. For 6 of the trials, the sea cucumbers were originally placed on the dark side, and for the other six they were placed on the light side of the aquarium. The side of the aquarium that was covered was also switched for half of the trials.

Sediment analysis

The sediment along the transects was analyzed with respect to grain size and composition. Mineral composition ($CaCO3$ or basalt) was determined by color and by examination under a microscope at 20x. To

(figure 3) Profile of transect #2 on fringing reef
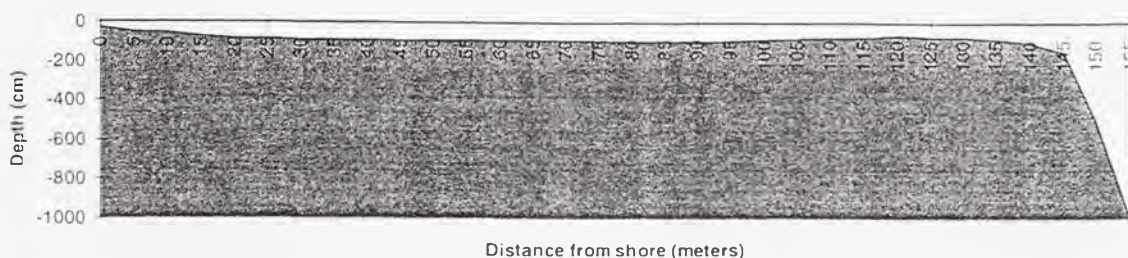
(figure 4) Profile of transect #3 on barrier reef
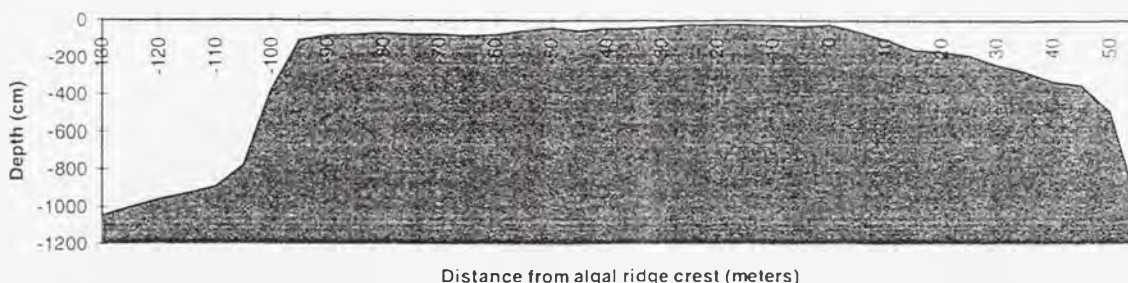
determine classes of grain sizes, the sediment was passed through soil sieves of 2mm, 1mm, and 0.77mm.

Samples were collected at eight locations, four on the fringing reef and four on the barrier reef. On the fringing reef, samples were collected at 15m, 40m, and 80m from shore and at 10m from the reef crest. On the algal ridge, samples were taken on the sea grass shelf, the back-reef slope, the algal ridge crest, and the fore-reef slope.

Results

Transect survey

Figures 3 and 4 show the profiles from both the fringing and barrier reefs. Transect #2 is the longest of the three fringing reef transects, and transect #3 is the longest of those on the barrier reef.

Table 1 lists the species that were found in all of the transects combined. (Voucher photographs are available at the Museum of Paleontology at the University of California at Berkeley.)

Table 1: Holothuroids found in transects

Species	# of individuals
H. atra	255
B. argus	65
H. leucospilota	64
"tiger"*	51
B. marmorata	11
S. horrens	10
"filter"*	7
T. ananas	6
A. mauritiana	2
H. pervicax	2
S. maculata	2
"synaptid A"*	1
"synaptid B"*	1
L. semperlanum	1
H. nobilis	1

* unidentified

The most commonly found holothuroid, *Holothuria atra*, was found both on the fringing and barrier reef. On the fringing reef, this species is found between 0m-100m from shore. On the barrier reef, *H. atra* was found only on the back-reef slope between 5m-80m from the algal ridge crest. In the shallow water on the algal ridge, *H.*

64

atra is found in densities up to 16 per 5m^2. On the fringing reef, the highest density found was 3 individuals per 5m^2. Figures 5 and 6 show the distribution of *H. atra* on the fringing reef and the barrier reef.

      Bohadschia argus, the species found in the second highest abundance was found both on the fringing and barrier reefs as well, but in different zones. On the fringing reef, this species was never found between 0m-40m from shore. It is found starting at 40m from shore all the way into the channel.

It was found in the highest numbers around 75m meters from shore. On the barrier reef, *B. argus* is found on both the fore-reef slope and the back-reef slope, but is absent in a zone extending 30m in both directions from the ridge crest. On the back-reef slope it is found in the greatest numbers between 50m-100m from the ridge crest. Scuba divers encountered *B. argus* individuals as deep as 65m in the lagoon channel. Figures 7 and 8 show the distribution of *B. argus* on the fringing reef and the barrier reef.

(figure 5) H. atra on fringing reef

# of individuals vs. Distance from shore (meters)

(figure 6) H. atra on barrier reef

# of individuals vs. Distance from algal ridge crest (meters)
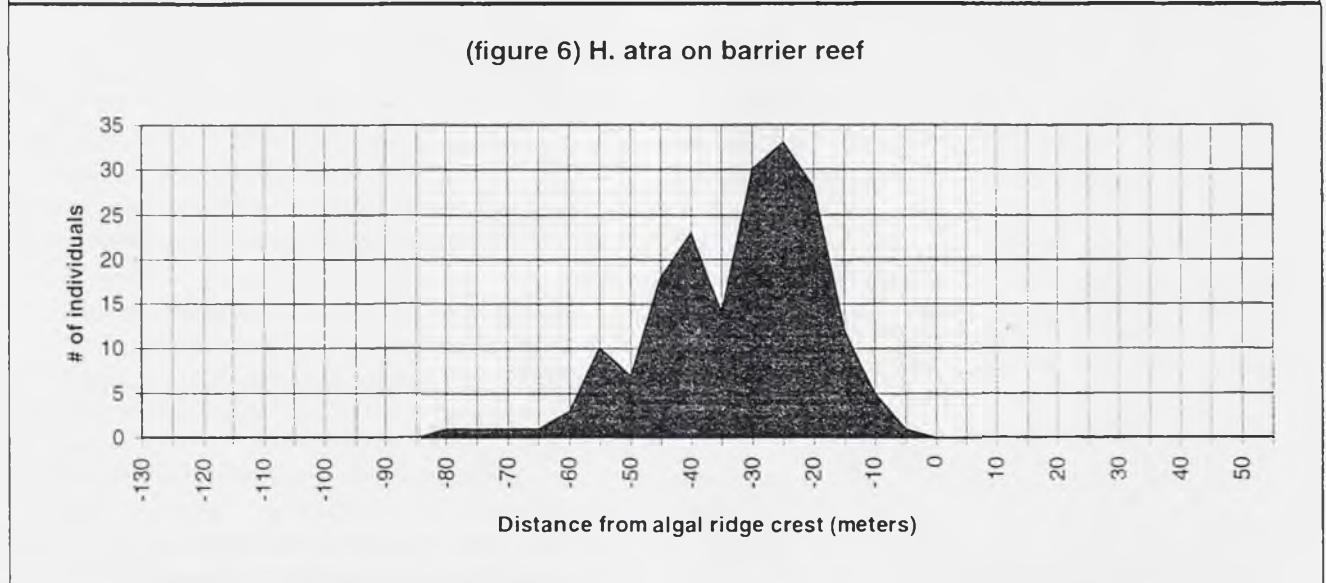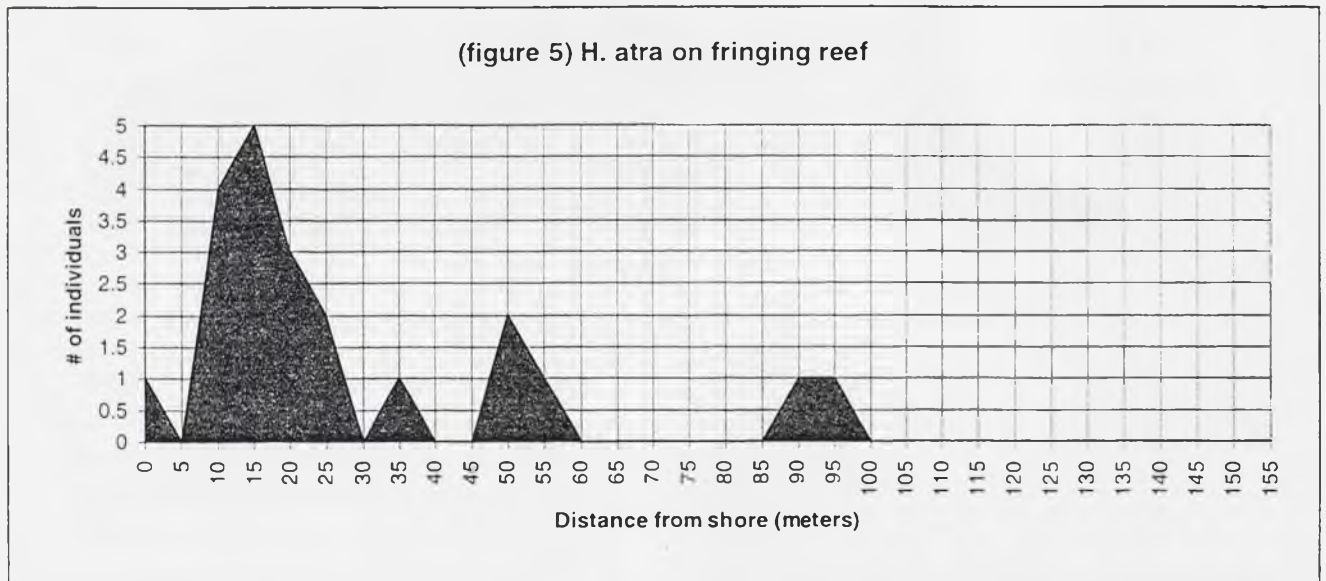
(figure 7) B. argus on fringing reef
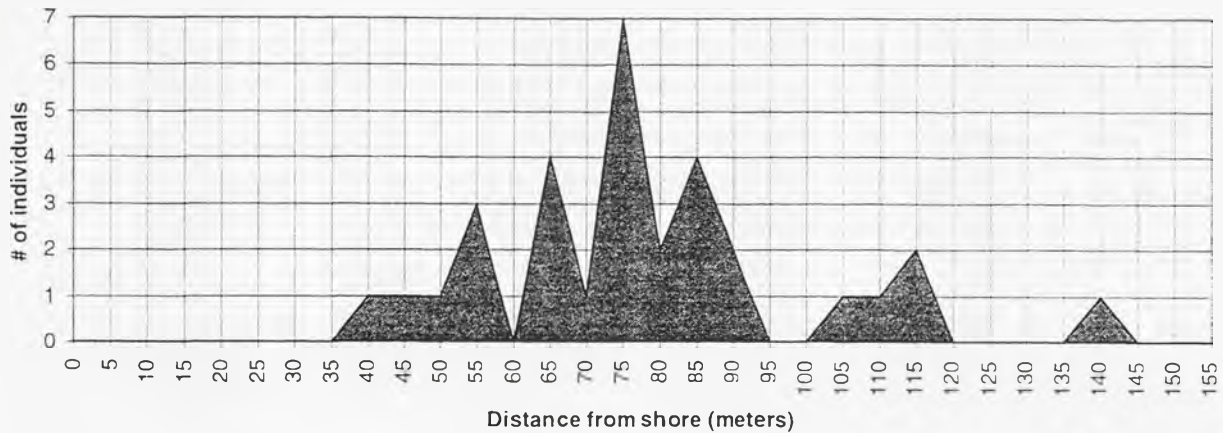
(figure 8) B. argus on barrier reef
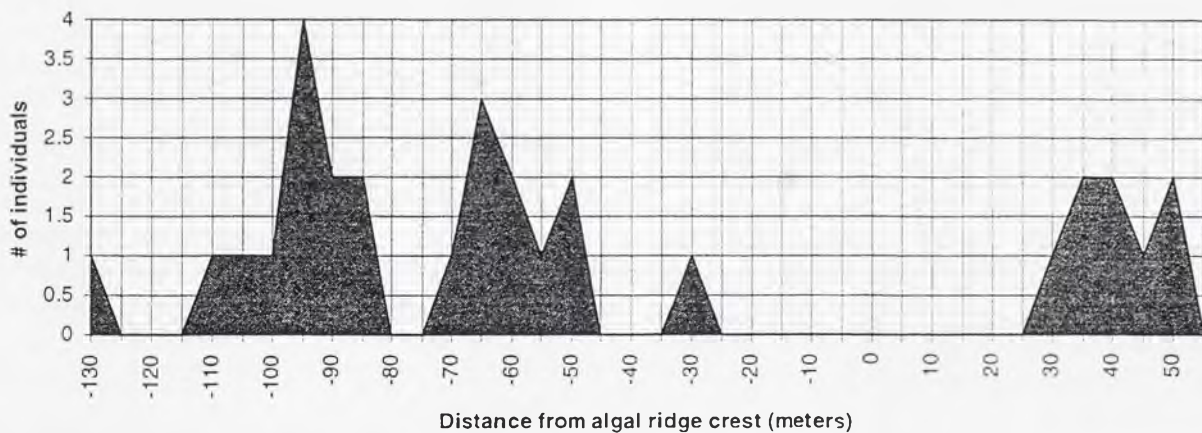
The species *Holothuria leucospilota,* *Stichopus horrens,* "tiger", "filter", "synaptid B" (*Euapta Godeffroyi?*), *Labidodemas semperlanum,* and *Holothuria pervicax* were all found exclusively (except for one individual *H. leucospilota*) under large coral rubble that is deposited by storm surges. This rubble was found in greatest abundance on the algal ridge crest and becomes less and less common until about 45m from the ridge crest on the back-reef slope where it was no longer found. "Filter" is found primarily under the rubble that is closer to the ridge crest. Those species that are found under rubble that were used in the light/dark preference experiment. Only the first four species listed were used because the others

are too rare and sufficient replicates could not be obtained.

Thelenota ananas was found on the back-reef and fore-reef slopes only at depths greater than 2.8m. The one *Holothuria nobilis* that was found was at a depth of 10m in the seagrass bed on the back-reef slope.

Bohadschia marmorata is always found burrowed under the sand during the day. It is found on the sandy shelves of the fringing reef and the back-reef slope, but not on the fore reef slope. There is particular confusion in the identification of this species. Not only do different guides refer to these spotted burrowers by many names, but they often divide individuals with different coloration patterns into different

species as well. In this paper, I refer to all burrowing holothuroids between 20cm-30cm in length as *B. marmorata*.

Actinopyga mauritiana is the only species that is found exposed in the high surf area of the algal ridge, and it is found nowhere else.

Synatpa maculata and "synaptid A" (*Synaptula media?*) were both found on the fringing reef. Both species were usually found hugging the base of a coral head.

Shannon-Weaver diversity index

The fringing reef diversity index was 0.997 while the algal ridge diversity index was 1.432. It must be noted that the area of barrier reef that was sampled was 16% larger than the fringing reef sample area. This increases the chances of finding rare species on the barrier reef, and thus may increase its diversity with respect to the fringing reef.

Water flow test

The first test of surface velocity showed that the algal ridge crest has the highest rate of water flow, followed by the back-reef slope and then the fringing reef. The fluorescent dye test, which measures flow in the middle of the water column rather than on the surface and is therefore not affected by wind, upheld the results of the first test.

Table 2: Water flow test results

Site	Surface velocity test	Fluorescent dye test
Fringing reef	0.055m/s	0.024m/s
Back-reef slope	0.083m/s	0.108m/s
Algal ridge crest	0.155m/s	0.210m/s

Wave Action

The average trough/crest difference of waves on the algal ridge was 53cm.

Night observations

Bohadschia argus was found to be more active at night than it is during the day. During the day their papillae are not protruding and they were never seen moving, while at night they were observed doing both of these things. Juveniles of this species were never observed during the day, but two were seen at night foraging. The night snorkels also revealed that *B. marmorata* comes out of the sand and forages on the surface at night.

S. maculata was found foraging in high densities, up to 5 per square meter in places. They were found in the highest densities around rubble and debris. During the day, they were rarely observed on this same section of reef adjacent to the Gump Station. *H. pervicax* was seen on the second night snorkel along with *H. leucospilota*.

Light/Dark Preference experiment

Figure 9 depicts the percentage of time spent in the light and the dark for all five species. Holothuria atra was found in the light slightly more often than the dark, while the other four species were found in the dark for a high percentage of the time. Figure 10 shows the percentage of time spent in the light by the four dark-preferring species at 4 different times during the day. A chi-square goodness of fit (Zar, 1984), was performed on this data. The null hypothesis that these five species have no preference for light or dark was rejected with a probability greater than 95%.

Sediment Analysis

On the fringing reef, the samples taken from 15m, 40m, and 80m from shore are similar in grain size. The sediment closer to shore was darker in color, suggesting that it contains more basalt particles. The fourth fringing reef sample has a larger percentage of large grains and has more halimeda flakes than the others.

On the barrier reef, the sample taken in the seagrass bed has a much higher percentage of fine particles and also darker in color (this darkness could be due to organic matter). Samples 6 (back-reef slope) and 7 (algal ridge) were similar in composition, while sample 8 on the fore-reef slope had a higher percentage of larger particles (see table 3).

(figure 9) Combined results of light/dark preference test
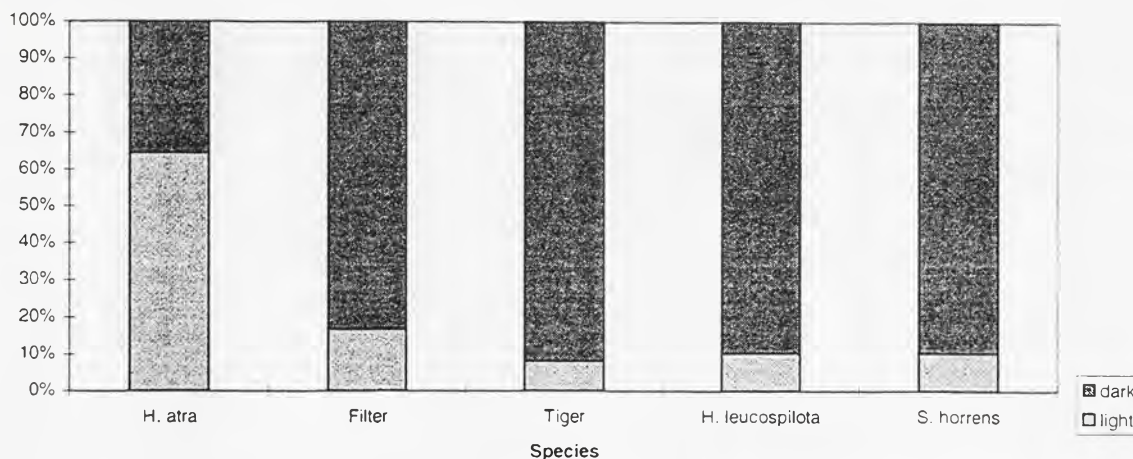
Table 3: Sediment particle size

Sample	>2mm	>1mm	>.77m	<.77mm
#1: 15m from shore	10%	15%	35%	40%
#2: 40m from shore	8%	12%	40%	40%
#3: 80m from shore	8%	12%	30%	50%
#4: 10m from reef crest	30%	20%	30%	20%
#5: sea grass bed	1%	4%	25%	70%
#6: back-reef slope	28%	29%	30%	13%
#7: algal ridge crest	10%	35%	40%	15%
#8: fore-reef slope	44%	44%	10%	2%

(figure 10) Percent of time spent in light by dark-preferring species

Discussion

Transect survey

The distributions found in the transect survey can be explained in a number of ways. Wave action can explain the absence of all species except *A. mauritiana* from the high-energy wave zone on the fore-reef slope. These results support hypothesis 1 with the exception of *A. mauritiana*. The morphology of this species may be a clue as to why it is the only species able to live here. The side body walls have buttress-like folds, creating a particularly wide ventral surface. This large ventral surface is helpful in gripping onto the rocky substrate where the waves break.

The distribution found for *H. atra* suggests that this species prefers shallower rather than deeper water. On the fringing reef they are found near shore, and on the barrier reef they are found near the ridge crest. These are the two shallowest areas occurring in the study site.

In contrast, *B. argus* seems to avoid the shallow waters where *H. atra* is found. It is never found within 40m of the shore on the fringing reef, and almost never in water less than 30cm deep where *H. atra* flourishes. It may be that in extremely shallow waters, *B. argus* would risk being exposed to the air during unusually low tides, seeing that this species is rather large and may reach 10cm in height.

B. marmorata is found only on the sandy barrier reef flat and on the sandy shelf of the back-reef slope. Rocky areas, such as the algal ridge and the fore-reef slope, are inhospitable for this species because there is rarely enough sand in these areas for *B. marmorata* to burrow into. The finer sand in the seagrass bed may be too dense for this species to burrow into.

T. ananas, being found only at depths greater than 2.8m, also seems to be avoiding shallow waters. This is the largest species that was encountered in the study, its length sometimes reaching 50cm. *H. nobilis*, which is also a massive species was only seen once, but at a depth of 10m. A pattern seems to emerge that the larger species on the reef are found at greater depths.

The distribution of the species *H. leucospilota*, *S. horrens*, "tiger" and "filter" is clearly correlated with the presence of objects to hide under (the other species found exclusively under coral rubble were found in such low numbers that it is difficult to make claims about their distribution). The only place they were found was on the algal ridge, and the algal ridge is the only area offering the microhabitat of dark, covered spaces. "filter" was always near where the waves break on the algal ridge crest. This is probably because it does not forage for food, but grabs food objects out of the water as they float by. The morphology of this species is a clue to its feeding strategy. It is the only species that was encountered that did not have its mouthparts oriented toward the ventral side for picking up food particles off of the bottom. Furthermore, "filter" was the slowest moving of the species tested in the light/dark experiment, supporting the idea that this species does not move around for its food, but suspension feeds instead.

Diversity and abundance

The barrier reef offers more microhabitats in general than the fringing reef. The fringing reef is basically a sandy plateau with scattered coral heads. It is a habitat that roughly corresponds with the back-reef slope. But the barrier reef has not only this habitat but a seagrass bed, the algal ridge and the fore-reef slope, all offering different niches to inhabit. This is one reason why the diversity of the barrier reef is higher than that of the fringing reef.

The fact that the water flow is generally higher on the barrier reef could also be a factor contributing to higher diversity and abundance on the barrier reef. Higher water velocity means more nutrient circulation in the area (Begon, Harper, & Townsend, 1986). On the fringing reef, where current speed was calculated to be between 0.024m/s-0.055m/s, *H. atra* is found in densities reaching only 3 individuals per 5m². On the algal ridge, where water flow was calculated to be between 0.155m/s-0.210m/s, *H. atra* is found in densities up to 16 per 5m². Furthermore, there were over six times as many holothuroids encountered on the barrier reef, in a sample area only 16% larger than the fringing reef.

Light/Dark preference

I found in the transect survey that *H. leucospilota*, *S. horrens*, "tiger" and "filter" are all found under rubble while *H. atra* is not. The question remained, "what effect does light have on this behavior?" The light/dark preference experiment showed that the species that are found under rubble use light to seek out this microhabitat while *H. atra* does not (figure 9). This suggests that they have some means of sensing visible light, although they have no eyes.

The experiment also showed that the dark-preferring species were found in the light most often at midnight (figure 10). This supports my fourth hypothesis that holothuroids are more active at night. In the wild, holothuroids come out of their hiding places to forage at night when it is dark, and potential predators cannot see them. In fact, this behavior was observed for many species during the night snorkels. It is possible that this behavior is engrained into the animals in the wild by the pattern of daylight and dark, as a result the animals continue to operate on this schedule although the light conditions in the aquarium are constant. Daily bio-rhythms such as these are called circadian rhythms (Drickamer, Vessey, &

Meikle, 1996) and would warrant further investigation in holothuroids.

Sediment analysis

In a similar transect study on the island of Raiatea, sediments from the lagoon were proclaimed "strikingly uniform in mineralogical and mechanical composition (Stark and Dapples, 1941). My results do not support this statement. It is true that the vast majority of the sediments are composed of calcium carbonate. The only exception is the sample nearest the shore, but this is most likely the result of the man-made retaining wall that has been built along the coast using blocks of basalt rock. Still, there were differences in the mechanical composition of the sediment in different places which can bring us to some interesting conclusions about certain holothuroids. For example, *B. argus* occurs in both the zone with the finest sediment, the seagrass bed, and the zone with the coarsest sediment, the fore-reef slope. Sediment particle size does not seem to be affecting its distribution. Another example is *H. atra* occurs on the relatively fine near-shore sediments as well as the coarser algal ridge sediments. Furthermore, if one looks at the fecal pellets of this species, there are particles of all size classes from silt, to stones up to 1cm in diameter. I personally observed a piece of rock approximately 3cm wide, leaving the anus of an *H. atra* individual! The conclusion is that both *B. argus* and *H. atra* are generalists as far as the mechanical composition of the sediment that they ingest.

Acknowledgments

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Comparative effects of the introduced mangrove, *Rhizophora stylosa* , and the native tree, *Hibiscus tiliaceus* , on the salt marsh grass, *Paspalum vaginatum*

Isa Woo
Integrative Biology
University of California, Berkeley, CA 94720

ABSTRACT. Studies were carried out to test the possible reasons for the exclusion of the salt marsh grass, *Paspalum vaginatum*, under mangrove aerial roots and *Hibiscus* canopies. Three hypotheses were made: (1) The exclusion of the grasses is due to soil chemistry inhibition; (2) The exclusion of the grasses is due to shading; (3) The exclusion of the grasses is due to root competition. To test the first hypothesis, a transplant study involved planting *Paspalum* into mangrove, *Hibiscus* and *Paspalum* soils (control). There were no noticeable differences between the growth of the plants in different soils at site 1. At site 2, plants grown in *Hibiscus* soils were shorter. To test the second hypothesis, a shading experiment was conducted. The experiment showed that *Paspalum* had a positive growth response towards shade. Shaded plants were taller and had longer internode lengths. In the field, plants adjacent to mangrove and *Hibiscus* areas are shorter than average. This suggests that shading may not be the sole factor in excluding grasses from mangrove or *Hibiscus* areas. To test the third hypothesis, soil root cores were taken to measure the dry root biomass of different vegetation types. Mangrove soils had the highest amount of dry root biomass while *Hibiscus* soils had the least. Root crowding may explain the exclusion of grass under mangrove soils. However, this hypothesis is not sufficient to explain the exclusion of grass under *Hibiscus* canopy. Although mangrove and *Hibiscus* areas both exhibit grass exclusion, the mechanism of this exclusion differs. Most likely, grasses near mangrove areas are limited by root competition, while plants near *Hibiscus* are limited by soil nutrients and shade.

Introduction

Salt marsh and mangrove ecosystems are intertidal plant communities which grow along low energy coastlines and are subject to periodic flooding (Kangas and Lugo 1990). Both communities play an important role in ecosystem processes by trapping sediments and stabilizing substrates (Chapman 1976).

More specifically, salt marsh grasses are useful in a variety of areas: they play an essential role in erosion control; they are nesting grounds for waterfowl and other birds; and they are used for stock feed, marsh pastures and green manure for rice and sugarcane (Chung 1992).

Mangrove plants are tropical intertidal forest communities found at the interface between terrestrial and marine ecosystems (Thomlinson 1986). Mangrove ecosystems play crucial roles in sediment trapping, and in sources of timber; and they are also nurseries for young marine animals.

Salt marsh and mangrove communities share similar habitat requirements but occupy different areas of the globe. Salt marshes have a wide distribution that extends from the Arctic to the subtropics (Kangas and Lugo 1990). Mangroves have a circumtropical distribution (Kangas and Lugo 1990, Thomlinson 1986). It is hypothesized that the southern extent of salt marsh distribution is limited by competition with mangrove communities (Kangas and Lugo 1990). Where these two communities occur together, mangal forests replace salt marsh grasses (Kangas and Lugo 1990; Lewis 1982; and Lopez 1989).

The island of Moorea, French Polynesia, offers a unique opportunity to study the competition between mangrove and grass species. The mangrove species, *Rhizophora stylosa*, was introduced to Moorea for oyster cultivation in the 1930s. Since then, mangrove populations have established and spread into areas of salt marsh habitat, displacing the grass, *Paspalum vaginatum*.

P. vaginatum Swartz was collected in the Society Islands in French Polynesia as

early as 1922 (Jepson Herbarium Museum specimen). It has been disputed that *P. vaginatum* is the same species as *P. distichum*; however, recent publications recognize both *P. vaginatum* and *P. distichum* as separate species (Kartesz 1994 and Harden 1993).

P. vaginatum is a perennial C4 salt marsh grass that has a high tolerance to salinity (Marcum and Murdoch 1990 and 1994). Salinity tolerance is not a limiting factor to *Paspalum* distribution on Moorea because it can be seen growing on the edge of the shore (Harden 1993, personal observation). Large populations of *P. vaginatum* are frequently found along the perimeter of Moorea where the shore is protected from wave action, such as: coastal coves, protected mud flats and estuaries. These same habitats have been colonized by *R. stylosa*.

Where both *Paspalum* and *Rhizophora* occur, the transition between grass and mangrove is sharp and distinct. *Paspalum* is excluded from directly beneath the mangrove's aerial roots. This observation is called the "halo effect" where a ring of bare soil forms a circle around the mangrove tree (Kramer 92, D'antonio pers. comm. 1996). The exclusion of *Paspalum* is also seen under the canopy of the native tree *Hibiscus tiliaces*, but the transition zone is not as abrupt.

On Moorea, *Hibiscus* trees form the inland barrier of *Paspalum* distribution, while the mangroves form the seaward boundary. In some cases, *Paspalum* is sandwiched between the introduced mangrove and the native *Hibiscus* trees (Appendix A).

The objective of this paper is to document and examine possible reasons why *Paspalum* is excluded from underneath the areas below the aerial roots of mangroves and to compare it to the absence of *Paspalum* under the *Hibiscus* canopy. Is the exclusion of *Paspalum* under mangrove roots and under *Hibiscus* canopies caused by the same factors? The factors that were chosen for study were: soil chemistry, shading and root density. Three alternate hypotheses are addressed: (1) *Paspalum* exclusion is due to soil chemistry where soil chemicals secreted from the vegetation hinders or prevents *Paspalum* growth; (2) The *Paspalum* exclusion zone is caused by shading from *R. stylosa* or *Hibiscus*; (3) *Paspalum* is excluded from underneath mangrove roots and *Hibiscus* canopy due to root competition.

Materials and Methods

Site description

Three sites were chosen based on the following two criteria: (1) All three species of *R. stylosa*, *P. vaginatum*, and *Hibiscus tiliaceus* occurred together; (2) Each site has pure stands of the three vegetation types and transitional ecotones from one vegetation type to another. Site 1 is a protected mud flat on the north side of the island near PK 24. The soils are relatively high in organic matter content and is predominately composed of mud. Site 2 is a sandy cove found on the west side of Moorea near PK 35. The soils are grainy, coarse, and sandy. Site 3 is located roughly 100 meters south of site 2 (Appendix B). The site contains a large undisturbed area of *Paspalum* and a pure and dense track of *R. stylosa*. At this site soils contained some sandy particles but had a higher proportion of organic matter than site 2. Unique to site 2 and 3 is the occurrence of a zone of short *Paspalum* adjacent to the *Hibiscus* zone

Coastal Paspalum distribution

The distribution of *Paspalum* was mapped on the west side of Moorea by personal observation. Four representative categories for the vegetation types were used : pure *Paspalum*, *Paspalum* dominated with some mangroves, mangroves dominated with some *Paspalum* and *Hibiscus* dominated with some *Paspalum*. (Appendix B)

Transplant experiment

Soils were collected from sites 1 and 2. At each site, soil was gathered from three areas: pure *Paspalum*, pure mangrove and under the canopy of *Hibiscus*. Enough soil was collected to fill ten gardening pots per soil category for a total of sixty pots. To minimize the effects of the soils' physical attributes (i.e. density and compaction), all

soils were sifted through a soil sieved with a quarter inch mesh. This produced a uniform soil clump size which would give plant roots equal probability of establishment in the different soils. The pots were labeled by site number and soil category. Plants were then collected after all the soils had been prepared. The roots were washed to remove as much soil from the roots as possible. *Paspalum* plants were transplanted into the three different soil types. The plants were set outside and watered every two days; however, they were not watered during rain showers. To stimulate shoot over root production, grasses were cut to uniform heights and recorded. As a measurement of plant health, percent yellow and percent green of the grass blades were recorded. The same procedure was followed for site 2. The potted plants were set outside in full sunlight. Plants from sites 1 and 2 were re-measured after thirty-one and twenty-five days, respectively. The tallest five blades were measured from each pot and the percent yellow and green of the blades were recorded again.

Shading experiment

Twenty quadrats of 0.5m x 0.5m were set out at site 1. Ten quadrats were shaded with a cloth and ten control quadrats were unshaded. A light meter from a camera measured a 75% reduction of light under the cloth. Grasses in all twenty quadrat areas were clipped to the ground to stimulate shoot production and to simplify growth measurements. After twenty five days, the five tallest blades from each plot were measured for height, diameter of stem and internode lengths.

Root biomass

Root biomass samples were taken at site 3. A cylindrical PVC pipe with a diameter of 7.3 cm was used as a soil core. Sample depth was 10 cm because most *Paspalum* root are found within this layer. The pipe was sharpened at one end to help cut through root mats. Four different areas were sampled: pure *Paspalum*, the transition between *Paspalum* and R *stylosa*, pure R. *stylosa* and under *Hibiscus* canopy. Five sample cores were taken randomly from the four habitats. The core was placed on a fine mesh screen and sprayed with pressurized water to separate soils from the roots. The roots were then dried and weighed.

Internode length measurements

At site 3, internode lengths were measured for four different *Paspalum* areas: pure *Paspalum*, the transition from *Paspalum* to mangrove, *Paspalum* in-between mangroves (but outside the 'halo zone') and *Paspalum* adjacent to *Hibiscus*. Thirty plants from each micro site were collected. Plant height, the number of branches and internode lengths from the root to the tip of the stem were recorded.

Voucher specimen of *Paspalum vaginatum* are located at the Jepson Herbarium, University of California, Berkeley.

Results

Transplant

All transplanted grasses were found to be healthy (i.e. green with little or no signs of yellow tipped leaves and no signs of wilting). Transplants from site 1 show no appreciable difference in plant growth between soil types. However, *Hibiscus* soils from site 2 did have significantly shorter grass blades (Table 1 and Figure 1).

Table 1.
Average Blade Height (mm) n=50

	Site 1 (mm)	Site 2 (mm)
Paspalum	160.68	116.26
R. stylosa	139.72	119.28
Hibiscus	121.96	95.22
ANOVA	P< 0.04	P<0.007

Figure 1.

Comparison of Average Blade Growths

Site 1 | **Site 2**
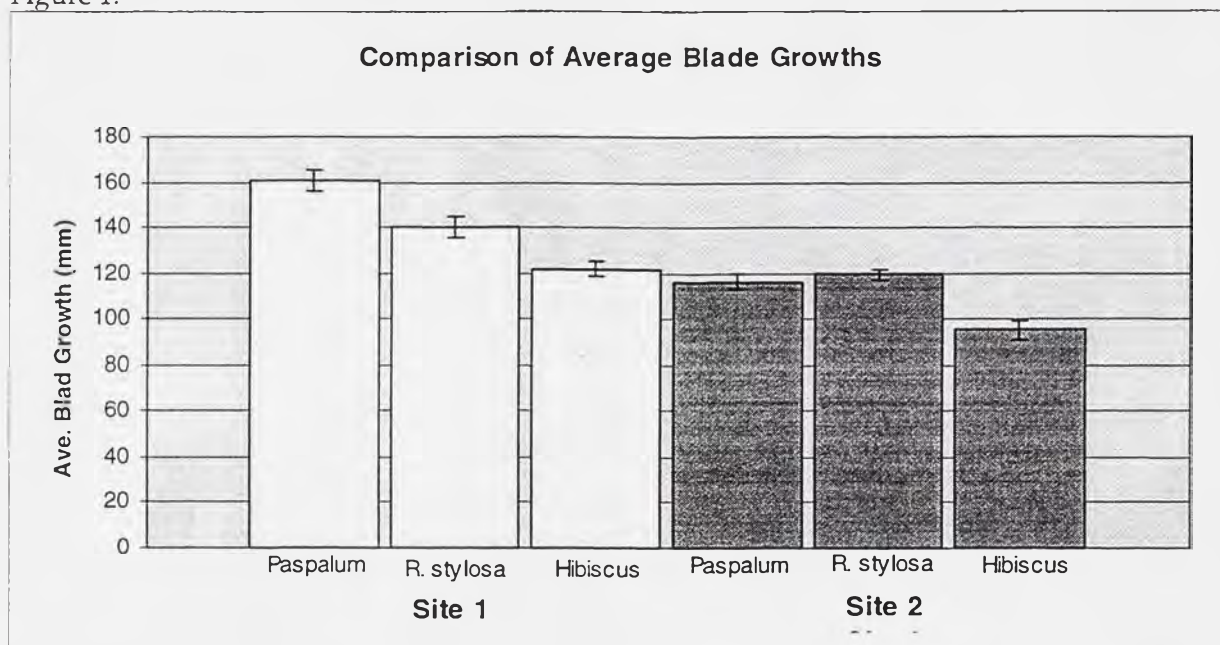
Shading

All plants survived the treatment of being clipped to the ground. Shaded plants had longer internodes, smaller diameter and were taller than the unshaded plots. (Table 2 Fig. 2 and Fig. 3).

Table 2.
Avg. diameter, internode-length and height (mm) n=50

	Shaded	Unshaded
Average diameter	2.5	3.91
Average internode	27.9	17.49
Average height	234.38	201.43
t-test	P<0.0001 for all three characteristics	

Figure 2.

Internode Length Comparison Between Shaded and Non-Shaded Conditions

Figure 3.

Height Comparison Between Shaded and Non-Shaded Conditions
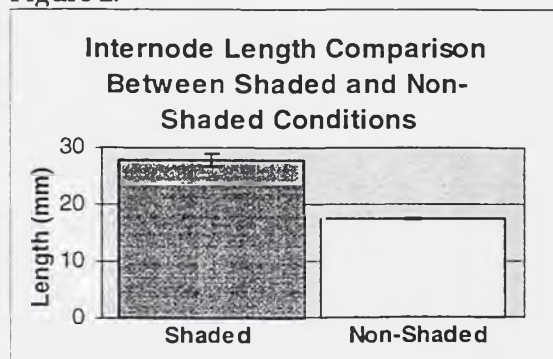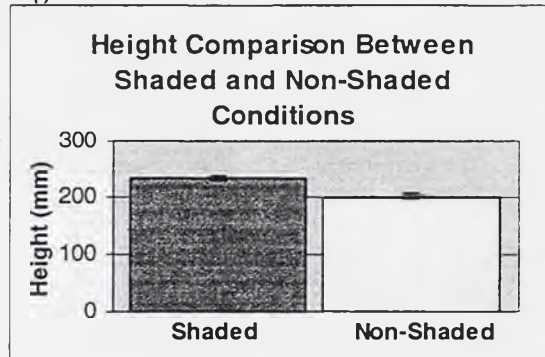
Root biomass

The dry weight of the mangrove roots were significantly higher than pure *Paspalum* or *Hibiscus* areas, but in *Paspalum* bordering the 'halo effect' there is no appreciable difference (Table 3, Fig. 4). *Paspalum* habitats showed no differences in the dry root weight in *Hibiscus* soils. And *Paspalum* bordering the 'halo effect' had significantly higher weights than *Paspalum* and *Hibiscus*. (Table 3).

Table 3.
Root Biomass Experiment n=5

Core diameter = 7.3 cm

Type	Avg. depth	Avg. dry root wt
M	9.6 mm	28.9 g
P-M	11.0 mm	23.2 g
P	10.4 mm	9.4 g
H	9.8 mm	0.75 g
ANOVA	P<0.0001	

M= mangrove   P-M= *Paspalum* adjacent to mangrove
P= *Paspalum*   H= *Hibiscus*

Table 4.
Internode Lengths. n=30

	Avg. internode	Avg. height
M	6.45	124.37
P	14.71	338.4
M-P-M	9.44	167.4
P-H	3.77	142.9
ANOVA	P<0.0001	P<0.0001

M=mangrove   P=pure *Paspalum*
P-H=*Paspalum* adjacent to *Hibiscus*
M-P-M= *Paspalum* sandwiched between
    mangroves

Figure 4.
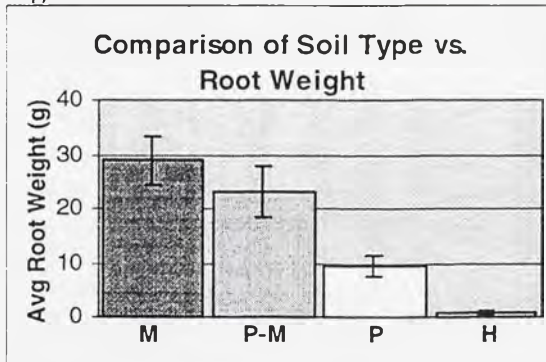
M= mangrove   P-M= *Paspalum* adjacent to mangrove
P= *Paspalum*   H= *Hibiscus*

Internode length measurements

Average internode lengths and average heights for shaded and unshaded plots are summarized on Table 4. *Paspalum* areas had the greatest heights and the longest internode lengths. These values were significantly larger than the values in mangrove and *Hibiscus* areas (Fig. 2 and Fig 3).

Figure 5.

Figure 6.

The first four internodes from the roots were averaged and   used as a character. *Paspalum* has greater average internode lengths than all other vegetation areas (Fig. 5).   *Paspalum* adjacent to mangroves has significantly shorter internodes than pure *Paspalum* and *Paspalum* sandwiched between mangroves, and has longer lengths than the grasses near *Hibiscus* stands. *Hibiscus* has the shortest average

internode growth measured. As for the height category: *Paspalum* ranks as the tallest vegetation habitat (Fig. 6). *Paspalum* near mangroves are shorter than *Paspalum* sandwiched between mangroves but no difference is indicated with *Paspalum* adjacent to *Hibiscus*. *Paspalum* near *Hibiscus*- and *Paspalum* in mangrove boundaries rank the shortest.

Discussion

Transplant experiment

Paspalum plants were transplanted into different soil types to test whether soil chemistry under certain vegetation types hindered plant growth. Transplants from site 1 indicated that there were no significant negative effects from the soils under mangrove or *Hibiscus* areas (Table 1 and Fig 1). At site 2, *Hibiscus* grasses grew significantly shorter than the control (Fig 1). This can be explained by the differences in soils at site 2. Soils under the *Hibiscus* canopy contained noticeably more sand. The *Hibiscus* trees were located along the edge of the road. The construction and maintenance of the road may act as a disturbance which can affect soil composition and particle size. This is a plausible reason for shorter grasses found near *Hibiscus* areas.

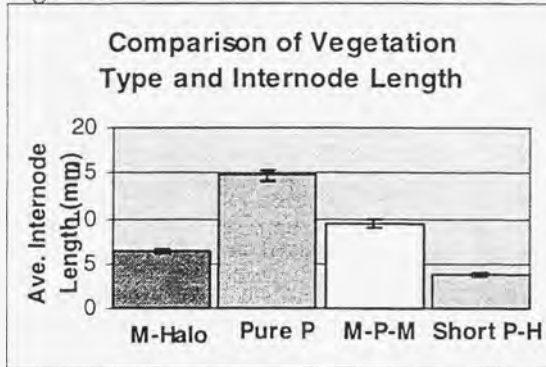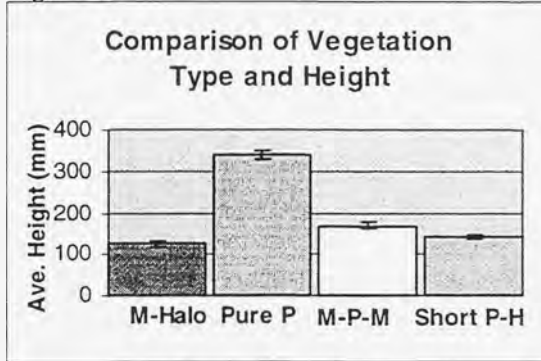Two concerns that may affect the experiment are: (1). The plants were watered with fresh water and not plant leachates, water containing plant extracts. However,, experiments by Clarke and Hannon show no evidence of inhibition by *Avicenna* mangrove extracts on other plants found in mangrove habitats. (2). The pots were set outside and during rain showers, some chemicals may have leached out of the soils. These concerns are possible problems that may skew the results. Some leaching may have occurred, but all pots were subject to the same environmental conditions and are comparable.

The results do not support the theory that chemicals in the soil play an important role in grass exclusion under mangrove aerial roots. However, further studies are recommended for *Hibiscus* soils. For both transplant experiments, *Hibiscus*

soils had the lowest measured growth which warrants further study.

Shading

Perhaps one of the most surprising results was that *Paspalum* grasses responded to shade by elongation. A preliminary concern was that the elongation was a temporary compensation effect, where the plant has high growth rates to reach sunlight. This may have some validity. However, a three year shading experiment by Wilson (Wilson 1996) confirm a positive response of shoot elongation to shade in tropical C4 grasses. Wilson reports that shade enhances organic matter breakdown and nitrogen cycling by reducing evaporation rates due to sunlight and a decrease in temperature (Wilson 1996). These results are supported by other findings that the shading of tropical grasses or other C4 grasses result in an increased allocation of dry matter to the shoots and stem elongation (Pierson 1990, Wong and Wilson 1980, Thompson 1993, Evans 1993). Yet, some sources attribute shading as the one of the most important factors that limit the growth of salt marsh grass under mangroves (Lewis 1982 and Lopez 1989).

Field observations show that grasses adjacent to mangroves and *Hibiscus* are shorter than in *Paspalum* habitats. This does not support the shading hypothesis because one would expect to see taller grasses in shaded environments. Rather, the opposite is seen: grasses were shorter in areas near mangroves and *Hibiscus*. A more believable theory is put forth by Kangas and Lugo (1990) : a combined effect of root competition along with shading may give mangroves a competitive advantage over grasses.

Field observations do not support the shading hypothesis in the case of mangroves. The boundary of the bare patches are directly below the mangrove aerial roots and do not necessarily follow the pattern of the mangrove's shadow throughout the day. It is more likely that the shading factor is more important under *Hibiscus* canopy than mangrove trees. *Hibiscus* trees have broad heart-shaped leaves. *R. stylosa* has small leaves that point

upwards towards the sun, minimizing the amount of sun intercepted by vegetation. Long term studies are necessary to clarify the affects of shade on *Paspalum* growth and establishment.

Root biomass

The dry root mass of mangroves were significantly higher than the grass (Table 3 and Fig.4). The data collected supports the hypothesis that root density may inhibit grass growth in tree inhabited soils (Belsky 1994). On the other hand, this is contrary to *Hibiscus* soils. There is no significant difference in the dry root weights of *Hibiscus* and *Paspalum* soils. This suggests that there is some other sort of process at work that inhibits *Paspalum* growth under *Hibiscus* trees: such as shading or inhibitory soil chemicals.

Internode length measurements

Internode measurements were used to compare the shading effect. If shading were the acting upon the grasses to exclude them from mangrove and *Hibiscus* areas, then a measurable increase in internode lengths would be expected (Wilson 1996). The internode measurements do not support the shading hypothesis.

Conclusion

The mangrove, *R. stylosa*, has successfully established itself in *Paspalum* habitats. In the presence of other mangrove trees, *R. stylosa* is often limited to the areas along the water's edge. In the absence of other mangrove competitors, such as the case of Moorea, *R. stylosa* spreads inland, displacing *Paspalum* habitat. In comparison, the native *Hibiscus* trees are found on the higher reaches of the salt marsh where inundation is less frequent. *Hibiscus* usually form the inland border of marsh habitat; rarely found within the marshland itself. This study analyzes possible reasons of *Paspalum* exclusion. This information would be useful in restoration of the salt marshes. Previous attempts to eradicate and control

R. stylosa's distribution involved cutting the mangrove trees down, but the root system remained intact. This may be effective in killing the individual tree, however; if the high density of *R. stylosa* roots can prevent the establishment and growth of *Paspalum*, the remaining root system may still prevent the reclamation of salt marsh grasses.

It is important to understand the factors limiting grass establishment and growth so that the remaining marshes can be protected. It would be too costly, time consuming and impractical to uproot mangroves where they currently exist. Once the ecological relationships of *Paspalum* and mangroves are better understood, perhaps some effort can be put into preserving what is left of salt marsh habitat.

Further studies

Further studies of the long term effect of shade on *Paspalum* plants are needed to distinguish between a light compensation effect or a long term shading response. The transplant of *Paspalum* plants, in its native soil, under *R. stylosa* canopy in the field would expose the grasses to natural light conditions and possible herbivory by *Tupa* crabs. More studies are needed to lucidate the morphological responses of *Paspalum* to herbivory and nutrient, light and water competiton.

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Vegetation profile of a typical coastal strand on Moorea, French Polynesia

Legend

Paspalum		Short *Paspalum*	
Hibiscus		Ocean	
Coconut		Road	
Verbenae		*Rhizophora stylosa*	

Paspalum Distribution on SW Moorea

PK 33

PK 34

N

PK 35

Site 2 →
Site 3 →

PK 24

Ha'apiti

PK 23

PK 22

PK 21

PK 20

Primary road
Stream
PK 19   Kilometer Post
●   Town
⚓   Church
━━━   *Paspalum*
⦙⦙ ⦙⦙ ⦙⦙   *Hibiscus/Paspalum*
▒▒▒▒   *Paspalum/Mangrove*
▪▪▪▪▪   Mangrove/*Paspalum*

1 mile

1 kilometer

0   500   1000 meters

Site 1

Area
of detail
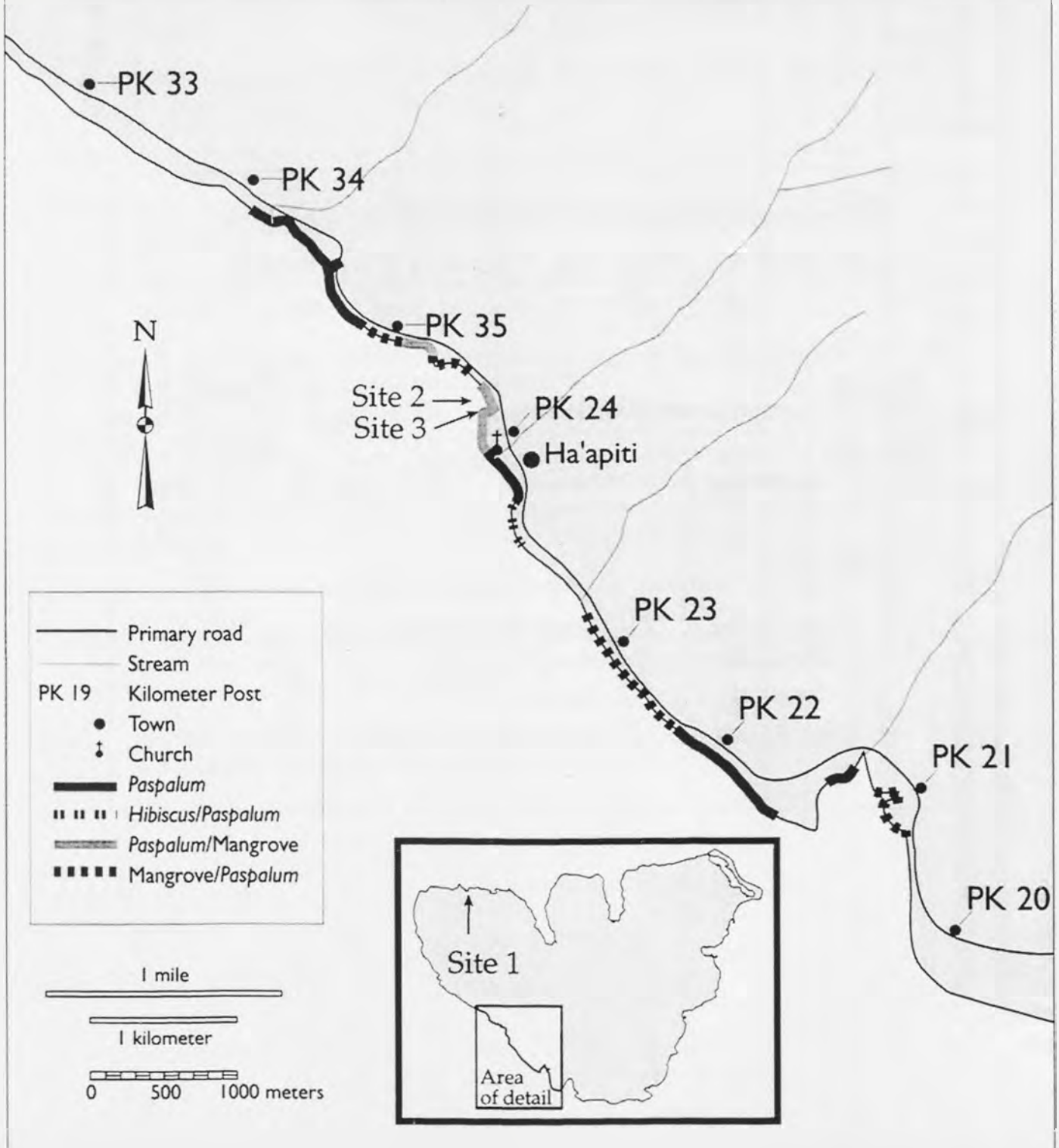
Establishment and Development of the mangrove fern *Acrostichum aureum* on Moorea, French Polynesia.

Ylva Carosone
Department of Integrative Biology
University of California at Berkeley, 94720.

ABSTRACT. The establishment and development of the mangrove fern *Acrostichum aureum* was investigated at five sites on Moorea, French Polynesia. Growth conditions of both the sporophyte and gametophyte generations were assessed. Sites ranged from moderately saline to extremely saline, and from well-shaded to very exposed to sunlight. From measuring fertile fronds at each site, mature sporophytes were observed to demonstrate reduced growth under saline, exposed conditions. Gametophytes were found to be growing on elevated microtopographical features such as fern stumps and mud clumps. Quantification of this phenomenon by measuring the elevation above maximum water level of gametophytes and young sporophytes growing along a river inlet showed that juveniles rarely grow in the zone frequently inundated by water. A salinity tolerance experiment investigated the tolerances of gametophytes and young sporophytes to saline solutions and found the latter to be more tolerant. A water inundation experiment subjected gametophytes and germinating sporophytes to inundation with saline solutions and found both growth stages to be deleteriously effected, even in freshwater. *Acrostichum aureum* is thereby found to have growth stages with differing tolerance levels, with a more sensitive gametophyte generation which establishes itself opportunistically on zones of lower salinity and water logging.

Introduction

Few ferns are known to be tolerant of saline conditions. The rarity of success of ferns in such hostile environments makes the distribution of the mangrove fern *Acrostichum aureum* in salty and waterlogged habitats particularly interesting. Much is known about mangrove tree species, however little is known of the mechanisms of establishment and survival for the mangrove fern in these same habitats (Medina et al. 1990).

Acrostichum aureum is the most widely distributed species of its genus, currently thought to consist of three or more species (Tryon 1982). The three species are found in environments such as mangrove swamps, lakes or ditches, displaying a range of tolerance to salinity from freshwater to tidal saltwater inundation. *Acrostichum speciosum* is found in tropical Asia and Australia and is the most tolerant of the three species to sea water (Lloyd and Buckley 1986). *Acrostichum danaefolium* is found in tropical and subtropical regions in fresh or brackish environments (Lloyd and Buckley 1986). *Acrostichum aureum* is pantropical in distribution and inhabits both brackish and salty conditions (Lloyd and Buckley 1986).

In order for the fern to be successful in its environment, both the haploid gametophyte and diploid sporophyte generations must survive and reproduce. Different growth stages of plants commonly demonstrate varying tolerance to environmental stressors. Typically the juvenile stages are more sensitive than their mature counterpart to factors such as salt toxicity (NSW Agriculture and Fisheries 1989). Studies on *A. aureum* and *A. danaefolium* have found that significant protection from salt toxicity of the mature sporophyte occurs at the root level. Sanchez-Peña (1994) found that concentrations of Na and Cl were about two times higher in the roots than in the leaves of *A. danaefolium*. Petersen et al (1990) hypothesized that the basis for salt tolerance in *A. aureum* is a Na/K pump working in tandem with a countercurrent Ca channel. It has not been established as to how the more sensitive gametophyte and juvenile sporophyte growth stages manage to survive saline conditions.

Previous studies have investigated the reproductive biology and gametophyte morphology of *A.danaefolium* and *A. aureum* in the laboratory (Lloyd and Gregg 1975, Lloyd 1980, and Lloyd and Buckley 1986), however the need for an ecological study of the gametophyte generation in

nature has been noted (Lloyd and Gregg 1975). Gametophytes have been observed growing upon elevated microtopographical features of the forest floor, such as mud clumps, and it is thought that such positions are favorable for gametophyte germination and growth due to increased leaching of salts (Medina et al. 1990).

This paper investigates the range of environments in which *A. aureum* persists on the island of Moorea and, through both field and laboratory observations, tests the hypothesis that the survival and establishment of gametophytes and young sporophytes is differentially limited not only by salinity but also by water inundation and water-logging of the soil.

Materials and Methods

Sites

My study of *A. aureum* was conducted during the months of October and November on the island of Moorea, French Polynesia (17°31' S, 149°50'W). Using Litinsky's climate classification, French Polynesia has a humid to subhumid maritime tropical climate with a rainy season from December to March (Atlas of French Polynesia 1993).

Study Sites of *Acrostichum aureum*, Mo'orea.

Legend:
- Coastline
- Stream
- • Town
- ● Study Site
  1. Opunohu
  2. Shrimp Farm
  3. Temae
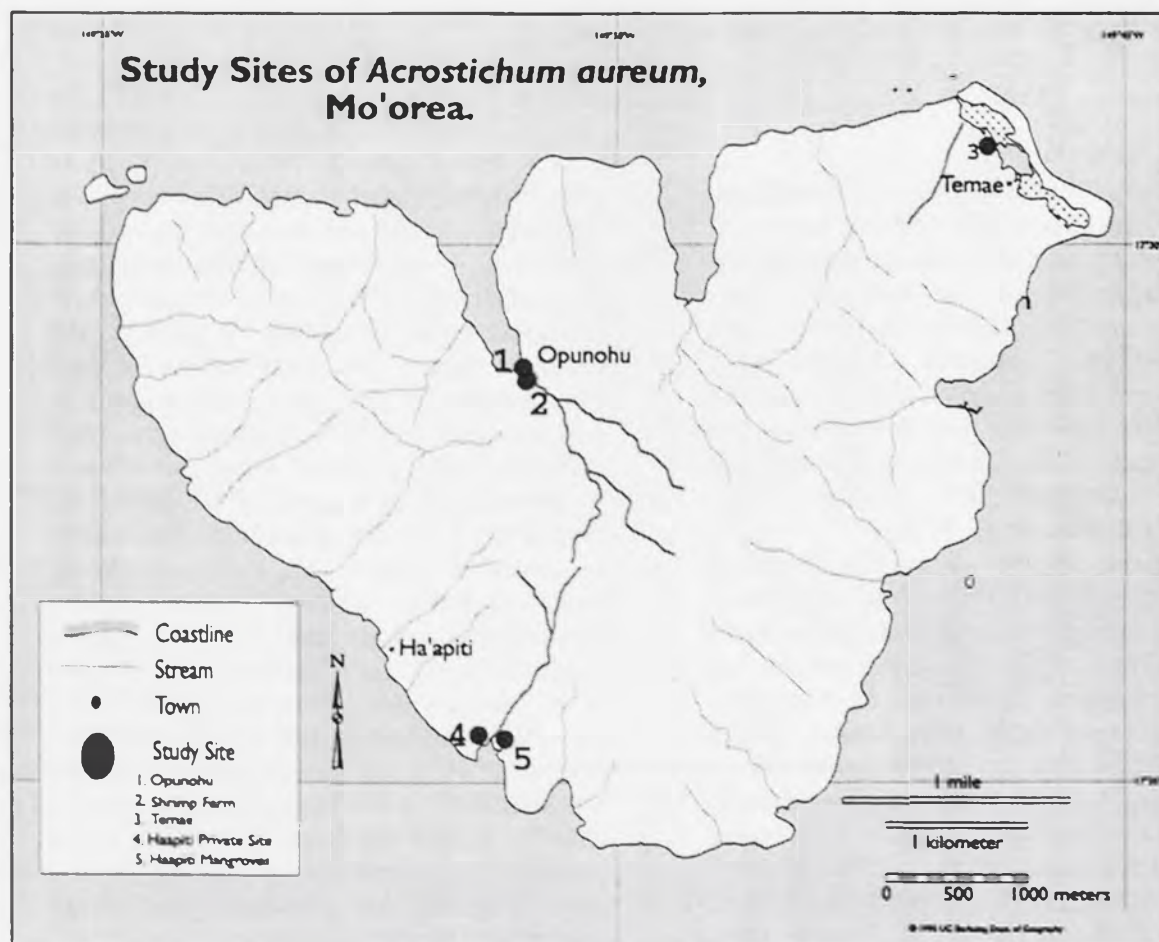 4. Ha'apiti Private Site
  5. Haapro Mangrove

Figure 1. Map of Moorea, French Polynesia, showing the five study sites chosen for the investigation of the establishment and development of *Acrostichum aureum*, the mangrove fern. Sites 1, 4 and 5 were estuarine habitats; site 2 was along the levy bank of a shrimp farm pond and site 3 was a large, open swamp area.

Five study sites were chosen for investigation:

1. Opunohu: a low-lying, well-shaded estuarine habitat adjacent to the mouth of the Opunohu River at PK 18. The overstory was dominated by *Hibiscus tiliaceus*. Mean annual precipitation in this area is 2500mm per annum (Atlas of French Polynesia 1993).

2. Shrimp Farm: a highly exposed area along the embankments of several shrimp ponds located near the Belvedere road turnoff at the base of Opunohu Bay, PK 18. Mean annual precipitation in this area is 2500mm p.a. (Atlas of French Polynesia 1993).

3. Temae: a large, open swamp area surrounding Lake Temae, near the circum-island road at PK 1.8. Mean annual precipitation in this area is 2000mm p.a. (Atlas of French Polynesia 1993).

4. Haapiti Private Site: the landward edge of a hibiscus-dominated mangrove area (on private property) close to the road at PK 21.7. Mean annual precipitation in this area is 2000mm p.a. (Atlas of French Polynesia 1993).

5. Haapiti Mangroves: an estuarine mangrove habitat dominated by hibiscus and *Rhizophora stylosa* near PK 21.4. Mean annual precipitation in this area is 2000mm p.a. (Atlas of French Polynesia 1993).

Site Conditions: Salinity & Exposure to Sunlight

The conductivity (total dissolved solids, TDS, in grams/liter) of soil and water samples collected at each site was measured. Conductivity is frequently used as an indication of salinity. Soil samples were prepared by taking 50g of soil and adding 250ml of water, stirring, and measuring the TDS of the suspension after 8 hours using a Corning Checkmate Meter. Additionally, soil samples were returned to the University of California at Berkeley and tested for conductivity. A saturation extract method was used as outlined by Carter (1993), and an Orion Research Model 101 conductivity meter was used to measure conductivity in decisiemens/meter. These were then converted to measurements in grams/liter.

A densiometer was used to calculate percentage cover at three points at each site. These three values were then averaged to get an overall measurement of canopy coverage.

Frond Measurements

Twenty fertile fronds were selected on mature sporophytes at each of the five sites to compare growth characteristics. Fertile fronds were chosen in order to maintain a degree of consistency between the ages of the fronds. Measurements were made of frond length, number of pinnae, number of fertile pinnae, length of the 3rd, 5th and 8th pinnae, and distance along the rachis between the 3-4th, 5-6th and 8-9th pinnae.

Gametophyte Distribution and Elevation

Field searches for gametophytes were made at all sites, in the understory and vicinity of the mature sporophytes. Gametophyte distribution on fern stumps, logs and exposed roots along the banks of an inlet creek at the Opunohu River site was recorded.
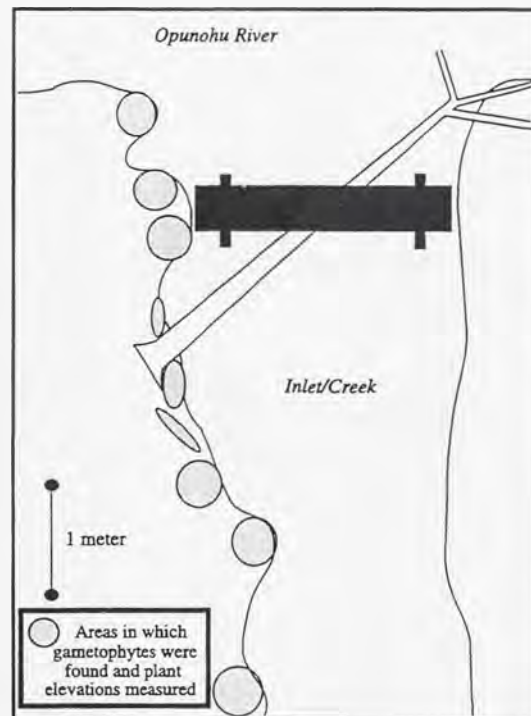
Figure 2. Areas in which gametophytes were found and plant elevations measured at the Opunohu site, Moorea.

The elevation above water level was measured for each plant found on the areas designated in Figure 2. Plants were classified into four growth stage categories (see Figure 3):
• gametophyte
• gametophyte with germinating sporophyte
• young sporophyte I (having multiple initial pinnae, usually 3-4, and being less than 1cm in height)
• young sporophytes II (having multiple initial pinnae, usually 5 or 6, and being less than 2cm in height).

In the absence of tidal records for this location, I assumed the average maximum water level to be the point of maximum corrosion along a metal barrier spanning the mouth of the creek. The elevation above this level was recorded for each plant on each stump or buttress. I continued to take tidal readings in order to gauge the accuracy of having chosen the corrosion line as a maximum water level.

Salinity Tolerance Experiment

Gametophytes and young sporophytes of the four stages discussed above and represented in Figure 3, were collected from Site 1 (bordering the Opunohu River). Two gametophytes and one of each of the other three growth stages were then transplanted into foil tins (diameter 11cm, depth 3cm) containing soil from the same site. These plants were placed in a shaded open-air laboratory and treated with solutions of varying saline levels prepared from boiled sea water diluted with boiled tap water. The control solution was freshwater, and the six remaining groups were treated with solutions of 2.5 g/L, 5.0 g/L, 7.5 g/L, 10.0 g/L, 25.0 g/L and 40.0 g/L TDS. Each group contained five replicate tins. Twice per day for 15 days, each group was treated with 25ml its respective solution. Prolonged inundation and burning of the leaves by salt was avoided by pouring the solution over the surface of the soil rather than over the leaves of the plant. Response of the plants was then observed and recorded daily. These observations were then converted to a
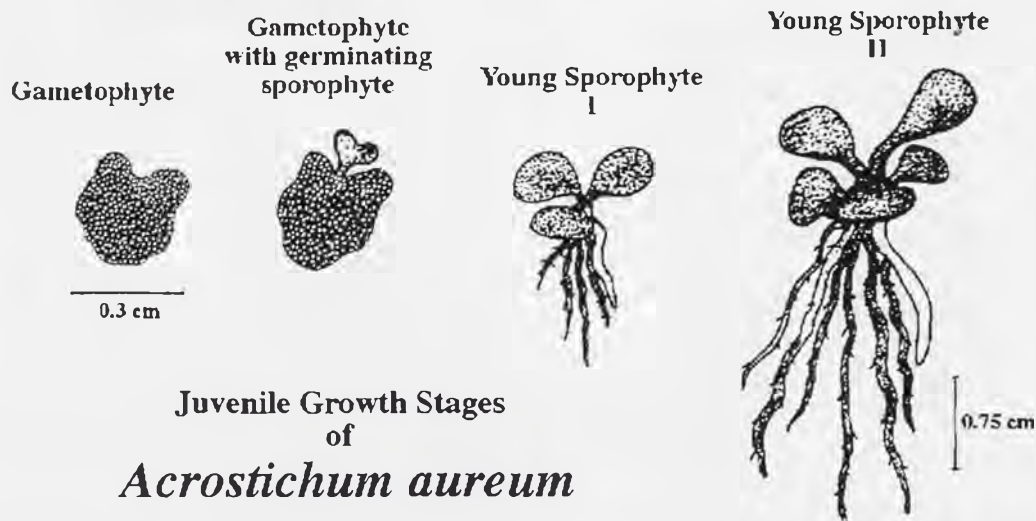
Figure 3. Juvenile Growth Stages of *Acrostichum aureum*. (Illustrations by the author).

numerical value from 10-0 according to the following scale:

Deterioration Index
10   healthy
9   dull, slight wilt
8   wilt
7   darkening, discoloration
6   dark, wet
5   dark, wet, transparent
4   brown
3   light rot
2   rot
1   bad rot
0   completely rotted

The values given for each of the five replicates were then averaged to obtain an overall value for each growth stage at each treatment level each day.

Inundation Experiment

Gametophytes and gametophytes with germinating sporophytes were collected from Site 1 at Opunohu (for growth stages see Figure 3). One of each of these two growth stages was placed in a petri dish and immersed in water. Five groups were established with five replicates in each: a freshwater control, and four saline solutions of 2.5 g/L, 5.0 g/L, 10.0 g/L, and 40.0 g/L TDS respectively. Response and mortality of the plants was then observed and recorded daily over a 10-day period. Deterioration of each plant was recorded as an estimation of the percentage of severe discoloration or rot of the tissues. A plant that appeared to be 40% rotted was thereby given a health rating of 60%. The values given for each of the five replicates were then averaged to obtain an overall average percentage health value for each growth stage at each treatment level each day.

Results

Site Conditions: Salinity & Exposure to Sunlight

Conductivity readings from the samples analyzed at the University of California at Berkeley were comparable to those obtained in Moorea, thus validating the techniques used at the field station in Moorea and its results.

Densiometer readings showed the sites to range from full exposure (0% cover) to 90% average cover.

Table 1. Average Conductivity of Soils and Percent Cover at each of the five study sites.

Site	Average Conductivity, g/L TDS	Average Conductivity, dS m^{-1}	Average Percentage Cover
1. Opunohu	2.07	9.0	90
2. Shrimp Farm	3.72	16.17	0
3. Temae	24.78	108.0	0
4. Haapiti Private Site	2.80	12.17	81
5. Haapiti Mangrove Area	3.67	15.96	84

The five sites can be generally characterized as follows:
- Opunohu: saline, shaded.
- Shrimp Farm: very saline, very exposed.
- Temae: extremely saline, very exposed.
- Haapiti Mangrove Area: very saline, shaded.
- Haapiti Private Site: moderately saline, shaded.

Gametophyte Distribution

Gametophytes were found at Opunohu, at the Shrimp Farm, and at Haapiti, however none were found at Temae. Gametophytes were found to be in proximity to mature sporophytes and growing on surfaces elevated above the waterlogged soil, such as mud clumps, root buttresses and old fern stumps. Gametophytes were rarely found growing on the flat surface of the forest floor or in open patches of the forest.

Gametophyte Elevations

The point of maximum corrosion on the metal barrier spanning the creek proved to be an effective measure of the average maximum tidal level. The water level was found to be at this height at high tide on the day of a full moon after several days of heavy rain. Only three plants were found to be growing below the maximum water level chosen along the metal barrier. There was a positive correlation (r=0.8018) between the total number of plants and elevation above the maximum water level.
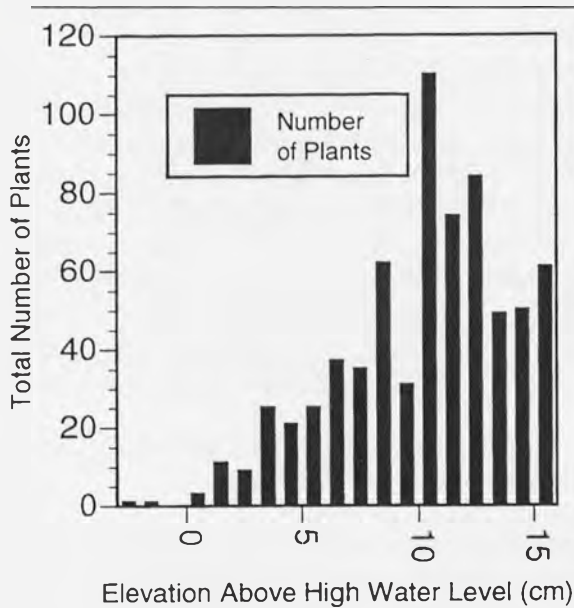
Figure 4. Elevation above water level of *Acrostichum aureum* gametophytes and young sporophytes, growing on fern stumps at the Opunohu Site, Moorea.

Salinity Tolerance Experiment

Mortality rates were highest in the high saline solutions, particularly those above 10.0 g/L TDS (see Figure 6). Mortality of the different growth patterns tended to follow this sequence: slight wilting of the sporophytes, darkening of the gametophytes, wetness of the gametophytes, rotting of the gametophyte with the germinating sporophyte (however the sporophyte initial remained healthy), rotting of the independent gametophytes, browning and eventual rotting of the sporophytes. All plants in the control group remained healthy. Notably, sporophytes were observed to exhibit growth under freshwater conditions.

Inundation Experiment

Gametophytes at all saline levels were shown to deteriorate rapidly to low levels of health (see Figure 7). These observations included rotting of the tissues or bleaching and discoloration of the cells. The highest rates of deterioration occurred in the solutions of higher conductivity. Sporophytes deteriorated less than gametophytes at the same saline treatment level. Likewise, rates of deterioration generally increased with increased TDS concentration, particularly at 40.0 g/L.

Frond Measurements

Notable differences in growth were found between the different sites, with the greatest reductions in growth and vigor occurring on saline and highly saline soils in exposed conditions i.e. at Temae and at the Shrimp Farm.
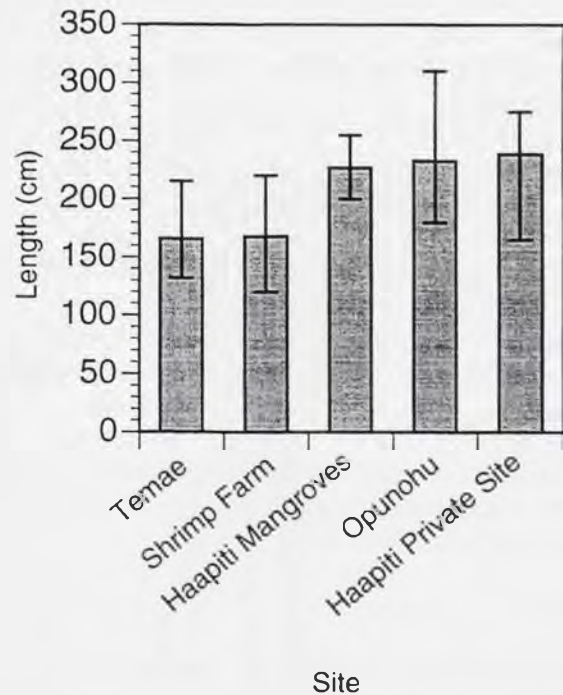
Figure 5. Average Length of Fertile Fronds of *Acrostichum aureum* at five sites on Moorea, French Polynesia. Note: the fine bars represent the maximum and minimum frond length at each site.
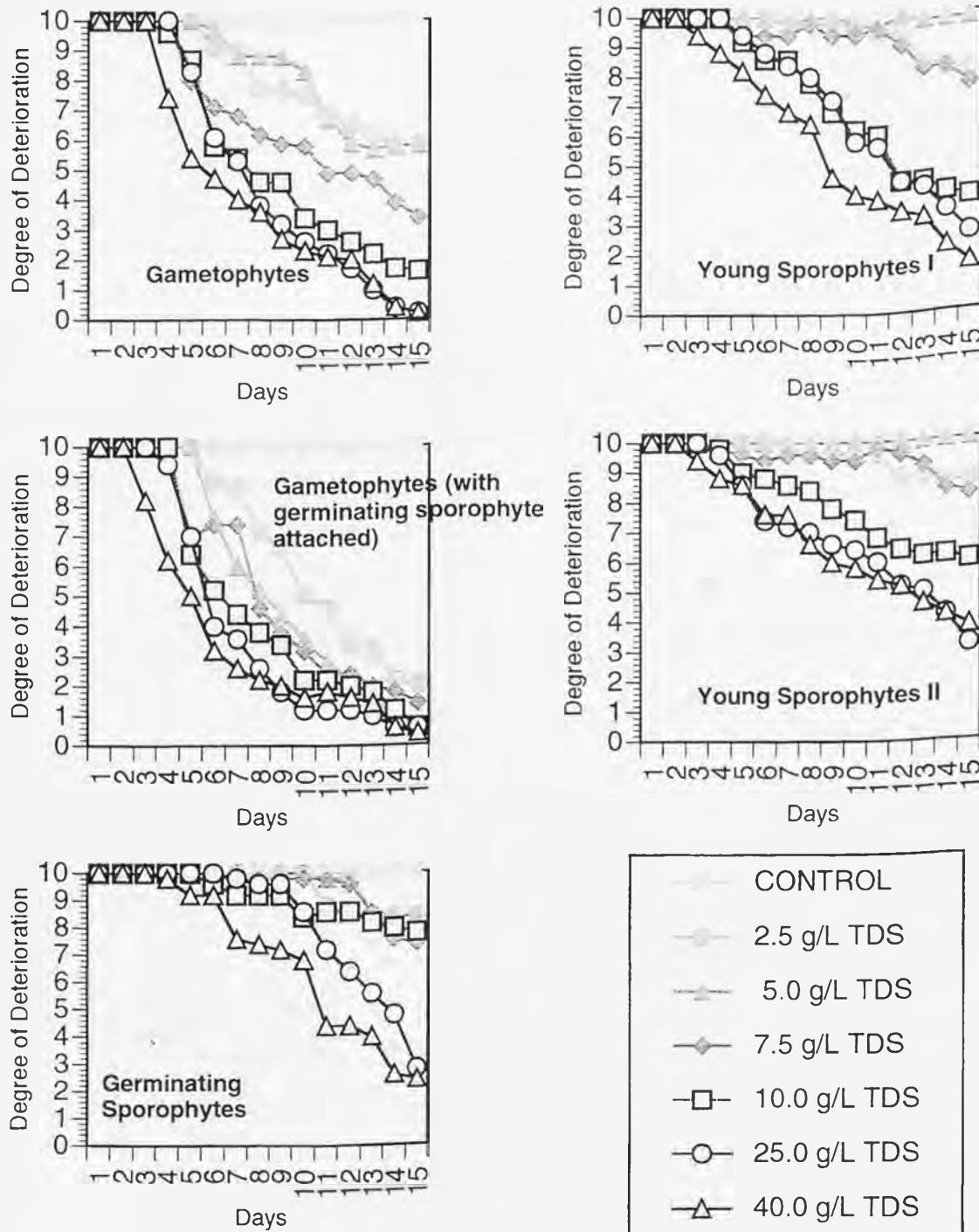
Figure 6. Deterioration of various juvenile growth stages of *Acrostichum aureum* treated with saline solutions
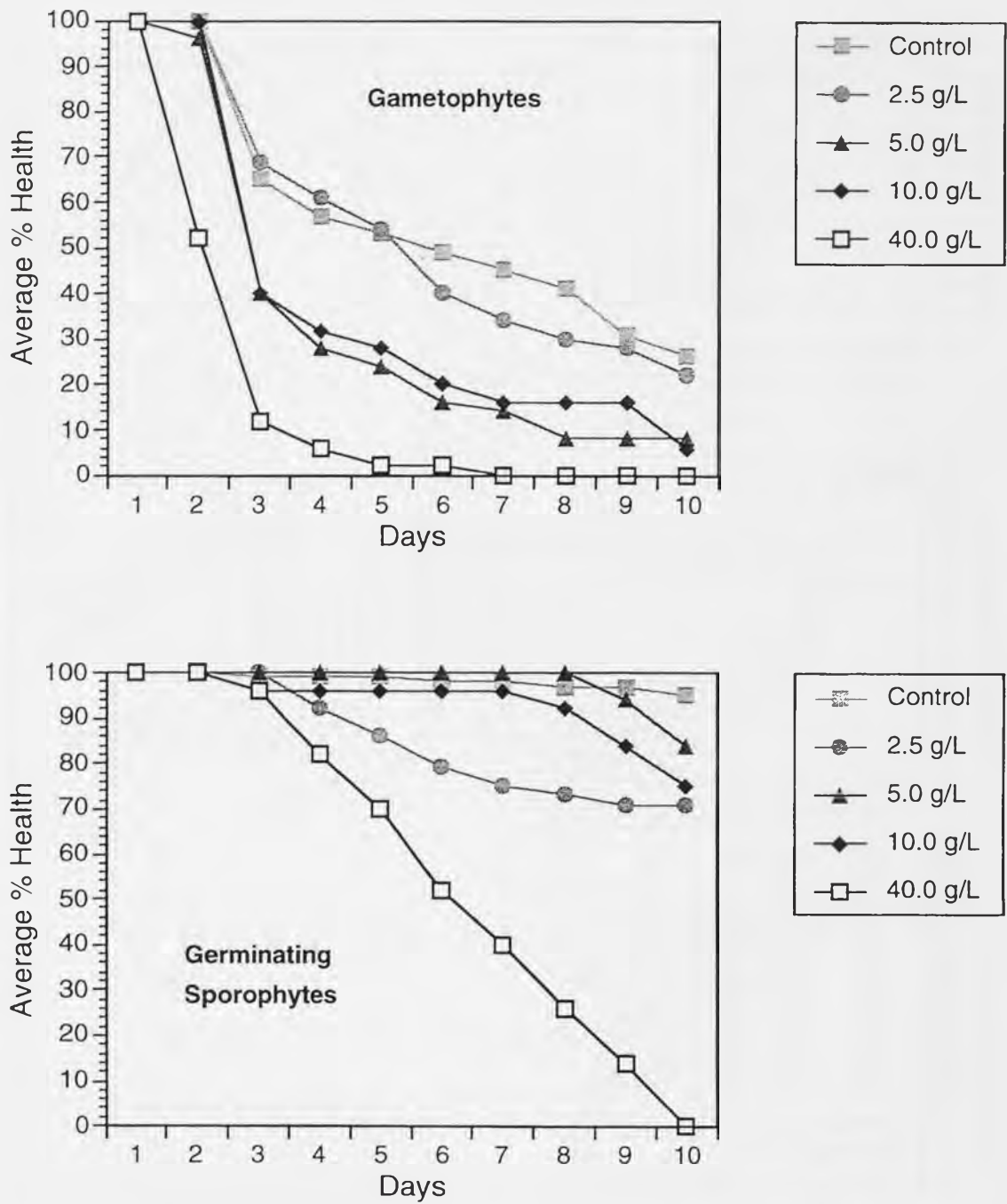
Figure 7. Average Percent Health of Juvenile Stages of *A. aureum* inundated with saline solutions.

SITE	1	2	3	4	5
1 Opunohu	1.00000				
2 Shrimp Farm	0.00012	1.00000			
3 Temae	0.00012	0.73120	1.00000		
4 H. Private	0.80404	0.00012	0.00012	1.00000	
5 H. Mangroves	0.99966	0.00012	0.00012	0.67702	1.00000

Table 2. Tukey HSD Multiple Comparisons. Matrix of Pairwise Comparison Probabilities for Frond Length

These frond measurements were then compared statistically using a Tukey test to create a matrix of pairwise comparison probabilities (see Table 2).

Results of the comparison of frond lengths showed Temae and the Shrimp Farm sites to be non-significantly different, and Opunohu and the two Haapiti sites to be non-significantly different, however these two groupings were significantly different from each other. Similar trends were noted for pairwise comparisons calculated for all of the frond traits (i.e. pinnae lengths and distances as outlined in Materials and Methods), with one exception. The number of fertile pinnae per frond was found to be non-significantly different between all of the sites. The average number of fertile pinnae per frond ranged between 9.8 and 11.35.

Discussion

Site Conditions: Salinity & Exposure to Sunlight

Conventionally, saline soils are those regarded as having conductivity levels above 4 dS m^{-1} (NSW Agriculture and Fisheries 1989). The conductivity levels found in this paper show that *A. aureum* is growing under considerably saline conditions at the sites studied, ranging from twice to twentyfive times the level considered to be saline. This, accompanied by the fern's wide tolerance of exposure, make *A. aureum* able to inhabit a range of extreme conditions not tolerated by other ferns.

Frond Measurements

The significant differences found in frond length appear to be a consequence of a combination of the environmental factors of salinity and exposure to sunlight. Lower salt levels in shaded environments facilitated the growth of large ferns. Shading substantially decreases the salt accumulation in leaves of *A. aureum* and salt stress is reduced due to lower evaporative demands (Medina et al. 1986). Medina et al. (1986) state that decreased growth in highly saline water may be due to the larger amount of energy invested in a sodium-exclusion pump at the root level to exclude ions that may otherwise accumulate to toxic levels. The decreased growth at Temae and at the Shrimp Farm as opposed to the growth at the three other sites may be due to such a mechanism. Considerable differences in frond length despite comparable conductivity levels at the Haapiti Mangrove site and at the Shrimp Farm (3.67 and 3.72g/L respectively) would suggest that other factors are at play in determining growth. Exposure to sunlight is likely to be of primary effect, given the large difference in average percentage canopy cover at each site (84 and 0% respectively). An analysis of the nutritional requirements of *A. aureum* and of the mineral contents of the soils on which it grows is yet to be published and would make a valuable compliment to the body of knowledge about this species.

The remaining frond traits that were significant (such as the number of

pinnae per frond or the measurements of pinnae length and distances, seem largely to be a factor of scale; that is, larger fronds have larger pinnae. Interestingly, despite significant differences in the number of pinnae per frond, the number of fertile pinnae per frond was non-significantly different. The reproductive capacity of *A. aureum* at each site may still be affected, however, as spore output would decrease with decreased surface area of fertile pinnae. Therefore, the smaller sized fertile pinnae at very salty, exposed sites would lead to an overall reduction in spore output. Another avenue of investigation into the reproductive output of *A. aureum* would be to assess the relationship between the number of fertile fronds produced per plant under different environmental conditions. The plants at the Temae site had noticeably fewer fertile fronds than those at the other sites, perhaps due more to the exceedingly saline conditions present rather than the exposure at this site (i.e. the same observation was not true at the Shrimp Farm site where the average percent cover was also 0%). Investigation into both the size and number of fertile fronds per plant would enable these parameters to be quantitatively factored into considerations of spore output as a factor in gametophyte distribution.

Gametophyte Distribution

The only site where gametophytes were not found was at Temae. The lack of gametophytes at this site is likely to be due to the extremely saline conditions at this site and the often dry conditions observed. As discussed, the plants at this site are also likely to have a lower spore output than the other sites studied, however, given the massive spore release that would still be occurring, there should be sufficient spores released to lead to many germinations. Germinations are not likely to occurring at Temae due to saline, dry conditions above those that can be tolerated by gametophytes. These conditions may change considerably during the rainy season, with increased availability of free water and increased leaching of salts. A longer term study that could incorporate any possible seasonality

of spore production and germinations would be valuable.

Another possible distribution factor, though likely to be minor, is predation of the juvenile growth stages by land crabs. This was observed to be occurring at the Opunohu site.

Gametophyte Elevations

The distribution of juvenile plants on elevated surfaces, the strong correlation between an increased number of plants and increasing elevation above water level at the Opunohu site, accompanied by the low number of gametophytes found to be growing on the forest floor, suggests that these elevated areas do indeed provide regions of more favorable growth conditions for gametophytes. Given that surface soils may have salinities of 2 - 100 times that of subsoils (Lloyd and Buckley 1986), the gametophyte stage is often subjected to incredibly harsh beginnings and any surface that experienced an increased leaching of salts would be favorable. The strong correlation between plant growth and increased elevation above water level at Opunohu suggests that water inundation plays a significant role in determining gametophyte distribution at this site. The result that only three plants were found to be growing below the maximum tidal level is notable, as it shows that juveniles are not growing in zones inundated by water, despite the contrasting ability of the mature sporophyte to do so. This observation is likely to be the product of two important factors. Firstly, spores that might land in this zone of inundation are likely to be physically swept away by the force of the water, and secondly, inundation by saline water would be a very difficult environment for germinating and developing gametophytes. Lloyd and Buckley (1986) found that spore germination was highest in their control group and in a saline solution of 0.5% NaCl and significantly decreased above 1.5% NaCl, and spore germination of *A. aureum* was low in concentrations of 2.25 to 3.0% NaCl. Their research included an investigation of the development of the gametophyte, and they found that the

critical level which will limit the attainment of two-dimensional growth and gametophyte survival is a soil salinity of 1.75 to 2%. Their results indicate that the tolerance range for germination is lower than the tolerance range of the mature sporophyte. Thus, the gametophyte generation must develop in a microhabitat of more suitable salinity levels, e.g. a raised, leached surface.

There was no apparent zonation of growth stages over the range of heights observed above water level, however a longer term study which could monitor these populations more closely over time and assess comparative ages of the juveniles and survival rates would be useful. This could provide the basis for a demographic study of the population at a larger level.

Salinity Tolerance Experiment

There was a clear difference between the tolerance of the different growth stages to saline conditions. The higher tolerance to salt of the young sporophytes than that of gametophytes leads clearly to the question of how this younger, more sensitive generation manages to establish and give rise to the more tolerant sporophyte generation. Hypotheses for this were discussed above regarding gametophyte elevations. However it is unclear as to at what point the deterioration recorded was irreversible and at what point the reproductive capacity of the gametophyte was lost. It is advantageous to have a strong germinating sporophyte stage to get established and to quickly develop the necessary morphological and physiological features that assist the plant to tolerate saline conditions. This experiment showed that this can be the case - the germinating sporophyte was more tolerant than the both of the young sporophyte stages. The rapid deterioration of the gametophytes from which the sporophyte initials were germinating (at a faster rate than that of gametophytes alone) may be due to the increased age and strain on this gametophyte as it supports the growing sporophyte.

Inundation Experiment

Mortality was most rapid in solutions of higher salinity, however rates of deterioration were high in solutions of all concentrations. This suggests that inundation by water of any salt level is deleterious to the gametophytes. As found in the salinity tolerance experiment, the germinating sporophyte initial appears more tolerant than the gametophyte.

Given that bleaching and rotting of both growth stages (gametophytes in particular) occurred at all levels, even in the freshwater control group, it would appear that the juvenile stages of *A. aureum* are incapable of surviving extended periods of inundation by water. In their swamp-like habitats, this would prove to be a severely limiting factor on distribution. More investigation is necessary to determine the effects of periodic tidal inundation (as opposed to constant inundation) of juvenile growth stages.

All of these results combine to demonstrate the differential tolerance of the growth stages of *A. aureum* to various environmental conditions and the critical nature of the gametophyte in the establishment of the population. Although asexual reproduction of plants is often advantageous in difficult environments, *A. aureum* did not appear to demonstrate this mechanism. Stems did not have branching or creeping rhizomes connecting each plant. Instead the fern releases massive numbers of spores and, as Lloyd and Buckley (1986) state, even very low percentages of survival at higher salinities could result in millions of successful gametophytes. These spores appear to have the best chance of survival when landing on elevated surfaces of lower salinity levels, above the level of tidal inundation, but with free water available for fertilization. The distribution in salty areas despite seemingly preferring freshwater, as indicated by the growth of young sporophytes in the control group of the salt tolerance experiment, and by high rates of germination of spores and survival of gametophytes in freshwater and solutions of very low salinity (Lloyd and Buckley 1986) would be a fruitful area for

further study. Interestingly also, the herbarium at the University of California at Berkeley has several juvenile sporophytes collected from a freshwater area in Moorea, however field observations failed to find *A. aureum* in inland, freshwater environments. The fern gametophytes did not appear to be competing with any other plant in its first growth stages at the sites studied. Perhaps it is out-competed in freshwater conditions, and competition may also be different at various stages of the life cycle.

The gametophytes of *A. aureum* and *A. danaefolium* have been shown to have a significantly greater tolerance to salinity than that of the gametophyte of *Ceratopteris thalictroides* (Lloyd and Buckley 1986). This fern is a freshwater aquatic and currently believed to be the outgroup of *Acrostichum*. The differing tolerances of the gametophytes and sporophytes of *Acrostichum* suggests that though the gametophyte may have evolved some ability to tolerate salt, it has not developed the necessary physiological nor morphological features to tolerate salinity to the same level as the sporophyte generation. Further investigation into the biology of *Acrostichum aureum*, its relation to the other species of its genus and to its outgroup, and its interaction with other plants at a community level would add not only to the knowledge about this particular species, but also to the study of the adaptive capabilities of plants and mechanisms for tolerance to extreme environments.

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The success of the introduced Common Myna, *Acridotheres tristis*, on the island of Moorea, French Polynesia, as demonstrated by foraging patterns related to human development and disturbance

Julianne Ludwig
Department of Integrative Biology
University of California, Berkeley   94720

ABSTRACT.   Since being introduced to the island of Moorea, French Polynesia in 1908, the Common Myna has come to dominate the island's avifauna. The reason for its success relative to native birds was hypothesized to be its keen use of human-modified foraging habitats. Thus, while native birds suffered from human alterations to the natural environment, the Myna prospered. Studies were done on the Myna's general foraging behaviour to determine to what extent it was using human-modified foraging habitats compared to more natural ones. An emphasis was put on how the Myna capitalizes on disturbances to increase its foraging ability. After determining the grass lawn to be its staple habitat, two lawns were chosen in areas of differing disturbance, one in a town and one in a suburban area. Myna density in the areas and foraging on the lawns was compared to dete rmine what levels of human disturbance the Myna prefers. Also, a study was done on Myna predator vigilance to see whether the Myna practices decreased vigilance as flock size increases in order to increase its time spent foraging. Lastly, the Mynas interactions with native Moorean birds were observed in an attempt to understand the bird's possible effects on the already human-impacted native avifauna. It was found that Mynas were using human-modified foraging habitats much more than natural ones, and that they were especially foraging in habitats with disturbances that maximized their foraging ability and food availability. They showed a preference for suburban habitats, and did not practice predator vigilance, but instead showed more interaction with conspecifics as flock size increased. Antagonistic interactions between the Myna and the Tahitian kingfisher, *Halcyon venerata*, were observed, giving support to previous beliefs that the Myna may be negatively impacting native birds.

Introduction

The Common Myna is native to India and adjacent regions, but through human introductions it has expanded its range vastly in the last 200 years. Mauritius was the first extra-Indian territory into which it was released (1762), following which subsequent introductions included several island chains in the Indian, Pacific, and Atlantic Oceans, as well as Australia, New Zealand, and South Africa. During the last century, the Common Myna has extended its original continental range from geographic India to Russian Turkestan, S. E. Persia, peninsular Thailand, and some former Indochinese countries (Sengupta 1982).

In 1865, the Myna was introduced to Hawaii by Dr. William Hillebrand to combat the plague of army worms that was ravaging the pasture lands of the islands. It spread quickly and was reportedly abundant in Honolulu in 1879, and extremely common throughout Hawaii by 1933 (Berger 1983).   In many cases, the Myna has demonstrated itself to be of considerable value to the agroecosystem by controlling such agricultural pests as grubs, locusts, and other invading insects (Berger 1972; Sengupta 1982; Parasharya et al. 1994; Shah and Garg 1988).

Its merits as an effective biocontrol agent brought about the Myna's introduction to the Society Islands, French Polynesia, in 1908. It was hoped that the bird would control the wasp population which plagued the fruit plantations (Raust 1996). However, as in many other areas of introduction, the omnivorous Myna soon expanded its food preferences to include, among other resources, the fruits it was intended to protect (Sengupta 1982; Raust 1996).

Ernst Mayr wrote (1945) that on several of the South Pacific islands, the Myna was rarely found away from the coastal coconut plantations. However, the Myna presently inhabits several of the Society Islands and neighboring chains, and occurs in a variety of habitats from seacoast to forest edge.   These include open

countryside, agricultural areas, residential gardens, and city streets. Only dense forest is excluded (Pratt et al. 1987).

As an introduced bird, the Myna's high population numbers raise questions as to the reasons for its success and its possible effects upon the already species-poor native Polynesian avifauna. Fifty years ago, the Myna was qualitatively perceived as a serious competitor of several species of native birds (Mayr 1945). Its long term impact on the indigenous land avifauna still remains poorly understood (Steadman 1991). Although the Myna does not seem to pose any threat of disease to indigenous birds, it may compete with native species for food or nest sites (Franklin and Steadman 1991).

The most obvious causes of decline in Polynesian land bird populations have been and continue to be human activities such as direct predation, habitat alteration, and introduction of predators and pathogens (Franklin and Steadman 1991). Fragmentation of forestland has been a crucial blow to native birds, many of which rely on natural undisturbed habitat in which to live and breed. But unlike such native bird species with narrow ranges of habitat requirements, the Myna is an adaptable species which occurs usually, though not always, in association with man, and often with domestic animals, thus flourishing with forest clearing and human development. It is therefore difficult to determine the true effect of the Myna on native avifauna when its success seems so closely linked with the major causation of landbird decline, human disturbance.

Since preliminary observations did not reveal Mynas competing directly with native birds, it is hypothesized that human development originally influenced the drop in native bird populations. When the Myna was introduced, it filled empty niches that new human-developed habitat provided. The Myna learned to use different resources in different habitats, capitalizing on the variety of diet possibilities in a developed island environment.

In order to test this hypothesis, it was planned to determine if Mynas are utilizing human-modified habitats more than (and possibly at the exclusion of) native habitats. A general study of myna foraging behaviour in different habitats was done to document how they utilize the different resources available to them at different sites. More in-depth observational studies were conducted to determine what levels of human disturbance the Myna prefers and whether it practices predator vigilance or not. All throughout these studies, any interactions with native bird species were noted.

Materials and Methods

General Foraging Behaviour

Expeditions to various parts of Moorea were taken between September 30, 1996 and November 22, 1996, including trips around the perimeter of the island as well as trips into Pao Pao and Opunohu Valleys, and along the road to Mt. Belvedere in the interior of the island. Each habitat where Mynas were seen to be foraging was characterized and recorded. The specific observations made at each site were: food resources utilized by the Myna, general Myna foraging behaviour, and any risk factors or disturbances present. The general categories of habitats sampled were: grass lawns, dumps, pastureland, domestic animal feedings, roadside, shoreline, hotels/restaurants, fragmented forest treetops and edge, muddy fields, and marsh.

Relative Myna Utilization of Lawns at Differing Urban Disturbance Levels

Two grass lawn plots in the vicinity of Cook's Bay were chosen, both approximately 1.2 hectares in area. One was a cleared but empty lot in a recently developed suburban residential area, and will be referred to as the Suburbia site. The other was a public lawn at the junction of the two main roads in the town of Pao Pao (Figure 1). The lawns were assumed to be comparable in the amount and types of small invertebrate food resources available to the myna, based on direct observations of the grass at each plot and on observations of food Mynas pulled up as seen through binoculars. The birds seemed to be equally productive at each site, pulling up food

from the base of the grass fairly often whenever they foraged.
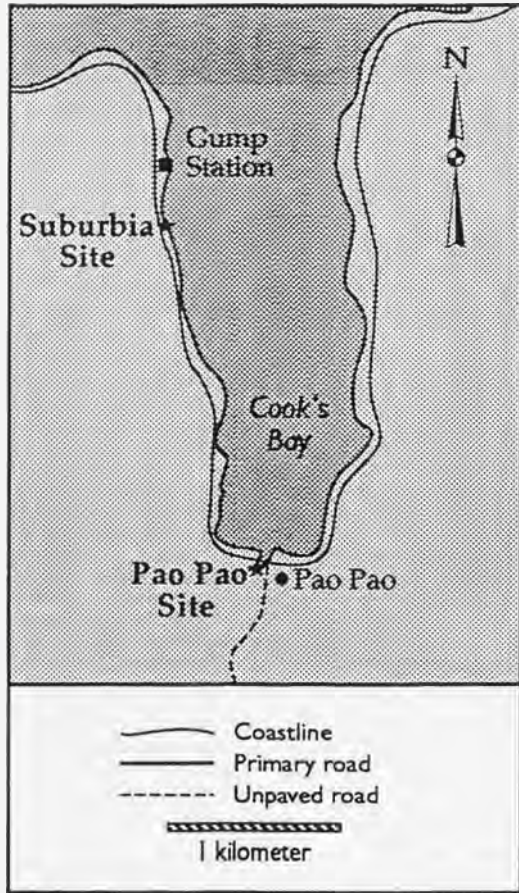
Figure 1. Location of the two lawn plots studied. The Pao Pao site represents a town setting, and the Suburbia site represents a suburban area.

Measurements were taken of the relevant characteristics of each site. The Suburbia site lay at the base of a slope, between two roughly parallel roads. One was a narrower residential road on its eastern side at the same level of the plot and 9 meters away. The other was the main circum-island road which was approximately 9.4 meters away but beyond the top of a slope on the plot's western side, thus making it invisible from the viewpoint of the plot itself . The nearest building was a house across the street , approximately 25 meters away. Percent cover was zero as there were no trees on or near the lawn. An odd-shaped plot was

chosen because one corner was overgrown with tall grass in which mynas were not visible. The point of observation was on the slope at a corner of the plot, approximately 3.5 meters away. Figure 2 shows a detailed map of the surrounding area.

The Pao Pao site was bordered by the circum-island road on its northern side, the road to Opunohu valley on the east, and a dirt driveway on the west. Its southern side was delimited by a muddy strip which served as an infrequently used driveway to the next door house. All were on the same level of the plot. The circum-island road and Opunohu road were each 2 meters away from the plot and the driveway was 1 meter away. The nearest building was a house that was 14 meters away. Percent cover was 3 percent. The two sides bordered by the main roads were lined with hedges about 1 meter tall. Just outside the plot, lining the western edge alongside the driveway, there were five trees total: 2 *Casuarina equisetifolia,* 1 *Hibiscus tilaceous,* 1 *Pandanus tectorius,* and one *Plumeria rubra,* accounting for the 3 percent cover of the plot. On the southern side of the plot, the lawn extended and there was a *Tournefortia argentea* tree, 15 meters from the edge of the plot, under which the observation point was located. Figure 3 shows a detailed map of the surrounding area. Only palm trees were included on the map because they were the only tree species of clear importance to mynas as nesting sites. The other trees apparently served merely as perching sites for Mynas or as stopovers while they were flying through, and thus were not relevant to the study.

Sampling of the sites was done in two hour blocks from 6:00 a.m. to 8:00 a.m., 11:00 a.m. to 1:00 p.m., and 4:00 p.m. to 6:00 p.m., alternating sites each sampling period to randomize for daily weather conditions. Thus, if the Pao Pao site was visited during the morning session, the Suburbia site would be visited in the afternooon, and then again the Pao Pao site in the evening. The following day, observations would begin at the Suburbia site instead, and continue in such an alternating fashion. This method was successful in ensuring that measurements at

Figure 2. Detailed map of surrounding area of Suburbia site. The path taken when walking density transects is shown, along with an outline of the transect area surveyed. The transect began just north of the stop sign and continued south to the cul de sac in the road. All birds seen in the outlined "visible transect" area were counted.

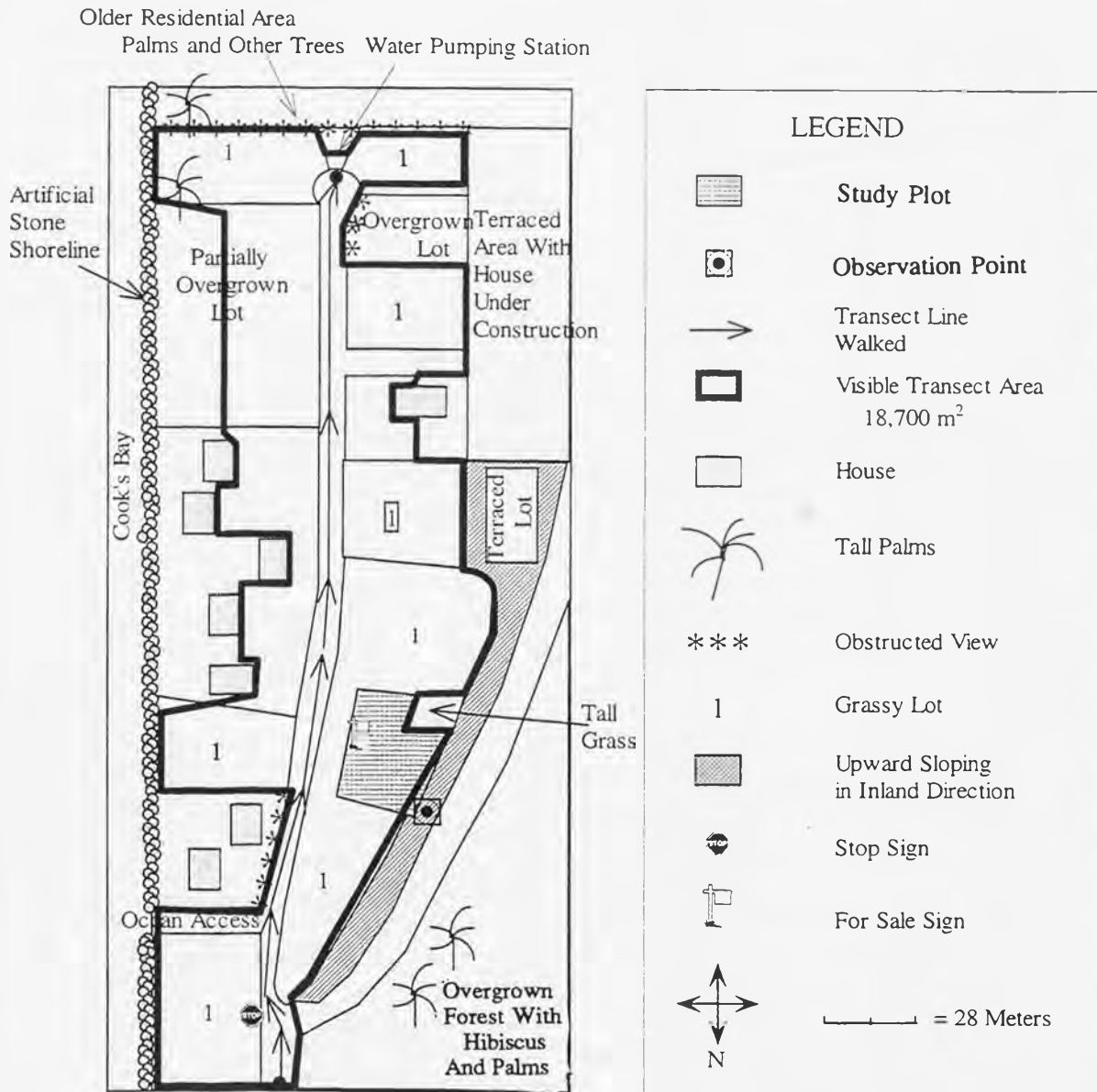**Figure 3.** Detailed map of the surrounding area of the Pao Pao site. The path taken when walking density transects is shown, along with an outline of the transect area surveyed. The transect began just south of the canal, and continued north and out onto the main circum-island road, terminating at the snack shop. All birds seen in the outlined "visible transect" area were counted.

Cook's Bay
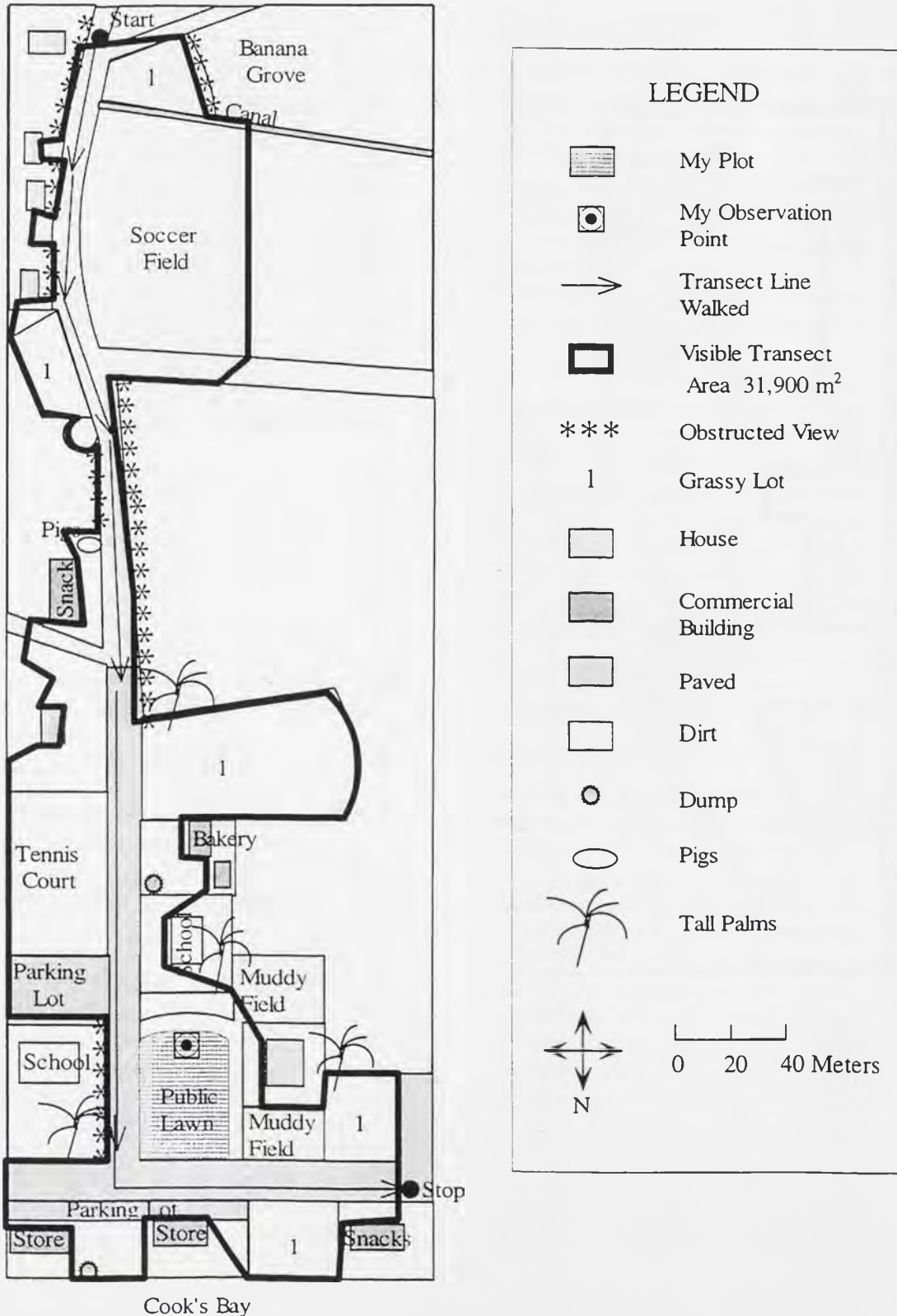
each site were taken in comparable weather conditions. These sessions were repeated until six replicates at each site for each time block were completed, totaling 36 sessions. The dates of sampling were November 1, 1996 to November 19,1996.

To measure traffic levels at the two sites and thus give an idea of relative levels of human disturbance, a count was taken of vehicles with and without motors, pedestrians, and domestic animals passing through the plot or on the bordering roads. This was taken at the ninth minute of observation, and then repeated every ten minutes for the duration of the two hour sampling period.

During sampling blocks, an initial count of Myna birds standing on the plot was taken, and then repeated at each ten minute mark until two hours passed. These sample values were then averaged for that session to give the mean number of Mynas on the plot at any given point in time (average instantaneous number of mynas) during that session.

Focal animal sampling was done if any Mynas were present on the plots in the nine-minute intervals between the other measurements. A Myna was randomly picked and watched for a one minute sample period, with binoculars if needed. If the bird could be kept in sight for longer, a longer sample may have been taken and then later broken up into one minute intervals. If a bird flew before the end of a minute, the data were discarded. Durations of time spent foraging vs. not foraging were recorded on a tape recorder, and later timed. Foraging was characterized as any behaviour associated with food, including searching for, obtaining, or consuming it. Walking while looking for food was thus considered as foraging behaviour. Because the number of foraging samples taken at each session varied from none to many, the samples from all replicate sessions at that site and time of day were averaged together to find the mean time an individual myna spent foraging during that time block at each site.

Thus for each time block at each site, there were six numbers denoting the average instantaneous number of mynas for each of the six replicate sessions. Each of these was then multiplied by the mean time an individual myna spent foraging during that time block at that site. This number was then multiplied by the total time of 120 minutes to give the utilization of the lawn during that two hour block in myna*minutes. For example:

The first 6:00 a.m. session at Pao Pao had an average of 0.08 Mynas on the plot at any given time throughout the two hour sampling period. From all the foraging samples of that session and its other five replicate sessions at Pao Pao at 6:00 a.m., the average proportion of time spent foraging by an individual Myna was .9279. Multiplying 0.08 Mynas x .9279 x 120 minutes = 8.91 Myna*minutes of lawn utilization during that first 6:00 a.m. session at Pao Pao. This calculation was repeated for each of the six replicates at each of the two sites at each of the three times of day to give 36 utilization values. A two-way ANOVA was then run on this data to examine the variance by site and time of day, and the interaction between site and time of day. Graphs, however, were made using the averages of the six replicate session values of mean instantaneous number of mynas at each site at each time.

Myna Density Relative to Disturbance Levels

Relative myna density was compared at the two sites using walking transects and flushing techniques (Leopold 1939). The transect counts were taken by walking down the road for a short distance at each site through a representative section of the areas (Figures 2 and 3). The total visible area in which mynas were counted was calculated to be 18.7 hectares at the Suburbia site, and 31.9 hectares at the Pao Pao site. Transects were run at each site at 6:00 a.m, 8:00 a.m., 11:00 a.m., 1:00 p.m., 4:00 p.m., and 6:00 p.m., six times each, totaling 72 counts. A general note was made of what activities the Mynas sighted were engaged in, especially as pertained to places of foraging. Bird counts divided by calculated transect area yielded the relative density for each replicate at each site at each time of day. These 72 density

counts were then analyzed using a two-way ANOVA to examine variance by site, time of day, and the interaction between site and time of day. Graphs were made using the averages of the six replicated sessions of density counts at each site at each time of day.

Predator Vigilance

Also recorded during the one minute focal animal samples was the duration of time the bird spent with its head down vs. head up while foraging (feeding vs. scanning.) Head down, from this point on referred to as a non-vigilant posture, was defined as a posture low enough for the beak to touch the ground. The flock number at the time of sampling was recorded in order to determine if Mynas were practicing predator vigilance. For the Pao Pao site, flock sizes greater than or equal to 4 birds were grouped together due to the instability of flocks once they reached 4 or above in number. The same was done with the Suburbia data for flocks of 5 or more birds (Catterall et al. 1992). The samples for each site were plotted on a scatter plot and the relationship between flock size and proportion of time non-vigilant was tested with a regression analysis.

Interactions With Native Birds

Because there are few native bird species on Moorea now, and even fewer whose territories overlap with or border on Myna territory, interactions between the Myna and native Moorean birds were random and observed purely by chance. Any observations were noted while doing general bird-watching or sampling Myna foraging behaviour in different habitats.

Results

General Foraging Behaviour

Grass Lawns -- Areas observed included both public and private lawns, soccer fields, and muddy fields. Mynas walked while foraging, pecking intermittently and sometimes struggling with some larger prey item. They fed at the base of the grass most of the time, though occasionally darted after some flying object or gleaned off the blades.

They were observed to pull up earthworms, grasshoppers, crickets, and beetles, though they must also have fed on grubs too small to see. They foraged similarly on areas which were predominantly mud, and ate similar insects. They also picked skinks, small geckos, and fruit off of trees on the lawns. Such grassy areas were often traversed by people, dogs, cats, and sometimes vehicles.

Dumps -- Dump-type habitats observed included the fruit factory dump, residential dumps, drainage runoff sites, and public trash bins. At the fruit factory dump, mynas appeared to be sifting through the rotting fruit remains for insect larvae, but at all other places, they were observed to eat human food scraps and trash. At the stone trash bins, they would actually jump inside to forage.

Pastureland -- Areas observed included fenced off pastures, some extremely overgrown with grass the height of a human, and some just with tall grass about 1 to 1.5 feet in height. Mynas were observed to forage only with each other at times, but much more often in the presence of sheep or cattle. In the latter case, they would actually ride the animals, using them as a perch and then jumping down to forage on the ground. The grazing animals paid no attention to their passenger birds, even when they dismounted and fed within a foot of the animal's grazing mouth. The Mynas were most likely eating crickets and other insects that the cattle stirred up, since a brief walk taken through an overgrown plot revealed a high abundance of small crickets that were stirred up by the disturbance.

Domestic animal feedings -- Feedings of dogs and pigs were observed. Mynas would hover nearby at dog feedings until the dogs left and then climb into the bowl and rapidly eat the rice and canned mackerel therein. The dogs would often return and chase the Mynas off a few feet. Mynas were also seen feeding outside a pig cage, eating the scraps that fell out, as well as feeding alongside loose pigs in a front yard in Pao Pao. They would often hop up on sleeping pigs or stand on them as they wallowed in the ditch, most likely feeding

on grubs and insects the pigs turned up while foraging or rolling in the mud.

Roadside -- Stretches of the circum-island road were observed. Mynas would actually feed in the street on food trash and carrion such as dead land crabs and even a dead rat. They pecked at the pavement of the road for something too miniscule for me to discern. Cars, people, and bicycles passed frequently. Mynas often simply sidestepped passing traffic before returning to their street foraging. One pair was even seen feeding on a freshly run-over land crab on the runway of the airport in Papeete, Tahiti, just next to a jet plane.

Hotels/Restaurants -- A snack shop, and three resort hotels were observed. The mynas would wait until people left a table and then fly up and feed on food leftover on the plates. At the resorts, they would often fly several meters inside the open-air restaurants to forage on empty tables. People were quite prevalent at these sites but the Mynas seemed indifferent to them.

Fragmented Forest Treetops and Edge -- Forest edges and interior in Opunohu Valley were observed, as well as forest edge around a residential garden. Mynas would pick skinks off of trees in the edge region of forests. In Opunohu Valley, they also fed on the fruits of the *Castilla elastica* tree, picking the ripe fruit from its treetops which extended above the rest of the Hibiscus forest.

Marsh -- A marshy habitat at a spot where the ocean came within 2 meters of the road was observed. A group of Mynas sat foraging in the marshy grass. They seemed to be gleaning much more here, though I couldn't tell specifically what they were eating. Available insect food resources were most likely high, though, since the buzz of insects was loud.

Shoreline -- Natural sandy beaches were observed. Mynas picked amongst the seaweed debris, seemingly eating small insects of some kind. They also were observed to toss the sand about near dusk and snap at things in the air, perhaps sand fleas. A wave was seen splashing a Myna while it foraged close to the water. The Myna continued to forage wet but unbothered.

Relative Myna Lawn Utilization at Differing Urban Disturbance Levels

Traffic counts showed a clear difference in traffic between the Pao Pao and Suburbia sites at all times. Traffic in Pao Pao was consistently about twice as high as in Suburbia. However, traffic on the circum-island road which ran above the Suburbia site was invisible from the plot, and thus seemed to factor little into the disturbance level of the plot. If that traffic is ignored, traffic in Suburbia was even less compared to Pao Pao.

Figure 4. Traffic counts at the Pao Pao and Suburbia sites during the three different time blocks of the day. Traffic counts of vehicles with and without motors, pedestrians, and domestic animals either passing through the plots or on the bordering roads, were taken in one minute samples every ten minutes during each two hour session. These values were then averaged for the replicate sessions to find the mean level of traffic at each site at each time of day. These averaged numbers are graphed in Traffickers (units of traffic such as person, car, etc.) per minute.
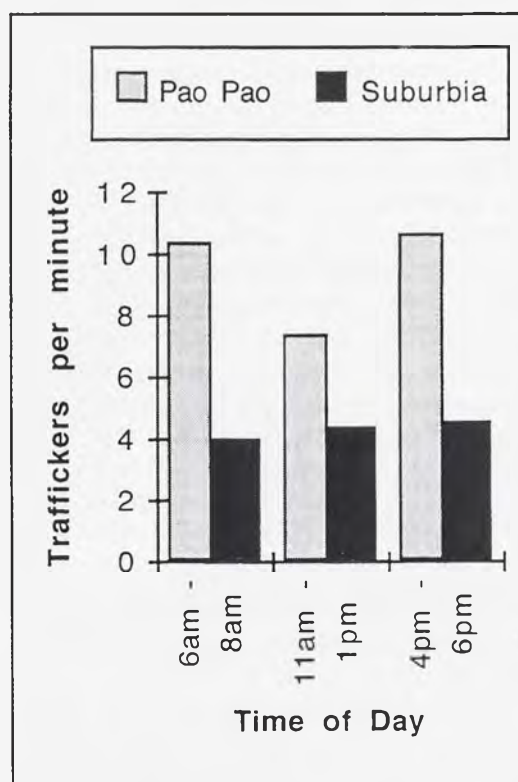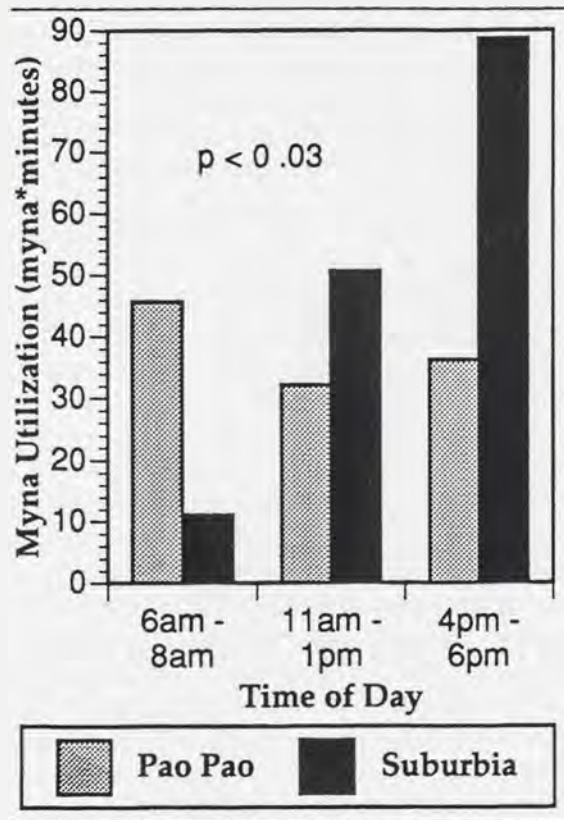
Figure 5. Myna lawn utilization at Pao Pao and Suburbia sites during the three time blocks of the day. The average instantaneous number of Mynas present on the plot (measured with scan samples every ten minutes during two hour sessions and then averaged for all sessions at that time of day at that site) multiplied by the average proportion of time foraging of an individual Myna (measured with one minute focal samples to determine percent time spent foraging and then averaged for all sessions at that time of day at that site) multiplied by the 120 minutes in a two hour session determines the average Myna lawn utilization value in Myna*minutes for that time of day at that site.

Relative Myna lawn utilization was shown to vary significantly based on site and time of day (whole effect test, $F = 2.83$, $p < 0.03$). The interaction between site and time of day was significant ($F = 4.01$, $p < .03$).
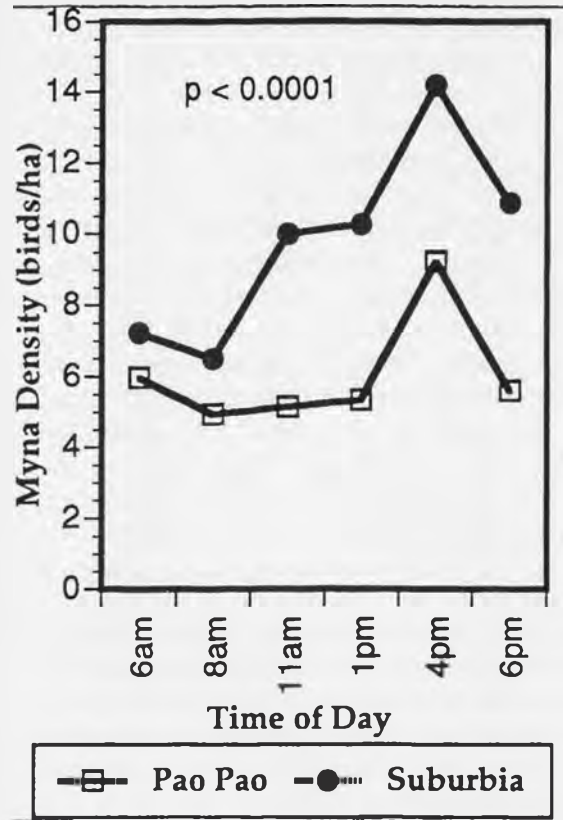
Figure 6. Relative myna density at Pao Pao and Suburbia sites throughout the day. Six replicate density counts for each time of day at each site were averaged to give the average density of Mynas at that time of day at that site.

Myna Density Relative To Disturbance Levels

Myna density was shown to significantly vary between site ($F = 25.2$, $p < 0.0001$) and time of day ($F = 4.9$, $p < 0.0008$). The interaction was insignificant ($F = 1.1$, $p > 0.3461$).

Predator Vigilance

Mynas foraging at Suburbia showed an insignificant effect of flock size on proportion of time non-vigilant ($Rsq. = 0.005$, $p > 0.21$). Those foraging at Pao Pao showed a significantly negative effect of flock size on proportion of time non-vigilant ($Rsq. = 0.134$, $p < 0.0059$).

103
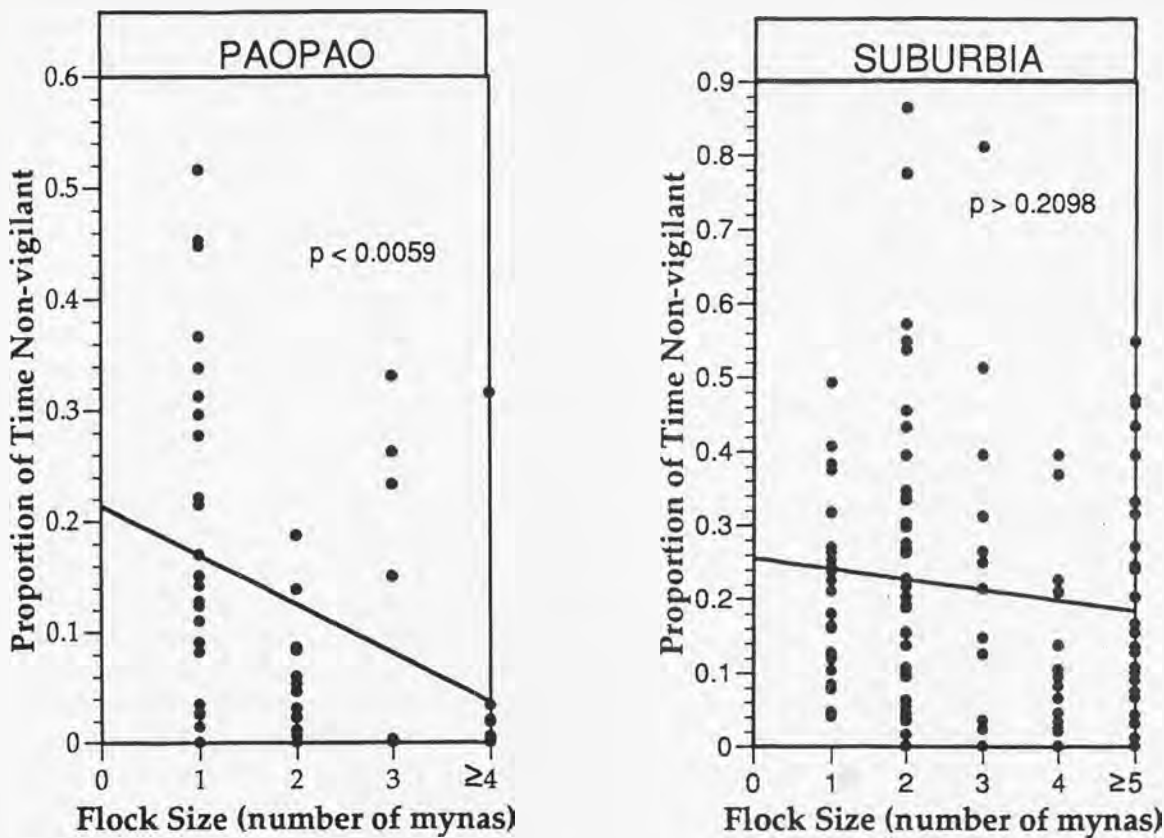
Figure 7. Myna vigilance. One minute focal animal samples were taken and the proportion of time spent non-vigilant was recorded along with the flock number at the time of the sample.

Interactions With Native Birds

Significant interactions observed between the Myna and native Moorean birds were minimal. With the Pacific Reef Heron, *Egretta sacra*, and Brown Noddy, *Anous stolidus*, large and medium-sized seabirds respectively, the Myna seemed deferent. It would move off a bit when one would fly up. Small seabirds like the Wandering Tattler, *Heteroscelus incanus*, and Plover, *Pluvialis fulva*, which tended to be more skittish themselves, would often fly a bit when a Myna came to feed near them on the shoreline. But they soon resumed feeding and were often within a few feet of the Mynas, both seemingly ignorant of the other.

The Tahitian Kingfisher, *Halcyon venerata*, was the only inland native bird which was seen to interact with the Myna, and several definite aggressive interactions

were observed between them. In one instance, at marae Tetiiroa, a kingfisher was observed diving at and calling harshly to a Myna at the forest edge near the parking lot. It dove twice at the Myna and then disappeared into the treetops behind it. The Myna flew off and disappeared into the forest edge on the other side of the parking lot. On a different day, at this same location, two mynas were seen to land in the treetops near a group of at least three kingfishers. One of the kingfishers immediately took flight and aggressively pursued the Mynas overhead, chasing them out of the area before returning to the others.

In Opunohu Valley, an event similar to the ones described above may have taken place at the edge of the riparian forest in which a kingfisher pair had been observed to reside. A bird swooped at a Myna in the cow pasture and

there was some squawking, but it was dusk and thus the aggressor was difficult to identify.

Indirect interactions between the Myna and kingfisher can only be postulated, but a myna pair was observed emerging from a nest of cavities in a softwood tree along the coast. These cavities much resembled a similar series of nest-like holes in a tree in the riparian forest of Opunohu , nearby known kingfisher territory.

Discussion

General Foraging Behaviour.

Mynas showed a distinct preference for human-modified foraging habitats. Of the habitats recorded, only the forest treetops, marsh, and shoreline could be considered natural. The grass lawns, dumps, pastureland, domestic animal feedings, roadside, hotels/restaurants, and forest edge all exemplified habitat that had been either altered or completely created by human disturbance of some kind. The largest flocks of mynas were observed in the cow pastures when cows were present, or on grassy lawns just after having been mowed. Thus the mynas were taking advantage of a human-introduced disturbance which maximized their foraging ability. In one case it was the disturbance of cattle walking and grazing, in the other it was the lawnmower shortening the grass and disrupting the insect population below.

It is this acute perception for favorable foraging disturbances that makes the myna potentially valuable to the agroecosystem. In India, it has been commonly observed that mynas follow behind ploughs as fields are ploughed, picking up the grubs exposed. Experiments conducted found that the birds reduced the pest grub population significantly, so that the plant stand of second crop raised in bird exposed field was higher in the experimental plot compared to the control (Parasharya et al. 1994; Shah and Garg 1988) In keeping with this, Mynas were observed feeding nearby as a plough was operating in a field in Opunohu valley. And at one point during a sampling session

at Suburbia, the noise of the lawnmower being turned on in the next lot immediately drew a flock of ten or fifteen birds from several lots away. They waited in the surrounding area and then moved in to feed when the lawnmowers were done. A similar event took place on a private lawn near a house.

The lawn itself is the staple foraging habitat of the myna on Moorea. Even if not recently mowed, the lawn represents a habitat that would not be possible without the human technology of lawnmowers. In a place as lush and humid as the tropical Pacific, the rapid growth rate of greenery would not allow a "natural" lawn to persist. As ground-feeders whose principal diet consists of insects, the myna on Moorea benefits greatly from man and his lawn.

Obviously, the lack of such human-modified habitats prior to human development meant that native birds did not evolve to forage in such conditions. They were specialized for feeding in natural, undisturbed forested environments, on the shore, or at sea. During these studies, only two situations in which native birds had seemingly adapted to use human-modified habitats were observed. There was a Great Frigatebird, Fregata minor, which would receive fish from a trainer at the dolphin tank of a resort. And there were plovers, Pluvialis fulva, which sometimes fed on some of the same grassy lawns that mynas used. All the other birds that utilized similar human-modified habitat and food resources were introduced. Such birds included the Zebra Dove (*Geopelia strata*), the Red-vented Bulbul (*Pycnonotus cafer*), the Grey-backed White-eye (*Zosterops lateralis*), the Red-browed Waxbill (*Aegintha temporalis*), the Common Waxbill (*Estrilda astrild*), the Chestnut-breasted Mannikin (*Lonchura castaneothorax*), and the Jungle Fowl (*Gallus gallus*).

All of these species introduced to Moorea seem to be quite successful, but none has as wide a range of foraging habitats as the myna. One possible exception is the Jungle Fowl which was introduced centuries ago by the early Polynesians and now roams wild throughout Moorea. But even it does

not dominate as much as the myna does. Since all of the currently successful and prevalent landbirds were introduced, it is clear that human development created new niches to which native birds were unsuited. They were mostly forced to retreat with the retreating forest, and introduced birds filled in the new empty niches. The generalist myna, with its wide range of foraging habits, and plastic ability to adapt itself to new and disturbed foraging habitats, was able to fill more of these empty niches than most of the other introduced birds. Thus the reason for its current dominance.

Relative Myna Utilization of Lawns at Differing Urban Disturbance Levels

Because of the lawn's value to the myna as its staple foraging habitat, it seemed a good site choice for comparison in this study. An added benefit was the ease with which the myna could be observed foraging in grass. Furthermore, the lawns were comparable enough in all their relevant aspects that any difference in foraging myna abundance could be attributed to the differing urban disturbance levels of the surrounding areas in general. Though the site in Pao Pao had more trees just outside the edge of the plot, these trees were species that mynas used only for perching between foraging bouts or as stopovers while flying. Mynas at the Suburbia site would use fences and houses for similar purposes. The only relevant tree to the myna was the coconut palm, because mynas often nested and roosted in these. At Pao Pao, there was a pair of mynas nesting in the palm tree just behind my observation point (see Figure 3), but it was far enough that territorial aggression within my plot did not occur often. The average size of territory that the myna actively defends against intrusion has been found in a study by Sengupta (1982) to be 117 square meters. Neither of the study plots had palm trees or buildings close enough such that myna breeding territory overlapped with the plots.

The plots did differ in the amount of traffic passing on the bordering roads. Traffic in Pao Pao was consistently about twice as high as at Suburbia (Figure 4).

Furthermore, there was often traffic by dogs and people passing directly through the Pao Pao plot, though this rarely happened at the Suburbia plot. The Pao Pao site, with its two intersecting busy roads, had high amounts of traffic on two sides of the plot. In Suburbia, however, though traffic counts included and mostly consisted of the traffic on the circum-island road that ran above and behind the plot, it was far enough above and out of sight that its traffic didn't seem to be a significant factor in site characterization. Thus the difference in traffic level between the two sites would be much more disparate than the graphical depiction suggests. There was no direct correlation between traffic and mynas observed. The mynas at the Suburbia site did not encounter much traffic at all, and thus had little opportunity to react to it. In contrast, the mynas at Pao Pao were accustomed to traffic, and thus were not phased by it.

Perhaps the most important difference between the plots was the diversity of habitat in their surrounding areas. Pao Pao had several types of human-modified habitat in the general vicinity of the plot, and the transects were run to include a representation of these sites. Places where I often observed mynas foraging were not only on the soccer field, private lawns, and other open public lawns such as the study plot, but also with some domestic pigs, at two snack shops, in store parking lots, at two dumps, and in the road. At the Suburbia site, there were only two main foraging habitats: the private and public grassy lawns, and the road.

Examining the data for relative density between the two sites, there is a significantly higher density of mynas in the Suburbia area for the greater part of the time sampled. I would argue that this is a result of the amount of lawn space available in each area surveyed. There was roughly twice as much lawn space per hectare in the Suburbia area compared to at Pao Pao. Since grassy lawns were the myna's staple foraging habitat, it makes sense that the more lawn space in an area, the more mynas that can be supported by the food resources provided in the grass. Therefore, mynas seem to prefer suburban

areas where there is plenty of cleared grassy land to feed on, and human homes to nest on, but not as much interfering traffic.

Interestingly, the slopes of the lines for each site (see Figure 6) almost parallel each other for all but the segments between 8:00 am and 11:00 am, showing a significant activity pattern of the myna. The unparallel stretch between 8:00 am and 11:00 am seems to result from the lower density of mynas in Suburbia during the morning from 6:00 am to 8:00 am. As they return to the area, the lines parallel each other closely and remain quite constant in their relative separation.

These graphical results are consistent with observations noted. During the morning sampling sessions, many birds were seen flying through and out of the Suburbia area, leading me to believe that they spend their mornings foraging in other habitats. By the end of the day, however, the birds have returned to their home nesting or roosting area. Therefore, the 6:00 pm density values are probably closer to the number of birds that actually live in the general area. The peaks at 4:00 pm perhaps result from other mynas from neighboring areas (perhaps nearby homes) flying into the areas to utilize its food resources, although it could just be that the birds are more active and thus more visible at this time. This latter explanation may be more supported since the ratio of bird densities at Suburbia compared to Pao Pao from 11:00 am to 6:00 pm retains a value comparable to 5/3. Such an even parallel trend between the two sites indicates more strongly a general myna activity pattern, rather than a daily influx of other birds, since its unlikely so similar a number of birds would commute to both areas.

The graph for myna utilization of the study lawns (Figure 5) shows that in Pao Pao, the lawn use peaked during the morning session, but not drastically, and so overall there was little fluctuation in the amount of myna lawn use throughout the day. In Suburbia, however, there was a definite increasing trend in myna lawn use as the day went on. In the morning, even though myna density in the Suburbia area was still slightly higher than that in Pao Pao, the lawn use at Suburbia was very low,

much lower than in Pao Pao. This also is supported by observations that the Suburbia birds were traveling to other foraging habitats during those morning hours. They then seemed to return in mid-afternoon and when their activity levels peaked at 4:00 pm, so did their foraging on the lawn plots. In Pao Pao, I think that the reason for such little variation in lawn use throughout the day probably stems from the diversity of foraging habitats in the general area. The myna can easily fly between the dump and the snack shop and the lawn, etc. at any time of day. Thus, it does not need to travel out of the area to forage and can instead divide its time evenly at the different foraging habitats throughout the day. Lawn use is lower at Pao Pao in general because of this convienent availability of other food resources in such close proximity.

Predator Vigilance

Lima wrote (1995) that a negative relationship between group size and levels of individual vigilance is widespread in socially feeding vertebrates. The main explanation of this 'group-size effect', the many-eyes hypothesis, is based on the simple premise that as group size increases, there are progressively more eyes scanning the environment for predators. Thus an individual forager can devote less time to vigilance (and more time to feeding) without any lessening of the group's ability to detect an attack. And individual foragers can spend more time feeding and less time scanning the environment for predators without any increase in their personal risk of being preyed upon.

Interestingly, the results of the predator vigilance survey showed no correlation in myna flock size and time spent non-vigilant. What would have been expected for most socially feeding animals, is a positive correlation between the flock size and time spent non-vigilant while foraging (equivocal to a negative correlation between flock size and time spent vigilant while foraging.) The more birds present, the more likely the Myna to forage a larger percent of its time with its head down rather than scanning the environment for predators. The results of

the myna data seem to stem from the lack of predators on Moorea. Except for some cats, dogs, and marsh hawks, *Circus cyaneus*, which seem to pose little threat to the myna, the island is predator-free.

A study done on a population of silvereyes, *Zosterops lateralis chlorocephala*, on Heron Island in the Great Barrier Reef showed there was no relationship between scanning behaviour and group size. Two possible explanations for the lack of correlation were that when predators are absent there is no advantage to adjusting scanning rates according to group size (predators were absent from Heron Island), or that silvereyes were partitioning their scanning behaviour between vigilance for conspecifics and vigilance for predators. In the latter case, the form of the vigilance/group size relationship becomes more difficult to predict (Catterall et al. 1992).

When the resulting data for Myna predator vigilance were split between the two sites, it was even more interesting to note the significant negative trend in the Pao Pao data. In the midst of town, Mynas were spending less rather than more time with their head down as flock size went up, as if they were spending more time monitoring their conspecifics. This is supported by observations of antagonistic interactions as flock size went up. In an area where there was less lawn space to go around, the Mynas seemed to be competing more for its resources. Even in the busier town area, where dogs were quite prevalent and on the loose, Mynas felt secure and comfortable enough in their environment to dispense of the practice of predator vigilance. Though Suburbia still showed no significant correlation, it was definitely noted that as flock size went up, particularly toward the end of the day, there was much more social interacting going on and less concentrated feeding. The interactions included not only aggressive behaviour but courtship exchanges as well.

Interactions With Native Birds

The minimal interactions observed between native birds and the myna can be explained by the lack of habitat overlap between native and introduced species. As mentioned earlier, introduced species fill the human-modified habitats while native species tend to remain more at sea, on shore, or in natural forested areas. Since the myna spends the majority of its time in human-disturbed habitats, its interaction with seabirds, shorebirds, and forest birds is relatively rare. However, it has long been suspected that it may exert pressure on the native forest bird species.

As documented for Hawaii, East Polynesia, New Zealand, and elsewhere, the spread of people across the Pacific was accompanied by massive losses of species and populations of birds. Forest clearing and agriculture began when humans first arrived and intensified with time. As a result, most surviving populations of forest birds are small, isolated, and perhaps sensitive to even minimal disturbance (Franklin and Steadman 1991). When a bird as aggressive and generalist as the myna comes into contact with such vulnerable species, there is likely to be some effect on the more sensitive native birds.

Studies done on the Tanga'eo kingfisher (*Halcyon tuta ruficollaris*) on Mangaia, the southernmost island in the Cook Islands group, showed similar interactions with the Common Myna as those observed on Moorea. Rowe and Empson wrote (1996a) that the presence of Mynas in modified and small forest tracts may be a significant factor in limiting Tanga'eo abundance in these areas, since Mynas competed with Tanga'eo for food (lizards and invertebrates such as stick insects, cockroaches, caterpillars and spiders) and were observed to harass breeding Tanga'eo and cause nest failure. Both sexes of kingfisher were seen to chase off intruders such as Common Mynas from the vicinity of the nest tree (Rowe and Empson 1996b). The chases witnessed between Tahitian kingfishers and Mynas were thus probably territorial aggression of kingfishers and protection of either their nest sites or their young. Of course, the aggression could simply stem from competition, since its quite possible that the birds' diets overlap in a similar fashion to that observed on Mangaia.

Furthermore, Rowe and Empson (1996b) described kingfisher nest sites as holes excavated in tree trunks. Three or four holes in a single tree-trunk were common. These descriptions exactly fit the two multi-holed trees observed in this study. Also consistent with the observation of a Myna flying out of one of these types of holes , is the fact that they also saw Mynas investigating two nesting holes in their survey area. Since multi-holed trees may indicate a strong attachment to a nest site, especially since there were usually several apparently suitable nesting trees in each territory, it seems significant that such a tree was seen being either investigated or inhabited by a Myna. For whatever reason, it would seem that kingfishers are abandoning some of their preferred nesting sites, and as their habitat shrinks in area, the Myna is filling in rapidly. It seems quite possible that the Myna could be steadily driving the sensitive kingfisher back into the interior of Moorea. Unfortunately, the kingfisher lives mostly in lowland secondary forests, and is absent from higher altitude forests (Thibault and Rives 1988). As the interior of Moorea consists of high peaks, the Tahitian Kingfisher does not have far to retreat before it faces another boundary to its range.

Conclusions

The Common Myna utilizes a huge range of food resources. On any given observation day of the bird, it seemed as if a new food item could be recorded. Such a plasticity of foraging habits no doubt plays a huge role in the apparent success of this introduced bird. On an island where human development has created new and disturbed habitats, the myna has been able to find plenty of unique food resources around which to build its omnivorous diet, and has especially taken advantage of disturbances which tend to maximize its foraging ability and food availability.

The prime example of such a disturbance that the myna capitalizes upon for its own benefit is the cleared grass lawn. Without the human disturbance of lawnmowers, these lawns would not even

exist, let alone persist. However, the Myna uses these grassy areas as its staple foraging habitat. They seem to prefer suburban levels of disturbance, and thus a higher density of birds is observed in suburban areas vs. more urban towns. The ideal situation for the Common Myna nesting pair seems to be a nest in a coconut palm or under the rooftop of a house, with a nearby residential lawn in which to forage regularly. Almost every house observed on Moorea had a myna pair nesting somewhere nearby and foraging on the lawn. At the research dormitory, there was actually a pair on either corner of the dorm, and thus one pair focused on the front lawn and one on the back lawn. It is no wonder the Myna does so well on Moorea. It is a small island with considerable human development, almost all of which can be classified as suburban. Only a few small towns exist, the rest of the island is mostly houses and their lawns lining the circum-island road just along the coast. In combination with the prevalent coastal coconut palms, this ring of human-modified habitat allows the Myna to dominate all around the island.

Further evidence of the Myna's success is its apparent lack of predator vigilance while foraging. The Myna is apparently secure and comfortable enough in the predator-free environment of Moorea that it spends more time competing with conspecifics when in large flock sizes rather than using the large group as a safety buffer from predators or other dangers.

The Myna's interactions with native birds seem to show a tendency for the bird to learn to use new foraging habitats from watching other birds. The Myna forages on the shoreline alongside the Wandering Tattler and Plover and appears to forage quite similarly to them, though its shorter beak probably keeps it from foraging at the same depths as they do. Similarly, the antagonistic interactions witnessed between the Myna and the kingfisher seem to result from the Myna pushing its way into kingfisher territory. It may be watching and learning from the kingfisher. There definitely is a potential for dietary overlap between the two, as the forest floors crawl with skinks

and spiders, both of which are definitely palatable to the Myna and probably to the kingfisher since the Tanga'eo kingfisher feeds on these prey items in Mangaia (Rowe and Empson 1996b.)

The Myna on Moorea may be following in the path of its Hawaiian conspecifics. In Hawaii, Mynas were introduced forty-three years earlier than in the Society Islands. Berger describes them as long as twenty-five years ago as occurring in forested habitats up to 8.000 feet. However, Mynas in Moorea presently occur everywhere but dense forests and high altitudes (Pratt et al. 1987). Perhaps in another twenty years, the Myna on Moorea will have invaded even the island's interior mountains and forests, as did its Hawaiian relatives.

Ehrlich et al. wrote of Hawaii (1988) that the islands are a place where the process of extinction that threatens our planet's birds is already well advanced, with only the remnants of an intriguing endemic fauna hanging on, and where a constantly changing fauna of introduced species, dominated by Common Mynas, can be observed. It is the sort of monument to human disturbance of natural systems that may soon be found in North America if great care is not taken to prevent it. The future of Moorean avifauna seems to be traveling a parallel path to that of Hawaii. Unfortunately, it is hard to condemn a bird like the Common Myna. Little blame can be directed toward a bird who owes its successful spreading and establishment to human disturbance of the natural environment. Rather the blame for its dominance and any consequences thereof must fall directly on the shoulders of man and his alteration and destruction of the natural environment. After all, the Myna simply fills human-modified niches and then expands outward from there. Its resourcefulness and cleverness in adapting its behaviours to make use of a wide range of habitats are not evil traits, but instead resemble the similar characteristics of man in the macropicture of the biological world. A truly amazing bird, the Myna has chosen its allies well. Undoubtedly, it will continue to prosper so long as man does.

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Factors influencing the early life cycle of *Inocarpus fagiferus*

Sandra Trujillo
Department of Environmental Science, Policy, and Management
University of California, Berkeley 94720

ABSTRACT. The seed dispersal, seed germination, and seed predation of *Inocarpus fagiferus* (Fabaceae) was examined in the Opunohu Valley of Moorea, French Polynesia. To test the probability of natural seed dispersal to the island, seeds were submerged for long periods of time in saltwater and freshwater. Overland flow and stream dispersal were tested as possible dispersal mechanisms. The effect of seed and seedling density, distance to stream, slope, and canopy cover on percent germination and percent predation was tested. Seed predators were also identified. Seeds have a low probability of surviving when submerged in saltwater and freshwater for extended periods of time, indicating that *Inocarpus fagiferus* may have been introduced to Moorea. Heavy rains are required for appreciable seed dispersal by overland flow and high elevation stream dispersal. The probability of germination is low in the Opunohu Valley because seed predation is a major component of seed mortality. While moth larvae are the most prolific predators of *Inocarpus* seeds, rodents are the most destructive to seeds. Although predation pressures are high, recruitment is occurring under dense adult canopy cover.

Introduction

The life cycle of a plant may be described as the continuum from seed, released from the parent plant, to adult, capable of passing on its genetic information. Changes in the number of individuals occur at each step of the life cycle: from seeds to seedlings to juveniles to adults (Solbrig 1979). The early life cycle of a plant is subject to the highest mortality in the life of a plant (Howe et. al. 1982). Janzen (1970) proposed that only seeds that are dispersed away from the parent tree have any significant chance of escaping discovery by seed predators and germinating. On the other hand, Harper postulated that the number of seeds that germinate is determined of the number of "safe-sites" that are available, whether it be under the parent tree or at a distance. A safe-site is a microhabitat that provides suitable environmental conditions for germination and establishment. It has become increasingly apparent that seed characteristics are major determinants of the success of plant populations (Solbrig 1979). However the experimental and quantitative data on the characteristics of seeds of island flora are sparse(Louda et al 1985)

Island flora is distinctly characterized by the manner in which the plant initially colonized the island. Plants found on islands reflect the plant's ability to produce propagules that disperse over long distances. If the plant was not naturally introduced to the island then the plant's role in human life becomes an important factor in understanding insular plant dynamics. Habitat interactions are constrained on islands by the few pollinators, animal dispersers, and predators that occupy the island (Carlquist 1974). Insular species interactions are also determined by the element of time, particularly recently introduced species. Therefore, the species specific relationships that are typical of continental systems may not be present in island communities (Janzen, 1971).

Inocarpus fagiferus (Parkinson) Fosberg is a leguminous tree that is distributed from the East Indies to as far east as the Southern Society Islands (Brown 1935; Hermann 1974). It is known as the Tahitian chestnut or *mape* to Tahitians. There is debate as to whether the tree was naturally dispersed to the high island of Moorea in the Society Island chain or whether it is the product of human introduction. On Moorea, it primarily occupies riparian areas but, throughout the Pacific, it can be found growing within the coastal strand community (Ridley 1930). *Inocarpus fagiferus* flowers and fruits during October and November. The pollinator of the small white fragrant flowers is unknown. The large single seeded fruit require one year for development. When a seed falls to the ground, it becomes part of a seed crop that consists of seeds from the past two years of seed production. Seeds germinate above ground. During the first two years of growth, the seed pod remains attached

at the base of the seedling until it decomposes. *Inocarpus fagiferus* is a sacred tree to Tahitians and is often found in association with a ceremonial site known as a Marae. The roasted seeds of the Tahitian chestnut are popular food items among Tahitians (Kirch 1989).

The objectives of this study were to investigate: 1) seed dispersal; 2)seed germination; and 3)seed predation of *Inocarpus fagiferus*. To illustrate the plausibility of Inocarpus being native to Moorea, the effect of water dispersal on the viability of seeds was examined. The mechanism of water dispersal on the island by overland flow and streams was also investigated. I evaluated the effect of different environmental variables on the probability that a seed will germinate. Finally, seed predation was explored as an important factor in seed mortality.

Materials and Methods

Site description

The study was performed on Moorea, French Polynesia (149°50'W,17°32'S) during the months of October and November 1996. Moorea experiences two distinct seasons: a wet season from November to March and a dry season from April to October.

Five 50 m x 20 m sites were established along an elevational gradient in the Opunohu Valley (Figure 1). Sites were chosen within riparian areas along the east fork of the Opunohu River. There were three criteria used in site selection: 1)Accessibility from the road was important; 2)The site's canopy had to be dominated by *Inocarpus fagiferus*; 3) The site had to be large enough to enclose a 1000m^2 area.

The low elevation site, at 20 m above sea level, is the flattest site, with average slope of approximately 4°. The east fork of the Opunohu River runs through the site and periodically floods the banks. The site is surrounded by *Hibiscus* and is encroached upon by agricultural activities.

The middle elevation site, at 110 m above sea level, borders the west fork of the Opunohu. The river cuts deep in the banks of the predominately *Inocarpus* forest. The slope varies from 6°near the stream to 30° as one moves towards the borders of the stand.

The high elevation site, at 240 m above sea level, borders the very narrow east fork of the Opunohu, near its headwaters. The site slopes uniformly towards the stream at an approximate average of 15°. Overland flow may be influential at this site during heavy rains. The borders of the site are influenced by *Hibiscus*.

The Marae site, near the Marae Tetiroa, is at 120 m above sea level. The mape trees at this site were probably planted by Polynesians, as it is a sacred site. On each side of the river, the slope quickly rises at an average of 15°.

The *Partula* site, at 230m above sea level, is located near the *Partula* exclosure. The site lies within a large *Inocarpus* forest that is affected by overland flow during heavy rains. This is the only site chosen where *Inocarpus* is still prevalent at 35m from the stream. The topography is similar to the Marae site.

Seed dispersal: Seed Viability

The ability for seeds to withstand submersion in saltwater and freshwater was tested by two methods: 1)To test the likelihood of dispersal to the island by saltwater, ten one year old minimally damaged fruits were submersed in an outdoor, unsheltered, saltwater tank for 53 days. 2)To compare the effect of saltwater and freshwater dispersal on seed viability, ten one year old, minimally damaged fruits were placed in an outdoor, sheltered freshwater tank and an outdoor, sheltered, saltwater tank for 24 days. As a control, ten one year old minimally damaged fruits were placed in the same outdoor shelter for 24 days but no water treatment was applied. After the submersion period, fruits were examined for level of fruit decay, permeability of seed coat, and hardness of seed. Those seeds that did not have hard, intact seeds were classified as incapable of germinating or unviable.

Seed Dispersal: Overland flow dispersal

To test distance fruits travel as a result of the forces of overland water flow, fifteen marked fruits were placed at 5 m and 10 m from the stream at the high elevation site and at the low elevation site. The slope where the fruits were placed was recorded for each site. After
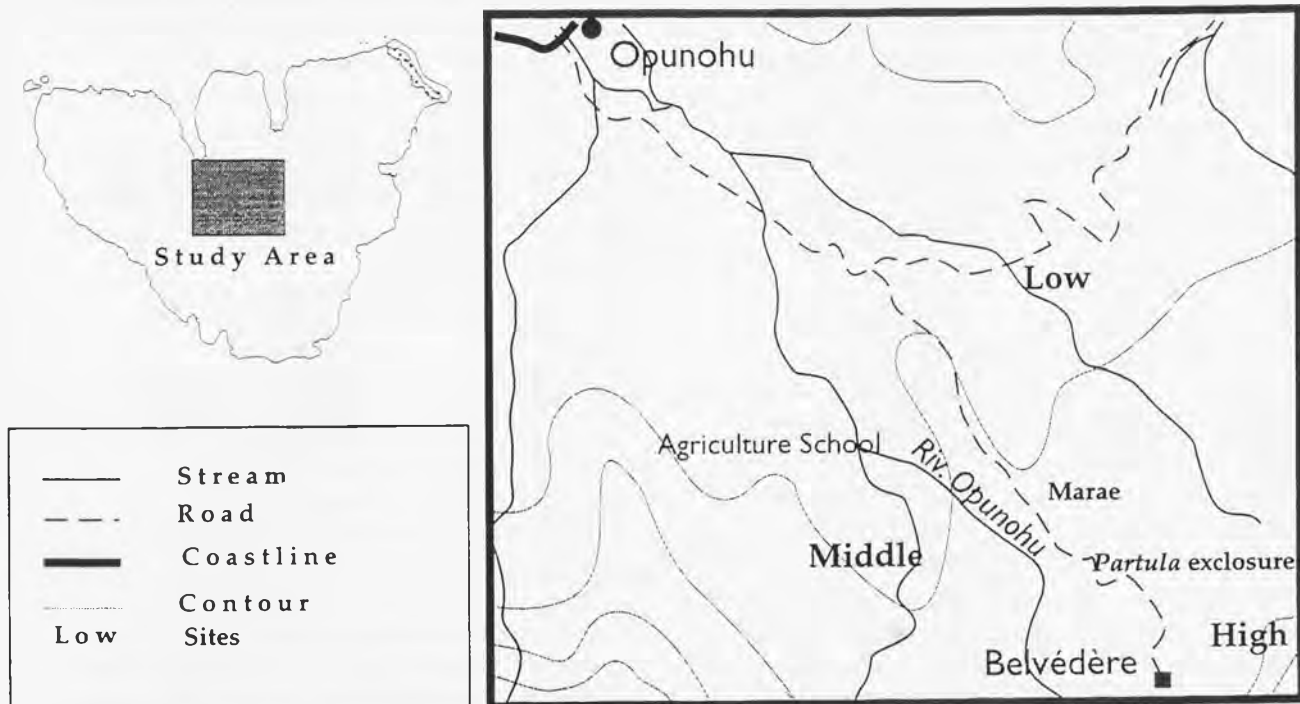
ten days, in which it rained three days, I measured the distance fruits moved from the origin.

Seed Dispersal: Stream Dispersal

To test the distance fruits travel downstream, thirty marked seeds were released in the east fork of the Opunohu river at high elevation, near the Marae Tetiroa, and at the low elevation site. Ten days after release, during which it moderately rained 3 days, distance traveled from release origin was measured for the first 15 seeds found. After the fifteenth seed was found, I measured the distance from release origin for all seed found within the following 150 m.

Seed germination

To determine what environmental factors affect germination, I examined the number of seeds that germinated of all seeds found within sixty 2 m x 2 m plots. Fifteen 4 m² plots were randomly placed at the high, medium, and low elevation sites. Randomness was executed using numbers from a random

number table as coordinates, to be used in locating plots within a 50 m x 20 m grid established at each site. At the 120 m site, nine 4 m² plots were established between 0 and 10 m from the stream. At the 230 m site, six 4 m² plots were established between 25 and 35 m from the stream. Seeds were classified into three categories: germinated, unviable, and viable. Seeds were classified as unviable if the seed had been damaged or destroyed by predators. If the seed had not germinated and the seed coat and seed were hard and intact, then the seed was classified as viable, although predators may have slightly damaged the fruit. Seedlings with seeds still attached at stem base were also tallied within the plot. Heights of seedlings were measured. Percent germination was calculated as number of germinated seeds and seedlings divided by total number of seeds and seedlings. Percent predation was calculated as number of unviable seeds divided by total number of seeds and seedlings. Percent germination and percent predation is reported on a per meter squared basis and reflects percentages for the seed crop of the past two

years. At each plot, I measured three microsite variables: 1)distance to the stream; 2)percent canopy cover, using a spherical densiometer; 3)slope, using a Silva compass. A regression analysis was used to relate percent germination to seedling height, distance to water, percent cover, slope, and percent predation. Seed and seedling density were also compared to percent germination, distance to water, percent cover, slope, and percent predation using a regression analysis. A one-way ANOVA was used to compare percent germination and percent predation between low, medium, and high elevation sites.

Demographic structure

To establish whether the demographic structure of the low, medium, and high elevation sites was similar, I measured height, using a clinometer, and diameter at breast height (dbh) for every tree greater than 3 m tall. For trees less than 3 m tall but greater than 1.5 m tall, I measured height. In five 5 m x 5 m plots that were randomly placed within the sites, using the method described above, height was measured for all trees under 1.5 m tall. A one-way ANOVA was used to compare the height and diameter of trees between sites. A regression analysis was used to relate height and dbh of total trees measured.

Seed Predation

Seed predation was evaluated using 30 fruit randomly collected from the middle elevation site. All macro-organisms on and within the fruit were identified. Any indicators of predation, such as moth larvae bore holes and rat gnaw marks, was also noted. Viability of seed was identified using the classification described in *Seed Germination* methods.

Pre-dispersal seed predation was observed using 30 fruit knocked down from trees. Indication of predator damage was noted for each fruit.

Voucher specimens

Voucher specimens of seed and seedling are located in the University of California at Berkeley Herbarium.

Results

Seed dispersal: Seed Viability

Of 10 seeds submerged in saltwater, none of the seeds were viable. The freshwater treatment was the least damaging to seeds, followed by the control treatment (Figure 2). Although control seeds were not damaged by water, predator attack damaged 6 of the 10 seeds while two seeds had withered.

Figure 2 Percentage of viable seeds after 24 day submergence in saltwater, freshwater, and no water treatment (control).
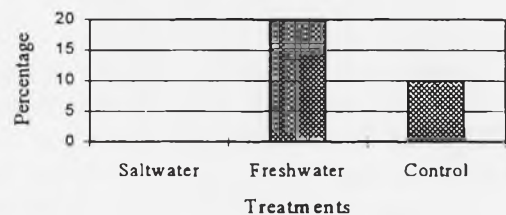
There was minimal movement of fruits by overland flow (Figure 3). At the high elevation site, one fruit of 15 moved. From the 5 m origin, three fruit of 15 moved . However, at the low elevation site, fruit did not move from the 10 m origin. From the 5m origin at the low site, three fruit moved. Of the three that moved, one fruit that moved 30 cm seemed to have been disturbed by forces other than overland flow, such as a pig. The area around this fruit had been completely cleared of the leaf litter that I had placed the fruit upon. One fruit moved backward 10 cm from the 5 m origin. There was no indication of flooding at the low elevation site.

Figure 3 Fruits that moved during the overland flow experiment at high and low elevation sites.
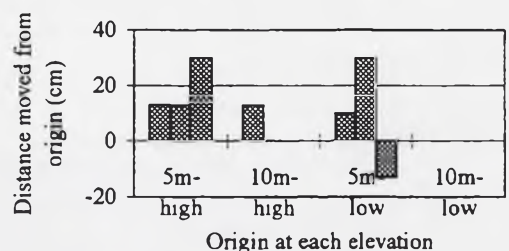
Fruit moved further downstream at low elevation than at middle elevation. Fruit traveled from 17 m to 235 m downstream at low elevation while fruit traveled from 0 to 12 m at middle elevation (Figure 4). The stage of the stream was higher after the 10 day period at low elevation than at middle elevation. Fruits were found in riffles, behind woody debris dams, in side pools, and sunken in pools.

Figure 4 Distance traveled downstream by fruits found after release at middle and low elevation streams.

Distance traveled downstream (m)
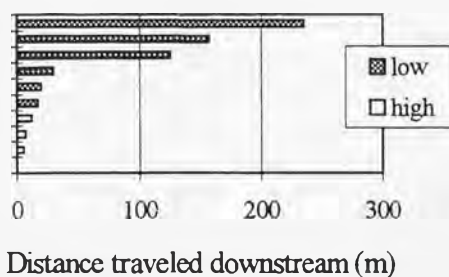
Seed Germination

Percent germination was not significantly correlated to seedling height, slope, or seedling density. Percent canopy cover was homogenous at all sites; Percent canopy cover ranged from 70 to 95% cover (Figure 5).

Figure 5 Percent canopy cover as related to percent germination ($n=60, p>.05, r^2<.1$).
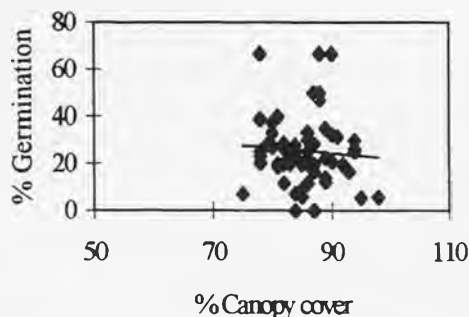
%Canopy cover

Percent canopy cover was not significantly correlated to percent germination. Percent germination was significantly correlated to distance to stream ($n=60$, $p<.05$, $r^2<.1$; Figure 6). Percent germination was most

significantly correlated to percent predation ($n=60$, $p<.05$, $r^2>.5$; Figure 7).

Figure 6 Distance to stream (m) as related to percent germination ($n=60$, $p<.05$, $r^2<.1$).

Distance to stream (m)
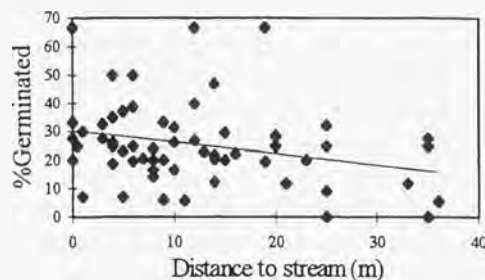
Figure 7 Percent predation as related to percent germination ($n=60$, $p<.05$, $r^2>.5$).
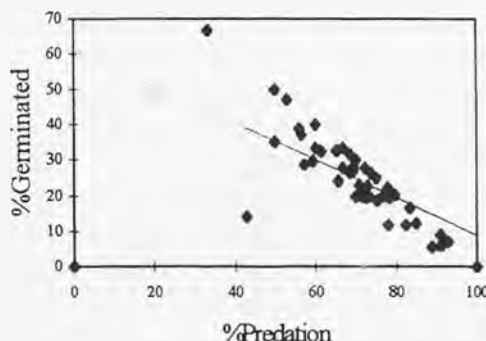
%Predation

While seedling density was not correlated to any microsite variables, seedling density was correlated to percent predation ($n=60$, $p<.05$, $r^2<.5$). As seed density increases, the number of viable seeds per meter squared also increases ($n=60$, $p<.05, r^2>.3$). However, the relationship between seed density and unviable seeds is a much stronger positive relationship ($n=60$, $p<.05$, $r^2>.9$).

Elevation did not influence percent predation and percent germination; there was no difference in percent predation or percent germination between sites.

Demographic structure

Height and diameter were positively correlated at each site (high: $n=81$, $p<.001$, $r^2>.5$; medium: $n=50$, $p<.001$, $r^2>.5$; low: $n=56$, $p<.001$, $r^2>.5$) and for combined data

$(n = 188, \ p < .001, \ r^2 = .56)$. There was no significant difference in tree heights or diameters between sites. The general demographic trend was for there to be a greater number of smaller trees and less larger trees (Figure 8).

Figure 8 Diameter distribution of trees greater than 3m tall at low, middle, and high elevations.
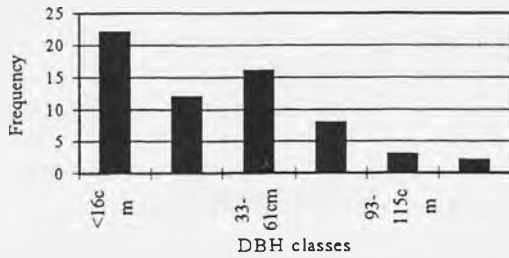
Seed predation

While there were 9 different predators that were found in association with fruit, only moth larvae and rodents were effective seed consumers (Figure 9). Although moth larvae were the most prevalent predators, rodents were the most destructive to seeds (Figure 10). Of 30 fruit knocked from tree branches, 24 of the fruit had been damaged by moth larvae and fungi.

Figure 9 Macroorganisms found in association with 30 *Inocarpus fagiferus* fruit.

Organisms
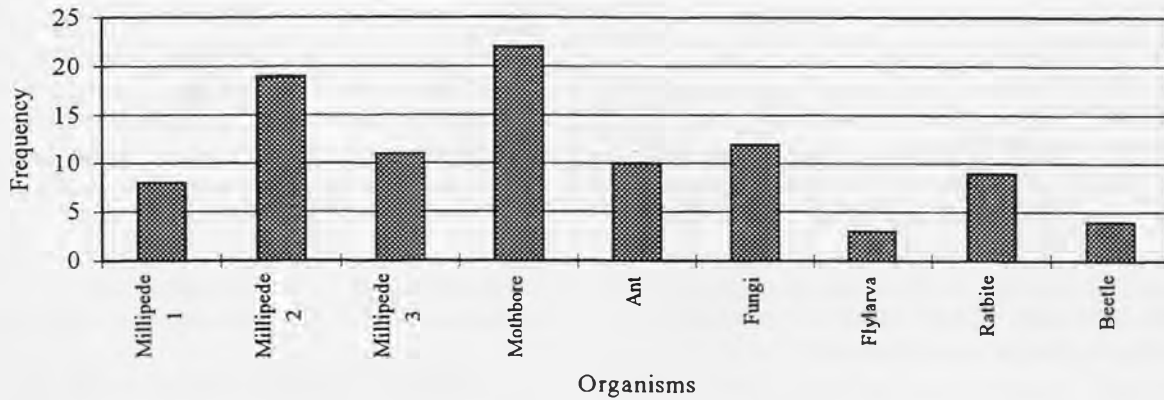
Figure 10 The effect of moth larvae and rodent predation on the viability of seeds.

Seed type
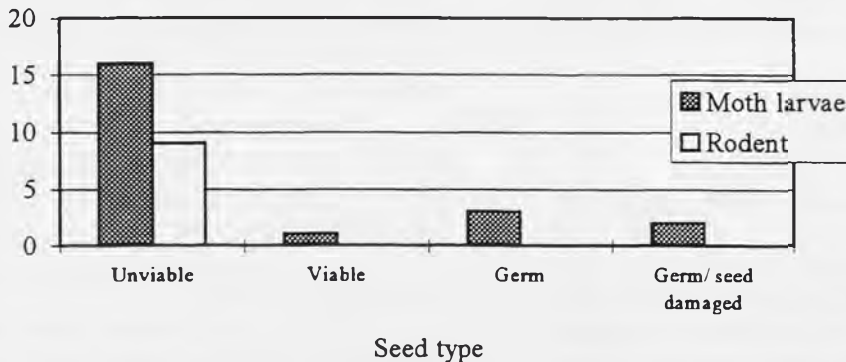
Discussion

Seed dispersal to the island

Whether *Inocarpus fagiferus* was naturally dispersed to Moorea by ocean currents or if it was introduced by Polynesians is important to the understanding of insular plant dynamics of the species. Although Ridley (1930) claimed that *Inocarpus* was naturally dispersed on account of its buoyant seeds, Guppy (1906) and Kirch (1989) reported conflicting evidence. Guppy found that although the seeds were buoyant, saltwater penetrated the seed coat and damaged the seed in all seeds that he found floating in the ocean. My results supports this argument. The cultural uses of the plant also lead Guppy to believe that Polynesians would have traveled with the seeds and introduced the species wherever they colonized. This line of argument was further supported by Kirch's archeological findings of the Lapita people, during second millennium BP, planting monocultures of the species throughout Oceania.

Seed dispersal on the island

Dispersal allows for the species to colonize new areas at a distance from the parent (Harper, 1977). At a distance from the parent, intraspecific competition is lower and the seed is isolated from predators that are attracted to the high density of seeds under the parent tree(Janzen, 1970). With greater seed density in Inocarpus stands, there was an increase in predated seeds. Thus, dispersal away from high seed density should increase seed survival. However, dispersal itself may decrease the longevity of seed life because water is damaging the seeds in the majority of cases (Figure 2; Guppy 1912). It is only for the small percentage of seeds transported without seed damage that dispersal is increasing the probability of survival.

In the Opunohu Valley, heavy and consistent rains are needed to disperse the seeds, particularly in upper elevation streams (Figure 4). If the seed does not land in the stream, then the seed must wait for heavy rains for overland flow and flooding to occur. Flooding and overland flow of great magnitude would have the most likely chance of occurring during the peak of the rainy season when the stream stage is high and the soil is saturated. The beginning of the rainy season is concurrent with the final

stages of fruit fall in October and November when there would be the greatest number of fruit on the ground. The synchronization of fruit fall with flooding may be important in the establishment of *Inocarpus fagiferus* in new habitats (Kubitzki et al. 1994).

Seed germination

If the seed survives dispersal, the seed then must defy the low probability of reaching a safe-site where germination is possible. There are several environmental variables that are related to low percent germination. There is a lower probability of germination for seeds that are further from the stream (Figure 6). Moisture may be a microsite variable regulating germination. However, percent germination is being affected by other factors, such as, most significantly, seed predators. While Boucher (1981) found that high seed density was associated to a higher probability of germination because seed predators were satiated, this is not occurring in *Inocarpus* forests in the Opunohu Valley. Although there is a greater number of viable seeds with a higher seed densities, there is also a more significant positive correlation between seed density and number of unviable, predated seeds. For predator satiation to occur, the predator must be host specific, which is a trait unusual in island communities (Janzen 1971). Janzen claims that it is not only release from competition that produces pure stands of a single species on islands but it is also the release from host specific seed predators.

Demographic structure

Lepofsky et al (1996) uncovered archeological evidence in the Opunohu Valley, suggesting that Polynesians cleared primary forest to develop *Inocarpus fagiferus* arboriculture during the late Holocene. Their conclusions are important in explaining stand history and structure. The arboriculture of *Inocarpus fagiferus* would affect the structure of the forest by creating dense stands in the Opunohu Valley of even aged structure. The fact that relict stands were arboricultures may also explain why stands predominately appear in riparian areas. Riparian areas are suited to agricultural activities because of natural irrigation and the flat topography as compared to the dominating ridges of the island.

Although dispersal allows seeds to move away from intraspecific competition,

intraspecific competition within stands may not be regulating seed mortality and establishment. Seeds are successfully regenerating under a closed canopy of *Inocarpus fagiferus* (Figure 5). The demographic structure (Figure 8) of stands in the Opunohu valley follows an inverse J-shaped curve that is typical for a stand that is experiencing recruitment (Daniels 1979). If the stands studied were located in areas of relict stands, the historical even aged structure has progressed to an uneven aged structure.

Although dispersal is necessary for the species to colonize new habitats, dispersal is not essential for the species to continue to exist in the Opunohu Valley. *Inocarpus fagiferus* was introduced to Moorea where there are few dispersal agents because of the large fruit size (Carlquist 1965). On other islands, land crabs and bats have been observed to act as dispersers (Andrews 1900). Where there are other dispersal agents that do not drastically damage the seeds or where seeds are smaller, dispersal would be more important in seed survival and stand establishment in new habitats.

Seed predation

The primary predators of *Inocarpus* fruit in the Opunohu Valley are moth larvae and rodents. Moth larvae attack fruit before and after dispersal. After moth larvae bore into the fruit and emerge, secondary predators, such as ants, fly larvae, and millipedes, use the bore holes as access to the fruit and consume the frass produced by the moth larvae (Figure 9). Although in the majority of cases, moth larvae do consume the entire seed, the instance of moth larvae attack does not necessarily lead to inviability of seeds (Figure 10). Moth larvae are not always successful at boring through the fruit to the seed. Germination is also possible with minimal damage to the seed. Unlike moth larvae, when rodents attack the fruit, the entire

seed is also consumed in every case observed. Although the rat is not as frequent a predator of fruit as moth larvae, the rodent is more destructive to the probability of germination. When seed predators are introduced to islands, they may take a heavy toll on the seed crop (Clark et al 1981; DeSteven 1984). The seed predator is also released from its own predation pressures (Terborgh et al 1980). While *Inocarpus* stands in the Opunohu Valley are capable of successfully regenerating under the current predation pressures of rodents, it is possible that increasing rodent populations could negatively affect early recruitment of *Inocarpus fagiferus*.

In conclusion, seeds have a low probability of surviving when submerged in saltwater and freshwater for extended periods of time. While this leads me to believe that *Inocarpus fagiferus* is introduced, it also offsets the importance of seed dispersal as a way to release the seed from intraspecific competition and seed predation. Predation is a major determinant of seed mortality. However, predation is not to the extreme level where recruitment is being negatively in the Opunohu Valley.

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The distribution of corticolous epiphytes on *Hibiscus tiliaceus* in the Opunohu Watershed; Moorea, French Polynesia.

Solomon Dobrowski

Department of Environmental Science Policy and Management

University of California, Berkeley 94720

ABSTRACT. A study on the distribution of corticolous epiphytes on Hibiscus tiliaceus was conducted in the Opunohu watershed in Moorea, French Polynesia. The study involved three foci. (1) The first examined patterns of epiphyte distribution, total cover, and biomass over an elevational gradient ranging from 0 to 250 m (2) The second focus was aimed at assessing patterns of epiphyte distribution, total cover, and biomass within the structure of a tree. (3) The final focus attempted to correlate ecological trends observed in the distributional studies with results from two physio-ecological studies performed: a saturation capacity test and a desiccation tolerance test. Total cover and biomass were found to increase between low and high elevation sites. An ordination analysis revealed that two distinct corticolous epiphyte synusiae occurred between high and low elevation sites. The first synusia found at low elevation sites was composed of two members of the moss genus *Calymperes* and two members of the Lejuneacea family; *Leucolejeunea* sp. and *Thysananthus* sp. The second synusia found at the high elevation sites was comprised of the moss species *Ectropothecium sodale* and a group of epiphytic ferns. The patterns observed are believed to be due in part to macro-climatic factors changing over the elevational gradient. Results from the second focus of the study showed that differences in species distribution occur between height zones. and to a lesser extent between branches of different inclination. This is likely to be caused by a gradient of micro-climatic factors and varying substrate compositions within a single tree. Results from both the saturation capacity and desiccation tolerance tests were shown to compliment ecological patterns observed in the distributional studies.

Introduction

Tropical rain forests provide a wide variety of habitats for corticolous epiphytes because of their diverse micro climate and the variety of substrates available on which to grow. Micro habitats of corticolous epiphytes are determined by amounts of direct rainfall (throughfall and stemflow), mist and dew from cloud interception, and amplitude and distribution of relative humidity. They are affected by the amount of direct or indirect light and heat radiation and by the structure and chemical composition of the substrata on which they grow. In general tropical rain forests are characterized by high temperatures and an adequate supply of water from a variety of sources. The interior of the tropical forest is high in humidity with an uneven distribution of light while near the upper surface of the canopy ,water is often deficient (Pocs, 1982; Gradstein, 1989; Richards, 1984).

Studies of corticolous epiphyte distribution along altitudinal gradients in tropical rainforests have demonstrated three major patterns: (1) An increase in bryophyte cover and richness with elevation (Gradstein, 1982; 1989: Wolf, 1993). (2) An increase in Bryophytic epiphyte biomass with elevation (Gradstein, 1989: Wolf, 1993). (3) A maximum of species richness at intermediate altitudes for vascular epiphytes (Gentry & Dodson, 1987).

Studies of corticolous epiphyte distribution on a smaller scale, within the structure of a tree have shown a number of patterns. Hosokawa (1964) and Cornelissen (1989) found that the vertical distribution of epiphytic bryophyte species and growth form was determined by light and atmospheric humidity, the lowermost occurrence of cryptogram being determined by illumination and the uppermost occurrence of canopy species limited by relative humidity. Cornelissen (1989) and Richards (1984) state that cryptogramic species distribution might also be affected by the branch inclination because of its effect on the establishment of diaspores.

Ingram and Nadkarni (1993) showed that corticolous epiphyte biomass and composition were determined by branch inclination and size and by the distribution and abundance of other epiphytic species.

Relatively little research has been done on the ecology of corticolous epiphytes in tropical rain forests of the Pacific islands. Gradstein (1979) reported on the distribution of "mossy forests" in relation to rain- carrying winds with regard to the Galapagos islands. Whittier (1967) published preliminary studies on the taxonomy, ecology, and geography of mosses of the Society Islands. This treatment contained a delineation of three ecological zones based on climate and dominant vegetation types: (1) The Maritime zone, (2) The Mesotropical zone, (3) The Hygrotropical zone. These ecological zones provide a logical framework in which to study the distribution of corticolous epiphytes along an altitudinal gradient in the Society islands.

Although comparing the distribution of epiphytes on two or more host species can be useful for studying host preference of particular epiphytes, examining the distribution of epiphytes within a single host species is necessary in order to tease apart differences in distribution based on micro-climatic factors. However, studies of epiphyte distribution over a broad environmental range often involve comparisons across a number of host species as well. This difficulty can be minimized on remote oceanic islands; their native flora is often depauperate and successful colonists generally radiate over a broad environmental range (Vitousek, 1994).

I chose *Hibiscus tiliaceus* , the most prominent rainforest tree species on the island of Moorea. This island is located approximately 11 km west of the island of Tahiti within the Society island chain. *H. tiliaceus* ranges in elevation from sea level to the uppermost mountain ridges on the island of Moorea. It is the most prominent riparian tree species forming a continuous belt across all three of the ecological zones summarized by Whittier. This unusual habitat breadth makes *H. tiliaceus* an exceptional host species on which to study epiphyte distribution, both over an elevational gradient and within a tree.

Physiological studies are often associated with bryophyte distributional studies. Distributional studies are especially suitable for epiphytic bryophytes because of the dynamic nature of the canopy environment. Light intensity, humidity, and precipitation vary both temporally and spatially within the canopy, with extreme and rapid wetting and drying cycles (Ingram, 1993). This lends itself to distributional trends based on desiccation tolerance.

Oliver and Mishler (1993) described 3 different components making up the complex phenotype of desiccation tolerance. These were: (1) Carbon balance per unit mass of water. (2) Damage control. (3) Damage repair. Measures of damage control are most easily performed because they require only simple procedures. These measurements are based on the principal that cells of different species may differ in the extent of damage to the cell membrane incurred during a wetting and drying cycle. This damage can be indirectly measured by determining the extent of electrolyte loss during rehydration. Any differences observed can then be related to the adaptive abilities of species to survive in and colonize sites with different water availability, relative to other species at question.

Therefore, this study was aimed at the assessment of species distribution, interactions, percent cover, and biomass of corticolous epiphytes along an altitudinal gradient in the Opunohu watershed of Moorea, French Polynesia. Patterns of zonation within the structure of a tree were also examined. I hypothesize that: (1) total epiphytic cover and biomass will increase with elevation (2) community composition will change over the elevational gradient (3) epiphyte distribution will change within the structure of a tree (4) distributional patterns observed are based on the growth form of each species and the adaptive ability of each species to survive and reproduce under varying moisture regimes

	Elevation (m)	Mean Temp (c)	Mean Annual Precipitation (mm)	Associate vegetation
Site 1	0	25	2500	*Acrostichum aureum*
Site 2	25	24.8	3000	*Cocos nucifera* *Pandanus tectorius*
Site 3	100	24.4	3500	epiphytic ferns and orchids. lianas
Site 4	250	23.5	4500	*Inocarpus fagiferus* *Neonauclea forsteri*

Table 1. Site characteristics of 4 study sites chosen along an elevational gradient in the Opunohu watershed.

(5) and that results of a desiccation tolerance and saturation capacity test of three prominent bryophytic epiphyte species will lend support to ecological patterns observed.

Study Site

This study took place in the Opunohu valley watershed on the northern coast of Moorea, French Polynesia (figure 1). The island is subject to consistent north easterly trade winds. Total annual rainfall over the watershed ranges from 2500- 4500 mm. , most of which falls between the months of November and March. Mean annual temperature is 25°C with and environmental lapse rate of 0.6°C/100m.(Atlas of French Polynesia). Mist and cloud interception data is unavailable but may effectively double or triple the actual measurable rainfall at higher elevations (Whittier, 1976). Field work was carried out during the months of October and November.

The four sites are located across an elevational range from 0m to 300m. All sites are adjacent to the Opunohu river within *H. tiliaceus* dominated stands. Site locations and elevations are summarized in figure 1. The floristic composition and climate of the forest change markedly along the elevational gradient. Site 1 is
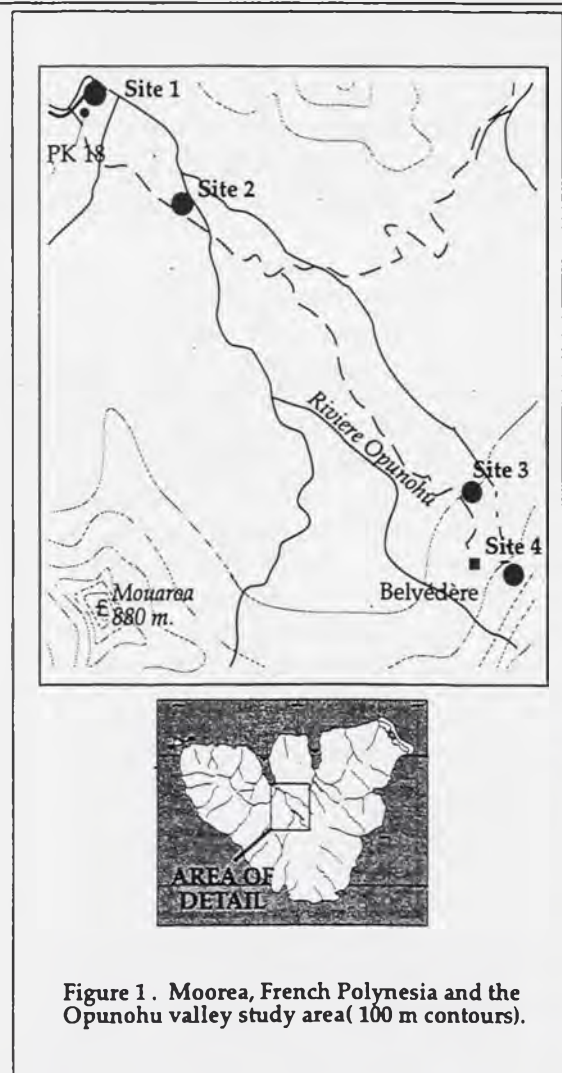

Figure 1. Moorea, French Polynesia and the Opunohu valley study area(100 m contours).

located in the Maritime zone within a mangrove, estuarine habitat. The overstory is 10-13 m. high with a understory of mangrove fern (*Acrostichum aureum*) that is subject to inundation and saline conditions. Site 2 is located in the Mesotropical zone. The primary *H. tiliaceus* forest is 13-15m tall with a few coconut palm (*Cocos nucifera*) emergents up to 25m tall. The understory is dominated by *Pandanus tectorius* and *Wikstroemia coriaceae*. Site 3 and 4 are located within the Hygrotropical zone. Site 3 has a dominant overstory of *H. tiliaceus*,13-15m tall with a dense understory of ferns and lianas. Vascular epiphytes are common including the Birds nest fern (*Asplenium nidus*), members of the Orchidaceae family, and other pteridophytes. Site 4 has a *H. tiliaceus* overstory, 16-20m. tall with Tahitian chestnut (*Inocarpus fagiferus*) and *Neonauclea forsteri* emergents, 25-30 m. tall. The canopy cover is complete and the understory is composed of ferns and forbs. Site characteristics are summarized in table 1.

Methods

Epiphyte distribution

Five trees were randomly chosen having a diameter at breast height(DBH) of 22cm. or greater from each site. Within each tree, three height zones were delineated: 30-60cm., 100-130cm.,170-200cm.(Height zones were based on accessibility from the ground). Plots were randomly located on accessible branch portions ($\geq$ 19cm. diameter) located within a specified height zone. Percent cover of all epiphytic plant species (excluding lichens) within the plot were measured using a 100 point grid, 15 cm. wide by 30cm. long. Any epiphyte species located beneath an intersection point was recorded. Intersected rhizomes were considered a hit for that fern species. Plots were placed on the upper side of the branch perpendicular to the branch direction. Three angle classes were defined based on degrees from horizontal): class 1= 0-20, class 2= 20-45, class 3= > 45. Angle class and branch circumference were recorded for each plot.

Epiphytic organic matter (EOM) was removed from each plot. The EOM was separated into two components: vascular epiphyte biomass (fronds, leaves, rhizomes, intercepted detritus) and bryophyte biomass. The contents were dried to constant weight for 120 hrs. at 48° C. The EOM was then weighed to characterize biomass between the different sites. Voucher specimens for all species were deposited at the University Herbarium, U.C. Berkeley.

Water Saturation Capacity The three most prominent bryophyte indicator species, *E sodale*, *Calymperes moorei*, and *Thysananthus* sp. were collected from all field sites. Ten samples were collected of each species. Samples were dried at 18°C for 120 hours and then weighed. Samples were placed on an acetate sheet. Water was added dropwise using a pipette until the sample reached its saturation point. This was denoted by the presence of water around the perimeter of the sample on the acetate sheet. The volume of water added / dry mass was calculated for each sample.

Desiccation tolerance Samples of the three indicator species were collected from sites 1 and 2. Samples were dried for approximately 1 week in a paper bag under standardized conditions during which they were transported to a laboratory at the University of California Berkeley. Samples were prepared by isolating the green apical portion of the plant from contaminating detritus and dead plant material. A subsample of each species was removed and hydrated in a growth chamber for 48 hours.

Desiccation tolerance was measured using the method described by Oliver and Mishler (1993). .02 g of the prepared samples were selected from each of the two treatments: (1) control - plants that were hydrated for 48 hours and; (2) desiccated - plants that were dried under the conditions described above. Plants were leached in 10 ml of distilled water. Change in conductivity (as a measure of electrolyte leakage from cells) was measured over a 20 minute period using a Corning M90 conductivity meter Three replicate measures were performed for each species

and for each of the two treatments; control and desiccated.

Statistical Analyses

All statistical tests were run on the JMP. statistical package. The five most prominent taxa were analyzed using a Principal Component Analyses. Associations between species were tested using a pairwise correlation table. Percent cover data on the three prominent liverwort genera belonging to the Lejeuneacea family were pooled into a single dataset and titled Lejeuneacea because of their lack of cover between all sites. Percent cover data on members of the *Calymperes* genus were pooled becuse of difficulty in identification to the species level in the field. All percentage cover data were Arcsin transformed to provide a normal distribution. The transformed data were used in a one-way ANOVA with a Tukey-Kramer means comparisons test to analyze the differences in cover between sites for all species.

Correlations among physical habitat factors (height zone, angle class, and plot circumference) and species were examined using a pairwise correlation table followed by a three-way ANOVA with tree and elevation as associate independent variables. Differences in total and bryophyte biomass between sites were tested using a one-way ANOVA with a Tukey-Kramer means comparisons test.

The saturation capacity and desiccation tolerance data for each species were compared using a one-way ANOVA with a Turkey-Kramer means comparisons test.

Results

Total Percent Cover and Biomass

Total percent cover of bryophyte species varied significantly between low and high elevation sites (F = 11.4, p < 0.0001). This same pattern was mirrored with respect to bryophyte biomass with significant differences occurring between low and high elevation sites (F = 13.57, p < 0.0001). Further inspection showed that biomass was positively correlated with the presence of *E. sodale* (r = .584, p < 0.0001)
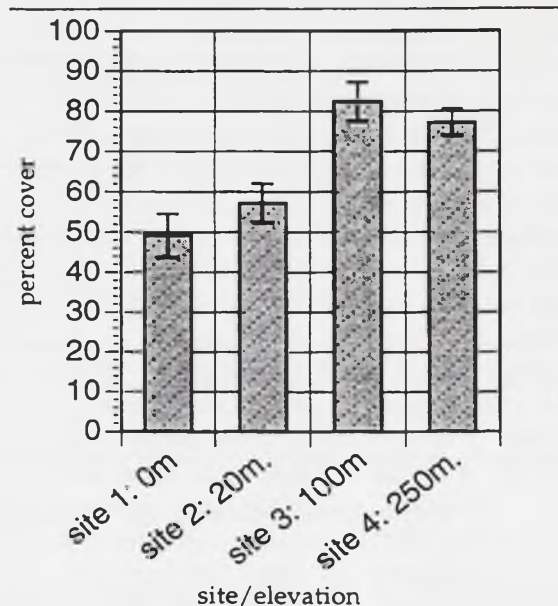
Figure 2. Total percent cover of epiphytic bryophytes on *H. tiliaceus* by elevation. Error bars represent one standard error.
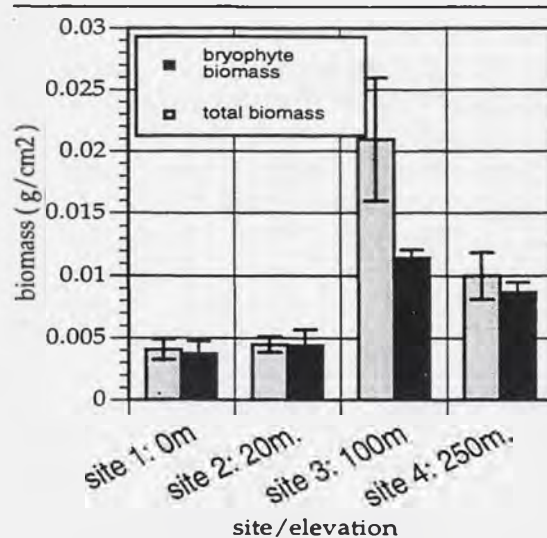
Figure 3. Total biomass and Bryophyte Biomass on *H. tiliaceus* by elevation. Total biomass consists of both bryophyte and vascular epiphyte components. Error bars represent one standard error.

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and was negatively correlated with *Calymperes* (r = -.300, p = 0.02). Total biomass at site three is nearly double that of bryophyte biomass because of the prominent vascular epiphyte community present at this site. Total percent cover and biomass are plotted against site/elevation in figures 2 and 3.

Epiphyte species distribution

The results of the principal component analysis show heaviest weighting along the x-axis with grouping occurring between sites 1 and 2 and between sites 3 and 4. The rotated components displayed (figure 5) show that *E. sodale* is negatively correlated with *Calymperes* sp., *Leucolejeunea* sp. and *Thysananthus* sp. and is found more prominently at upper elevational sites (sites 3 and 4). The PCA also shows a correlation between the presence of *Calymperes* and *Leucolejeunea* sp. at lower elevational sites (sites 1 and 2). Table 2 summarizes correlation values between species. *E. sodale* was negatively correlated with *Calymperes*, *Thysananthus sp., Leucolejeunea* , and Lejeuneacea (r = -.524, p<.001; r = -.258, p = .04; r = -.245, p=.05; r = -.512, p < .001, respectively). *Calymperes* is positively correlated with *Leucolejeunea* (r=.321, p<0.05).
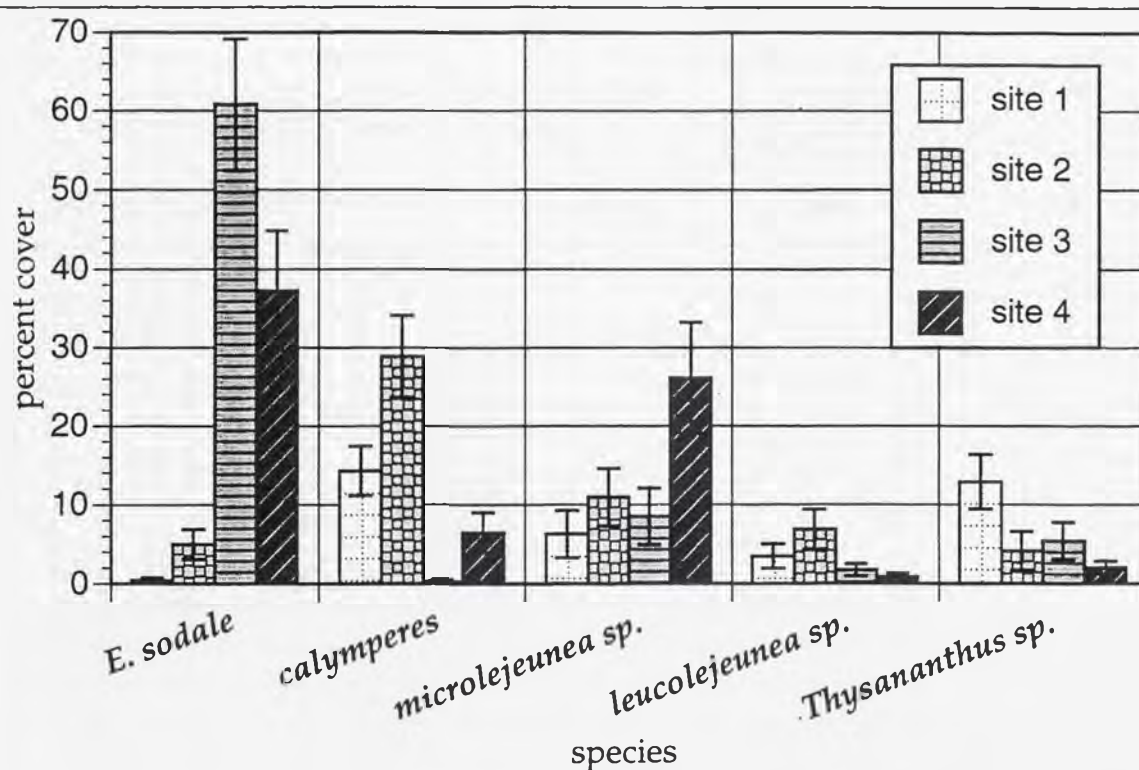
Figure 4. Epiphytic bryophyte cover on *Hibiscus tiliaceus* by species at 4 sites over an altitudinal gradient. Site 1-4 represent elevations of 0m, 25m, 100m, 250m respectively. *E. Sodale* and *Calymperes* are mosses. *Microlejeunea* sp., *Leucolejeunea* sp., and *Thysananthus* sp. are liverworts in the Lejeuneaceae family. Error bars represent one standard error.
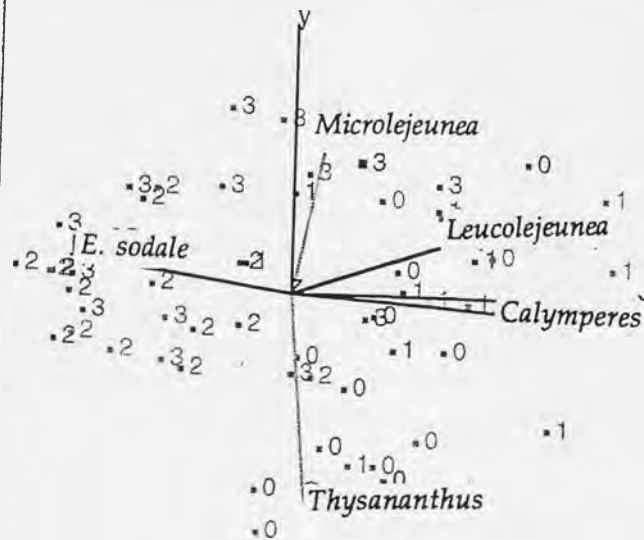
Figure 5. Principal component analysis biplot. Five taxa are E. sodale, Calymperes, Thysananthus sp. , Microlejeunea sp., and Leucolejeunea sp. Numbered points represent site locations: 0=site 1, 1=site 2, 2=site3, 3=site 4.

	E. Sodale	Calymperes	Microlejeunea	Leucolejeunea	Thysananthus	Lejeuneaceae	Total Cover	Height Zone	Angle Class	Circumference
Calymperes	-.524*									
Microlejeunea	-.225	-.091								
Leucolejeunea	-.245^	.321^	.005							
Thysananthus	-.258^	-.059	-.239	-.130						
Lejeuneacea	-.512*	-.009	n/a	n/a	n/a					
Total Cover	.625*	-.229	.186	-.056	-.170	-.001				
Height Zone	-.285^	.074	.134	.082	.225	.336^	-.069			
Angle Class	-.028	-.024	.364^	-.139	-.114	.230	-.112	.109		
Circumference	-.008	.208	.184	-.135	-.393*	-.106	-.070	-.495*	-.072	
Biomass	.584*	-.230^	.001	-.051	-.001	-.146	.495*	-.039	-.056	-.039

Table 2. Correlation values (r) for bryophyte percent cover data, Bryophyte biomass, and all measured physical variables. ^ P< 0.05 ; * P≤ 0.001

All species varied significantly between one or more sites. *E. sodale* cover varied between low elevation sites (1,2) and high elevation sites (3,4) and between sites 3 and 4 (F= 31.0, P<.0001). It comprised roughly 60% of the cover at site three, nearly twice as much as any other site. *Calymperes* cover showed significant differences between low and high elevation sites (F = 17.3, P< .0001) being most prominent at site 2. *Thysananthus sp.* cover varied between site 1 and all other sites (F = 3.41, P= .02). Percent cover of the five indicator Bryophyte species by site are summarized in figure 4.

Of the physical variables measured, percent cover was most closely associated with height zone. *E. sodale* showed a negative correlation (r = -.285, p = .027) with height zone. A three-way ANOVA, with tree and elevation as

Figure 7. Water saturation capacity of three epiphytic bryophyte species on *H. tiliaceus*. *E. sodale* and *Calymperes* are mosses. *Thysananthus sp.* is a liverwort in the Lejeuneacea family.

Figure 6. Epiphytic Brophyte cover on *Hibiscus tiliaceus* by height zone. *E. sodale* is a moss species. Lejeunacea represents three liverwort species in the Lejeuneacea family. Height zone 1: 30-60 cm., height zone 2: 100-130 cm., height zone 3: 170-200 cm. Error bars represent one standard error.

associate dependent variables, indicated that significant differences occurred betweenheight zones 1 and 3, with height zone 1 having roughly twice the cover as that of three (F = 8.09, p < 0.001). Lejeuneacea showed a positive correlation (r = .336. p = .009) with height zone, with the results of the three- way ANOVA indicating a difference between height zones 1 and 3 (F = 4.79, p = .0124). Percent cover of these species over height zone is summarized in figure 6. Among angle class interactions, *Microlejeunea sp.* was significantly correlated with the steeper angle classes (r = .364, p = 0.004). It was also noted that the entire Lejeuneacea family was positively correlated with angle class but not significantly (r = .230, p = 0.07).

Saturation tolerance varied significantly between all three species (F=135, p<0.0001). *E. sodale* held more
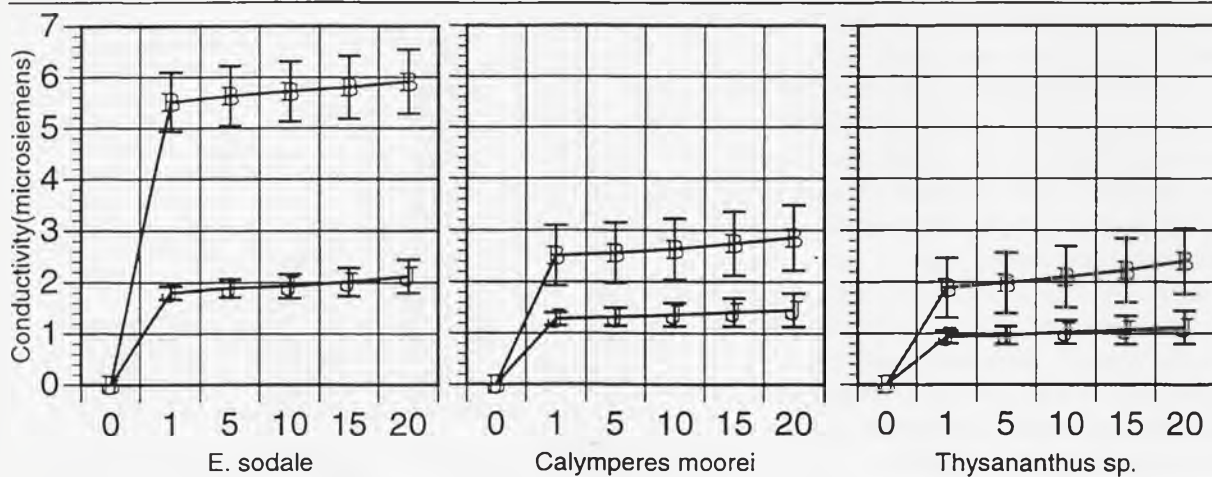
Figure 8. Conductivity of electrolyte leakage after a drying event for three epiphytic bryophyte species on H. tiliaceus over a 20 minut period. Squares represent treatments; circles are controls. *E. sodale* and *Calymperes* are mosses. *Thysananthus* sp. is a liverwort species in the Lejeuneaceae family.

than two times the amount of water as *Calymperes moorei* and *Thysananthus* sp. The conductivity measurements of all three species varied significantly from one another for both the treatment ($F=167$, $p<0.0001$) and the control group ($F=49.3$, $p<0.0001$). *E. sodale* had roughly 3 times the amount of electrolyte loss as *Calymperes moorei* and *Thysananthus* sp. in the treatment group. E. sodale also showed higher electrolyte loss within the control group as compared with the other two species.

Discussion

Total percent cover and biomass

Total cover and biomass of corticolous epiphytes on *H. tiliaceus* within the Opunohu watershed are greater in high elevation sites than in low elevation sites. This pattern is consistent with that of studies performed in mainland tropical rainforests (Richards, 1984; Gradstein, 1989; Pocs, 1982). It is generally assumed that climatic factors, especially the more favorable moisture conditions at higher elevations due to increased precipitation rates, increased cloud and mist interception, and higher relative humidity are responsible for the increase in epiphytic cover and biomass with elevation (Richards, 1984; Gradstein, 1989; Pocs, 1982; Wolf, 1993).

In addition to moisture conditions, the prevailing lower temperature at higher elevations is also cited as being an important factor in allowing for the development of bryophytic communities. Richards (1984) cites that it may be the high temperature of lowland rainforests (mean temp, 24-25 C) which is unfavorable for the development of a diverse and abundant bryophyte flora. He states that "the lack of tolerance of high temperatures might be because of high rates of respiration and because bryophytes are unable to maintain sufficiently high values of net assimilation at high temperatures and relatively low light intensities." The Opunohu watershed exhibits a climatic gradient with a relatively wide range of precipitation levels and temperature levels. Both the increase in available water and the decrease in the mean temperature over elevation are probable causal factors of the patterns observed in total cover and biomass.

Looking more closely at the results from the total cover and biomass data

shows that the trend of increasing cover and biomass is not linear and shows a peak in both total cover and biomass at site 3. This may be due in part because of the low light conditions at site 4 within the forest interior, caused by the overstory of *Inocarpus fagiferus* and *Neonauclea forsteri* emergents. It may also be due in part to more favorable conditions for vascular epiphyte growth at the mid elevations, thus explaining the peak in total biomass at site three. The high biomass and cover of vascular epiphytes at this site might be associated with the prominence of *Ectropothecium sodale* at site 3.

E. sodale is a moss that forms dense interwoven mats that provide an almost continuos layer of moss "carpet" over the branches and trunk of *H. tiliaceus*. This epiphytic "carpet" provides a substrate capable of intercepting spores and other propagules of vascular epiphytes. In addition to this, this bryophytic mat provides an exceptional water source for vascular epiphytes growing on it. Results from the water saturation test show that *E. sodale* can hold more than two times the amount of water as *Calymperes moorei* and *Thysananthus* sp. Nadkarni (1993) states that " bryophytes may favor their own displacement by providing vascular epiphytes with retained water, by forming humus, by accelerating bark decay, and /or by improving physical anchorage of seeds and propagules." The findings of this study support this statement. It is possible that *E. sodale* is creating a beneficial environment for vascular epiphytes and thus would explain the disproportionately high total biomass at the mid elevation site.

Epiphyte Species distribution

H. tiliaceus supports a diverse epiphytic community that changes over elevation and at a smaller scale, varies in distribution within a tree. Five prominent bryophyte indicator species were shown to vary significantly between sites, and were shown to be both positively and negatively associated with one another. A probable explanation of the patterns observed is based on the growth form of each species

and its ability to survive and reproduce under varying moisture regimes.

As stated earlier, *E. sodale* is a moss that forms dense interwoven mats. Mat forming bryophytes, because of their interwoven nature, form capillary networks in order to aid in the conduction of water through the plant. The capillary network occurs outside of the actual plant in the interstitial spaces of the mat, thus the majority of the water held by the plant is free water, or water that is not held within any cell membrane. Dense and interwoven mat growth forms are generally limited, to a strong degree, to locations with high available moisture (Schofield, 1981). Furthermore, results from the desiccation tolerance test show that *E. sodale* is the most desiccation-sensitive of the species tested showing a heavy loss of electrolytes during a wet/dry/ wet event.

The sum of this evidence supports the distributional trends found in this study. *E. sodale* is found extensively in the wet upper elevation sites but is practically absent from the drier low elevation sites. This trend was noted by Whittier (1976) in his ecological observations of the Society Islands. *E. sodale* is also found predominantly at the lowest height zones within a tree, which may be due in effect to the higher humidity and low insolation levels found near to the ground in a tropical rainforest.

The second bryophyte indicator taxon is the genus *Calymperes*. *Calymperes* is a pan tropical genus found frequently in lowland rainforests (Gradstein, 1989; Richards, 1984; Pocs, 1982). It is a cushion forming moss that has evolved a series of physiologically adaptive traits in order to retain water in dry environments. As the plant dries the leaves become imbricated and contorted, thus decreasing its surface area to evaporation. As the plant is rehydrated, the leaves tend to diverge widely, thus increasing its ability to trap water droplets (Schofield, 1981). In addition to this, the genus is characterized by enlarged hyaline cells within the leaf which are thought to aid in water storage and conduction (Richards, 1984; Gradstein, 1989; Pocs, 1982; Schofield, 1981). These

traits are all indicative of a plant adapted to dry lowland environments.

Results from the desiccation tolerance tests also show that *Calymperes moorei* is adapted for drier environments as compared with *E. sodale*. *C. moorei* has a greater desiccation tolerance than *E. sodale* based on its ability to minimize electrolyte loss after a drying event. Therefore, combining desiccation test results and physiological characteristics suggests that *Calymperes* is the dominant epiphytic bryophyte on *H. tiliaceus* at lower elevations because of its desiccation tolerance and its ability to retain water, and thus remain metabolically active, for longer periods of time.

Microlejeunea sp., *Leucolejeunea* sp., and *Thysananthus* sp. are all liverwort species in the family Lejeuneacea. This family is one of the most prominent families of bryophytes in the tropics, but yet one of the least taxonomically understood. All three species form mats of various types. *Microlejeunea* sp. forms a thin smooth mat that lays appressed to the substrate. *Leucolejeunea* sp. forms a thread-like growth form that creeps along the substrate in a sparing and irregular manner. *Thysananthus* sp. forms a mat that is smooth but is nearly five to six times the size of the previous two hepatics. Both *Microlejeunea* sp. and *Leucolejeunea* sp. are small and fragile plants as compared with *Thysananthus* sp. which is a large robust hepatic.

The small, fragile growth form of both *Microlejeunea* sp. and *Leucolejeunea* sp. would suggest that they are suited to moist environments. However, the data does not completely support this claim. *Leucolejeunea* sp. is found more prominently at the low elevation sites and higher within a tree, locations indicative of a drier environment. *Microlejeunea,* though most abundant at the highest elevation site, is also found higher within a tree and on more steeply angled substrates. The inclination of the substrate is of great importance to epiphytes. It affects their supply of water and nutrients, their exposure to sunlight, and their ability to establish themselves in new areas (Richards, 1984). Data for all three

liverwort species combined showed a trend of increased cover with increasing height zones and angle classes (though not significant). A possible explanation for this trend is the greater importance of microhabitat in the distribution of corticolous epiphytes, as compared with macrohabitat.

Microlejeunea sp. and *Leucolejeunea* sp., because of their small size and appressed growth form, occupy a microhabitat limited to a millimeter above the substrate. The microclimate within this millimeter may be considerably different than the macroclimate of the area. Furthermore, the nature of the substrate may play an important role in the distribution of these species. As a tree grows older the physical and possibly chemical properties of its bark change (Richards, 1984). The physical properties of the bark also change with height in the tree. The bark surface higher in the tree is much smoother and less complex than the surface near the base of the tree, which is much more fissured and complex. Pocs (1982) described the upper parts of tree trunks especially suitable for small or large patches of appressed hepatics such as the Lejeuneacea. This may be due in part to the smooth mat-forming or thread-like growth forms of these hepatics allowing these species to colonize upper tree trunk surfaces. Further studies are needed to quantify the differences between microhabitat and macrohabitat environments in relation to corticolous epiphyte ecology.

In addition to varying gradients in microhabitat, species interactions might account for distributional patterns observed. *Leucolejeunea* sp. was found growing in association with *Calymperes.* This liverwort was often found growing within the interstitial spaces of the much larger moss. This might suggest that *Calymperes* is providing a microhabitat for the development of *Leucolejeunea* sp. at lower elevation sites.

Thysananthus sp. was the only liverwort that showed a consistent pattern in its distribution. It was the prominent liverwort at site 1, the dry estuarine mangrove environment. It was also found at higher levels within trees at wetter sites..

As stated earlier, the species is a robust mat forming liverwort. However, when the plant dries the leaves and branches incurve in a ventral manner thus protecting it from extremely desiccating conditions. In addition, when the plant is dry the leaves are strongly imbricated forming a relatively continuous channel of interconnected chambers that enhance capillary conduction of water. It is also hypothesized that the sac-like lobules of some of the genera within the Lejeuneacea family may aid in water storage within the plant (Richards, 1984; Pocs, 1982).

These trends in distribution are supported by results from the desiccation tolerance tests. It was found that *Thysananthus* sp. showed the lowest electrolyte leakage as compared with the other species tested and also shows a characteristic growth form associated with dry environments. These findings compliment the ecological trends observed for this species.

In summary, there exists distinct epiphytic communities associated with low and high elevation rainforest types. Within the lowland rainforest of the Opunohu watershed their exists a distinct synusia of corticolous epiphytes. This synusia is comprised of *Calymperes* as the dominant epiphytic moss and *Leucolejeunea* sp. and *Thysananthus* sp. as associate liverwort species. In the mid to upper elevational rainforests there exists a separate synusia comprised of *E. sodale* as the dominant epiphytic moss and vascular epiphytic ferns as an associate set of species.

The findings of this study show that the community composition of corticolous epiphytes on *H. tiliaceus* varies over an elevational gradient and at a smaller scale, within the framework of a tree. These trends are based on macro and micro climatic factors. They are also based on the growth form of the epiphyte and the ability of each species to develop and reproduce under varying moisture regimes within the many microhabitats of the tropical forest canopy.

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Appendix. List of all corticolous epiphyte species found on *H. tiliaceus* by high(sites 3 and 4) and low (sites 1 and 2) elevation sites. Voucher specimens are deposited at the University Herbarium, U. C Berkeley.

Low elevation sites

    Mosses
        Macromitrium savatieri
        Macromitrium eurymitrium
        Calymperes moorei
        Calymperes tenerum

    Liverworts
        Thysananthus sp.
        Leucolejeunea sp.
        Microlejeune sp.
        Lejeuneaceae 1
        Lejeuneaceae 2

    Vascular plants
        Orchidaceaea
        Davallia dentiata
        Pyrosia serpens

High elevation sites

    Mosses
        Ectropothecium sodale
        Trichosteleum hamatum
        Calymperes tenerum
        Papallaria helictophylla
        Orthorynchiumcylindricum
        Macromitrium savatier
    Liverworts
        Thysananthus sp.
        leucolejeunea sp.
        Microlejeunea sp.
        Lejeuneacea 2
    Vascular plants
        Davallia epiphylla
        Ctenopteris blechnoides
        Asplenium nidus
        Pyrrosia serpens

Leaf retention and decomposition in a tropical island stream, Moorea, French Polynesia

Sapna B. Khandwala
Department of Integrative Biology
University of California, Berkeley 94720

ABSTRACT. Leaf retention and decomposition were studied in the Opunohu River catchment, Moorea, French Polynesia. The retention coefficient k was significantly higher in high elevation than low elevation reaches, and during high stage than low stage of stream flow at low elevation. Rocks were used more often than woody debris as a retention structure in high elevation reaches, but were used equally in low elevation sites, perhaps explaining the pattern in k observed. Comparative decomposition rates, based on percent leaf mass lost, were significantly different by elevation (high>low), microhabitat (riffle>pool), and leaf species (*Hibiscus tiliaceus*>*Inocarpus fagiferus*). Evidence for leaf shredding by shrimp (*Macrobrachium* sp. and *Caradina weberi*) was observed in the lab, where *Hibiscus* was shredded more than *Inocarpus*.

Introduction

Allochthonous organic material is a major source of energy input in small, forested streams (Minshall 1967; Cummins 1974; Vannote et al. 1980). Although the importance of this input has been well documented in temperate waters, the processes of leaf retention and decomposition are not well understood in tropical streams, with only a few published studies (Fittkau and Klinge 1973; Stout 1980; Dudgeon 1982; Pearson et al. 1989; Benstead 1996). Unlike temperate streams, which have distinct autumnal shedding, leaves enter the water relatively evenly throughout the year in the tropics. Thus, the nutrient input of these leaves may potentially be important year round.

Lobban et al. (1990) observed that most of the organic material found in streams on Yap in the Caroline Islands is allochthonously derived. Similarly, Resh et al. (1995) found that mid and low elevation streams on Moorea in French Polynesia receive external input from riparian vegetation. Maciolek and Ford (1987) described streams on Pacific islands as having stenothermally warm temperatures and lush riparian vegetation constantly contributing coarse particulate organic matter (CPOM). These characteristics suggest the possibility for a high decomposition rate breaking down these riparian leaf resources.

Winterbourn et al. (1981), in a classic paper demonstrating how the river continuum concept (Vannote et al. 1980) is not a generality true of tropical island streams, argued that breakdown and decomposition of CPOM were primarily carried out by microbial and mechanical means in tropical watersheds. However, they assumed this was because of the non-retentive and climatically unpredictable characteristics of tropical streams (Winterbourn et al. 1981).

Finally, both Haynes (1987) and Resh et al. (1990) found that the biomass of shredders in these tropical streams is negligible, and far less than what is found in temperate waters. Resh and De Szalay (1995) comment that it is not clear why streams of the Pacific Islands have so few shredders. They suggest that it may be a result of unretentive streams, heavily lignified riparian vegetation or island colonization dynamics.

In an attempt to understand the processes of leaf retention and decomposition in tropical island watersheds, the present study was conducted on Moorea, French Polynesia. The objectives of this study were: (a) to compare decomposition rates of two species of riparian trees, *Inocarpus fagiferus* and *Hibiscus tiliaceus*, in the absence of shredding organisms across elevational reaches and microhabitats, (b) to compare leaf retention abilities in high and low elevations during high and low discharge including analyses of retention structures used and leaf pack behavior, (c) to ascertain whether species of shrimp present in the stream are capable of shredding leaf material found within the stream, and (d) to estimate the amount of mechanical damage a leaf incurs in the absence of decomposition or shredding.

Materials and Methods

Study Sites

Leaf decomposition and retention studies were carried out from 18 October through 23 November, 1996 in the Opunohu River catchment, Moorea, French Polynesia (17°31´S, 149°55´W). Moorea (136 km^2) is the third largest of the Society Islands and the sister island to Tahiti, lying 18 km west of it, as part of French Polynesia. Moorea is 1.2 million years old and is made of a volcanic core surrounded by coral reefs. There are approximately 20 river basins on Moorea, arranged radially. Bedrock, boulders and cobbles dominate the substrata. Perennial streams reach approximately 150 m in some basins. The first 20 m in elevation slope is negligible (<5°), while after 20 m the incline is steep (up to 20° in 3 km). Rainfall, torrential at times, most likely regulates community structure and ecosystem processes within the streams. The riparian vegetation consists of *Hibiscus tiliaceus* and *Inocarpus fagiferus*, as reflected in the dominant leaf litter found in the stream. *Hibiscus* is a low growing tree with large, heart-shaped, flexible leaves. *Inocarpus* has ovulate leaves that are heavily lignified and is a believed nitrogen fixer.

Sampling dates encompassed both the hot and dry season (May-October) and the hot and rainy season (November-April). Average annual rainfall ranges from 200-400 cm per year across elevations. The climate is tropical with air temperatures ranging from 25-30°C and relative humidity of 80-90%. Stream water temperatures range from 20-

Figure 1. Map of study sites. Sites A, B, C, and D are designated low elevation reaches for cosites E and F which are designated high elevation.

28°C.

Table 1 describes the physical characteristics of the study sites. Figure 1 is a map showing localities of study sites. Locality A is the most downstream locality in the catchment, along an unnamed tributary from the Mouapu Valley that enters the Opunohu River 0.4 km from the mouth. Access to this site is from a road bridge on the Opunohu-Belvedere Road. Locality B is the next area upstream, accessed by a trail through a *Hibiscus/Inocarpus* forest, 0.5 km up the road. This is an unnamed tributary draining the Mouraroa valley. Locality C is upstream of locality B, just upstream of the second road bridge off the Opunohu-Belevedere Road. Locality D is east of locality C along the Opunohu River. Access here is by a dirt road travelling east from the main road. Locality E is at the Marae Tetiiroa and is composed of a continuous series of pools and cascades. The final locality, F, is located at the foot of the Three Coconut Trail, accessed behind the Agriculture School in the Opunohu Valley.

Leaf Retention

Freshly abscised *Hibiscus* leaves were collected from the riparian zone and marked with non-toxic flourescent yellow spray paint. Three hundred leaves were released at each of five low elevation and five high elevation sites after five days of no rain, designated a low water stage. Lamberti and Gregory (1996) suggest releasing enough leaves to have a

site	elevation	slope	order
A	2 m	<5°	4th
B	2 m	<5°	4th
C	<5 m	<5°	3rd
D	<5 m	<5°	3rd
E	100 m	10°	2nd
F	140 m	20°	1st

Table 1. Physical characteristics of the six localities sampled in the Opunohu River catchment. Slope and order data taken from Resh et al. 1990.
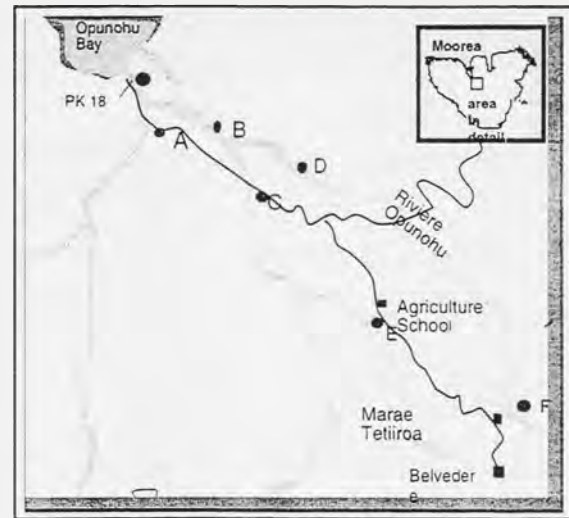
more than 90%. Pilot studies showed that 200 leaves were too few and 500 at locality B, too many. The release point at each site was chosen arbitrarily. Leaves were released individually and across the wetted width of the channel. This process took approximately five minutes. Meanwhile, those leaves not retained were collected downstream. Lamberti and Gregory (1996) also suggested that the wetted channel width multiplied by 10 be the distance downstream that unretained leaves were collected. Mean channel width was approximately 4 m, and so a 40 m reach was used for each replicate. A cumulative count of all the leaves not retained was taken every five minutes for 30 minutes. Pilot studies also showed that 97% of unretained leaves flow out in the first 20 minutes after release. Thirty minute intervals ensured the majority of unretained leaves would be collected. These data were then applied to an exponential decay model to calculate the retention coefficient, k:

$$P_d = P_o e^{-kd},$$

where P_o is the number of leaves released, and P_d is the number of leaves unretained a distance d from the release point.

In each 40 m stretch of stream the volume of woody debris was measured by treating each piece as a cylinder and measuring lengths and diameters in the field. Wetted lengths were taken of logs a minimum of 0.1 m diameter and 1 m length. In addition, the location of each retained leaf was mapped for the 40 m reach. Mean distance traveled by leaves as well as a two-way ANOVA comparing which retention structures (i.e. rocks, woody debris, vegetation, etc.) were calculated with this data.

Width and depth of the stream at 5 m intervals were measured. Stream water velocity was measured at three intervals along the reach by dropping twelve sticks into the stream and timing the course of six as they traveled a known distance.

Three hundred leaves were released again at the five low elevation sites during a high water stage (after a 24 hour period of rain) of the stream for comparative purposes. The same 40 m reach was observed for 30 minutes. Measurements of volume of woody debris and location of retained leaves was not repeated. A high stage k was calculated for comparison

to low stage data and analyzed for significance with a paired t-test.

Leaf Pack Retention

Ten leaf packs of 15 marked leaves were placed at locality E (high elevation) and at locality B (low elevation). Five of the packs at each locality were in riffles and five packs in pools. Leaf packs were placed in areas of pre-existing leaf packs and were observed for the first half hour after placement to ensure stability and submersion of each. Leaf packs were checked 1, 3 and 7 days after placement to observe retention capability of packs. A heavy rainstrom on day 6 was used to observe the effects of rain. Retention capability of leaf packs was compared between the four sites across the three days with a two-way ANOVA.

Leaf Decomposition

Fresh *Hibiscus tiliaceus* and *Inocarpus fagiferus* leaves were collected for the decomposition study. Circular disks of 7 cm diameter were cut out of the leaves. A control group of 25 disks of each species was maintained in a freshwater flow tank in the lab to observe effects of chemical leaching from these fresh leaves. A subsample was taken at six days and dried at 50°C for 48 hours to quantify the maximum mass lost due to leaching, to compare with field data.

When cutting disks, any obvious herbivory of the leaf was not included. Mesh bags (10 cm x 10 cm) were made with window screening (1 mm mesh size) and fishing line to house three disks of one species. Disks were dried at 31°C for 48 hours prior to being placed into a total of 144 bags. Of these, 72 bags were filled with *Inocarpus* disks and 72 bags were filled with *Hibiscus* disks.

Mesh bags were then grouped into bundles of six, three bags of *Inocarpus* disks and three bags of *Hibiscus*, and secured together with fishing line. One bundle was set in each of 12 low elevation and 12 high elevation sites. The 12 sites at each elevation consisted of six pools and six riffles and were chosen for convenience of access.

Mesh bags were secured together with twine and attached to existing vegetation and roots. If no stable structure was available, bags were attached to reinforcing bar secured to the stream bottom. To minimize loss of replicates, sites were checked after a

rain storm two weeks later to ensure integrity of the twine.

Mesh bags were placed on 18 October 1996 and collected 30 days later on 18 November 1996. Each bag was rinsed with freshwater to remove any sediment covering the disks, before they were dried at 31°C for 48 hours. Final masses were compared to the initial masses of the disks and a percent mass lost was calculated for each bag. A one-way ANOVA was used to statistically compare the effects of elevation, microhabitat and leaf species on decomposition.

Leaf Shredding

One species of Palaeamonid (*Macrobrachium* sp.) and one species of Atyid (*Caradina weberi*) shrimp were collected from the Opunohu River catchment and brought back to the lab for feeding experiments. *Hibiscus* and *Inocarpus* leaves covered with a periphyton layer were collected from the Opunohu River for feeding. Circular disks of 3 cm diameter were cut from these leaves. Each disk was dried with two separate paper towels to soak most moisture, and then weighed. This method of drying was used because complete drying of leaves would also destroy the nutritive periphyton layer.

Seven replicates of two treatment groups (*Macrobrachium* sp. and *Caradina weberi*) and one control group were set up in the laboratory in which approximately equal shrimp biomass was maintained in each 8 oz plastic cup. Water was changed every day for the ten days the experiment was conducted. After 10 days, disks were dried and weighed

in the same manner described above. A two-way ANOVA comparing both leaf species and shrimp species was conducted to analyze results.

Leaf Mechanical Damage

Newly abscised, near-perfect *Hibiscus* leaves were collected from the Opunohu River. Near-perfect was defined as whole leaves without evidence of herbivory greater than 1 cm^2 and perfect edges with no cuts. Leaves were marked with flourescent pink paint and soaked in freshwater for 72 hours. Soaking ensured neutral buoyancy when the leaves travelled downstream. Leaves were individually released in a mid-elevation (25 m) tributary at locality C, across the wetted width of 5 m. Leaves were retrieved for up to 100 m downstream from the release, 24 hours later. Each retrieved leaf was classified into no damage, small damage (<5 cm) or large damage (>5 cm). Each leaf was then further classified into punctured (through the middle of the leaf), torn (along the edges of the leaf) or broken. Leaves were collected from each 10 m interval past the release point.

	retention coefficient, k				
high	0.07	n/a	0.078	n/a	0.08
low	0.017	0.03	0.035	0.025	0.017

Table 2. The retention coefficient, k, across 5 low elevation and 5 high elevation reaches. N/A implies no leaves travelled a minimum of 40 m. Mean k in high reaches was 0.076 and in low reaches, 0.025.
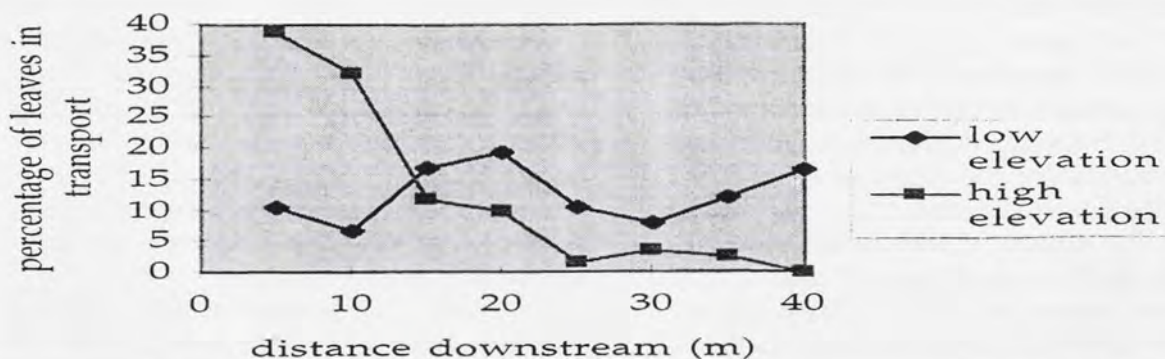
Figure 2. The mean number of leaves at each 10 m interval past the release point compared between high and low elevation reaches. Mean distance travelled in high elevation was 14.2 m, but 43.9 m in low elevation reaches.

Results

Leaf Retention

At a low stage, retention, measured by k, was significantly greater in high elevations than in low elevations (Table 2; t-test, df=4, p<0.001). The mean distance travelled by a leaf in low elevation was 43.9 m, while the mean distance travelled by a leaf in high elevation was 14.2 m (Figure 2).

Data within each elevation were pooled and the retention structures used by leaves between elevations were significantly different (Figure 3; two-way ANOVA, df=4, p<0.0001). However, the volume of woody debris was not significantly different between the two elevations (t-test, df=7, p=0.32).

One low elevation site was eliminated from the analysis comparing k between high and low water stage in low elevation because it was not comparable to the other sites. Site LL2 is an open stream with no overhead canopy. There was significantly greater retention in high water than low water stage in the remaining four, heavily forested streams (Figure 4; paired t-test, df=3, p=0.002). Finally,
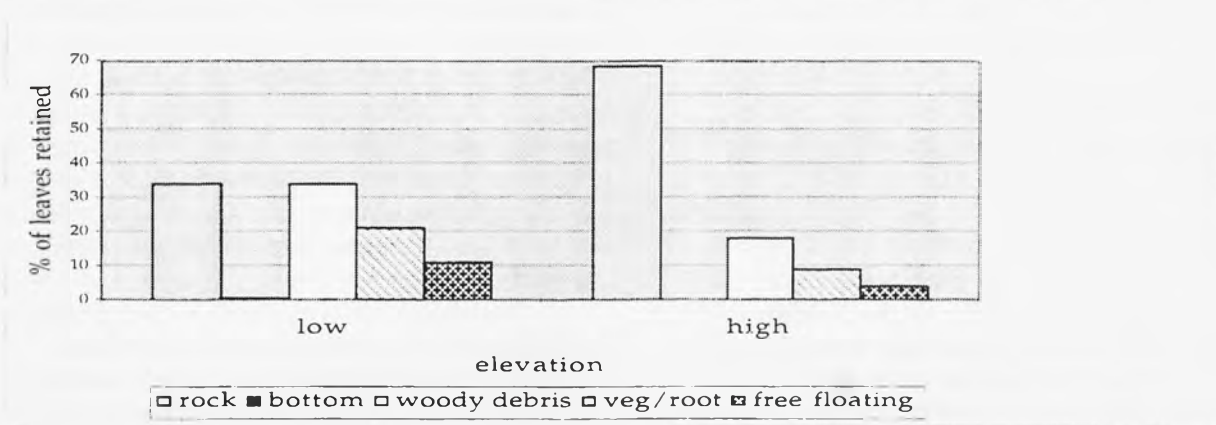
Figure 3. Mean number of leaves retained on one of five retention structure types compared between high and low elevation reaches.
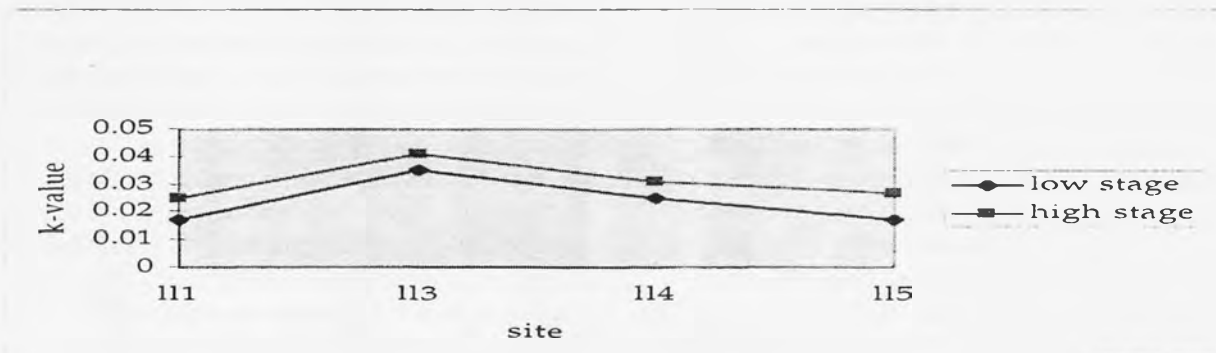
Figure 4. Comparison of the retention coefficient, k, between high and low stream water stages in four low elevation sites (p<0.002).

site	day		
	1	3	7
high riffle	13	13.8	7.8
low riffle	14	13.4	4.4
high pool	14.2	15.4	5
low pool	12	7.4	0

Table 3. Mean number of leaves remaining among five marked leaf packs placed in each of the four elevation/microhabitat types, out of a total of 15 leaves in each pack.

	elevation		microhabitat		leaf spp.	
	High	Low	Riffle	Pool	Ino	Hib
mean	48.67	38.08	48.99	38.90	41.73	46.69
F	18.3644		16.8666		3.6577	
p	<0.0001		<0.0001		0.05	

Table 4. Decomposition results from 144 mesh bags placed out in the Opunohu watershed for 4 weeks.

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there was a significant difference in number of leaves remaining in a leaf pack between days and microhabitats (Table 3; two-way ANOVA, df=3, p<0.004).

Leaf Decomposition

All three factors of elevation, microhabitat, and leaf species were significant when percent mass loss of leaf material was compared over the 30 day period (Table 4). A one way ANOVA showed that there was significantly more leaf decomposition in high elevation reaches than in low elevation (p<0.0001), in riffles than in pools (p<0.0001), and of *Hibiscus* leaves than *Inocarpus* leaves (p<0.03).

In the control group maintained in the laboratory, approximately 0.075 g were lost by *Inocarpus* and 0.01 g by *Hibiscus* due to leaching (approximately 6% mass lost) in the first six days.

Leaf Shredding

There was a significant difference in leaf mass lost between the two species of freshwater shrimp (*Macrobrachium* sp. and *Caradina weberi*) and the control and the two species of leaves, *Hibiscus* and *Inocarpus* (Figure 6; two-way ANOVA, df=2, p<0.0001). An analysis of these results found that the shrimp had a greater effect on *Hibiscus* losing mass than on *Inocarpus*.

Leaf Mechanical Damage

No significant relationship was found between damaged leaves and their position downstream from the release point. However, 40% of the leaves recovered incurred some kind of mechanical damage in the first 100 m from release within 24 hours.

Discussion

Retention Ability of Tropical Streams

Retention is significantly higher in the high elevation than in the low elevation stream reaches. One might expect retention to be less in high elevation reaches simply because of the slope. However, this is not supported by these data. Possibly, the pattern observed is because of the difference in discharge between elevations. The discharge in high elevation is lower than that of downstream reaches. Reaches in high elevation are generally first order streams, with typically low discharge. In comparison, reaches in low elevation are generally third and fourth order streams with typically greater discharge. Thus, the volume of water required to carry leaves downstream may not be great enough in upstream reaches, accounting for the difference in k between high and low elevation reaches.

Furthermore, the retention structures used in high and low elevation reaches were different from one another. Woody debris and rocks were used equally as retentive structures in the lower reaches, implying equal importance. However, in the upper reaches, rocks were used more often as a retention structure than woody debris (Figure 4), even though the volume of woody debris was not significantly different between elevations. Thus, it seems that rocks are disproportionately used more often as a retentive structure in high elevations.

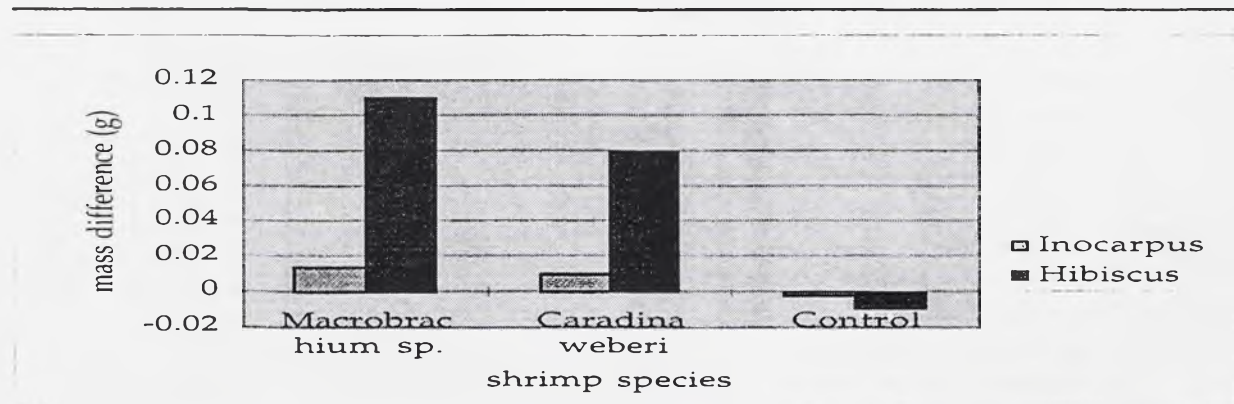Generally, the rocks found in high elevation reaches are much larger than those

Figure 6. Laboratory feeding trials were conducted for three treatment groups among two leaf species to test whether freshwater shrimp were capable of shredding leaf material in Opunohu watershed.

found in the lower reaches and may explain the pattern. These large boulders and cobbles are not submerged below the water level and a greater surface area is available upon which leaves can be retained. In lower reaches, where small cobbles and silt make up the substrata, not as much surface area is available for leaf retention.

However, it may be that woody debris plays the pivotal role in retention in lower elevation reaches. Retention is higher during high stages than during low stages in low elevation streams (Figure 2). This counters the suppositions of Winterbourn et al. (1981) and Maciolek and Ford (1987) that torrential rainstroms in the tropics flush out the rich riparian input in tropical streams. This result does suggest that woody debris plays an important role in the retentive abilities of the stream. For example, at high stream stage, although most of the rocks would be submerged, more of the riparian vegetation would be wetted, causing more leaves to be retained.

In fact, the site removed from the analysis depicted in Figure 5, was the only site with no woody debris found within it, and the only site that had a lower k at high water stage. These observations suggest that in terms of retention, rocks, boulders and the stream substrata are important in high elevation reaches, and woody debris, vegetation and the stream riparian are important in low elevation reaches.

Moreover, the retentive ability of a structure depends on water level. As the water level rises, the riparian roots and branches become more of a retentive structure and the cobbles/boulders in the stream become less of a retentive structure. Therefore, at low water stage of the stream, retention in the high elevation reaches is greater than low elevation reaches, explained by the stream's topography and supported by the data collected in this study. At high water stage, the dominant retention structure in high elevation reaches (namely rocks) would be submerged, flushing out any collected leaf material. Riparian vegetation and woody debris in the lower reaches, however, would be further wetted, causing greater retention in these reaches during high water flow, also supported by these data.

Not only are the number of leaves re-

tained and the structures the leaves are retained on different, but so is the pattern of retention between elevations (Figure 3). Leaves sampled in low elevation reaches were evenly spread out along the 40 m stream stretch, but were mostly clumped in their distribution in higher elevations. These data suggest that location of input is important when determining the retentive capabilities of these streams. If continual input into the stream does exist, then it would seem likely that the biomass of leaves found in the higher elevations would be greater than the biomass of leaves found in lower elevations during low stage flow.

The Extent of Retention and Decomposition in Tropical Streams

It is interesting that both retention and decomposition are highest in high elevation reaches. This brings clout to the idea that these leaves are not a wasted resource and makes the theory that these leaves are flushed out of the system less valid.

It is possible that the invertebrate communities are different in high and low elevations, contributing to the observed pattern. Kaushik and Hynes (1968) found that water temperature and quality, along with preferential feeding on decaying leaves by stream invertebrates affect rates of leaf decomposition. Although any possible "shredders" in the system were excluded by using mesh bags, microinvertebrates, such as midges, could still penetrate the barrier and evidence for their colonization was observed on the leaves (pers. obs.) The distribution of these chironomids may indeed be different in different elevations.

Temperature differences across the elevational gradient do not support these data. We would expect warmer temperatures in lower elevations facilitating higher rates of decomposition; this is not the case. Thus, it seems temperature has little bearing on decomposition rates in this watershed.

Decomposition rates were also significantly higher in riffles than in pools. Riffles may allow for faster leaching of the leaves as well as more efficient transportation of broken down leaf material. This is in contrast to the fairly stagnant state of leaves found in pools. In addition, leaf accumulations found in pools may become anaerobic and unable to accomodate the successive colonization of bacteria and fungi that initiate the decomposition

process.

Hibiscus decomposed more readily than *Inocarpus*, most likely because of the heavy lignification of the latter. Moreover, flexible leaves are more easily retained than stiffer ones (Young et al. 1978). The heavily lignified, oval shaped *Inocarpus* leaves are probably not caught on roots and branches as easily as *Hibiscus* leaves as they travel downstream, and are thus not as commonly found in these streams (pers. obs.).

Hibiscus is also more readily shredded by the shrimp species tested in this study. However, these shrimp are not always found within the leaf packs, suggesting that they may not preferentially shred leaves (Feldman, pers. comm.). Further study is necessary to quantitatively determine how much leaf material the shrimp are capable of processing. It is still unclear whether Winterbourn et al.'s (1981) treatise on New Zealand's streams can be applied to those of Moorea. Although a shredder for the system in the Opunohu basin has been found, decomposition may still be primarily microbial and mechanical. The extent of mechanical damage in a stream was also not clear from the results gathered in this study.

The differences in decomposition between microhabitats demonstrates the importance of localized effects in this stream system. Decomposition and retention are not occurring at the same rate in all reaches of the stream. Since the allochthonous input of leaf material provides the nutrient basis for the food web in these streams, where decomposition and retention are occurring becomes important in establishing community dynamics and population structures within the stream.

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Ecological and evolutionary implications of spines on the tropical stream snail, *Clithon spinosa*

Stephanie Yelenik
Department of Integrative Biology
University of California, Berkeley 94720

ABSTRACT. The spines of *Clithon spinosa* were studied on a functional and ecological basis with r egards to stream flow. Field data from the island of Moor ea, French Polynesia show that spine variation does not correlate with flow habitat. This may indicate that drag caused by spines is not costly or detrimental to the snail. Flow tank tests showed that *C. spinosa* move more in flowing than still water, but do not orient to flow, suggesting that the snails ar e not rheotactic. Spines do not af fect *C. spinosa*'s activity in the flow tank, and are therefore not used to per ceive direction or presence of flow. Snails with spines ar e more apt to land on their apertures than those without spines when falling thr ough a water column. This is not a usual str eam habitat, however, and may be an ancestral function of spines.

Introduction

Mobile organisms which are subject to aquatic flows are greatly affected by the force of drag (Vogel 1981). Streamlined shapes are often thought of as best suited for these environments, but rarely do organisms show this morphology. Many studies, therefore, have researched the function of organismal morphologies which deviate from this "optimal" condition. Gastropods shells have been studied for this purpose, as they vary in shape from smooth limpets to spiny snails. These form and function arguments, however, are difficult to prove (Carefoot 1995). Not only are many of the functional hypothesis untestable, but the forms themselves may not be of any useful significance to the animal at all. Often these protruding structures are remnants of ancestral adaptations and pleiotropic genetic effects (Carter 1967).

The snail family Neritidae contains a variety of shell shapes within its lineage. In the South Pacific, these snails are found in marine and freshwater habitats. Because both the marine and freshwater groups have species with and without spines, it seems to be a character which is easily lost and gained within the lineage. The diadromous life cycles of freshwater neritid snails (Resh 1992), in which the larvae must return to the marine environment for development, suggest that they evolved from marine ancestors. *Clithon spinosa* is a freshwater spined snail which in-

habits the high flow reaches of South Pacific island streams (Haynes 1990, Liu 1995). Although a species level phylogony has not been developed for *Clithon*, it is known that the marine species of the South Pacific does not have spines. It can not be assumed, however, that spines derived after movement into the streams because the marine ancestor could have lost the spines after the two lineages split. Especially in high velocity environments such as streams, where increased flow will increase drag coefficients (Vogel 1981), shell sculpture may impose constraints upon the ability of snails to remain attached to its substrate (Way 1993, Denny 1988). Due to the nature of neritid spines being lost or gained easily, there is a good possibility that a function exists as a trade-off of the drawbacks of drag.

Many hypotheses have been put forth to explain the function of shell sculpture in prosobranch gastropods (Carefoot 1995). Some of these include: (1) perceiving vibration, (2) protecting the snail from predators (Johansson and Samuelsson 1994; Barnhisel 1991), (3) destabilizing falls through water to increase chances of landing in an upright position (Palmer 1977), and (4) increasing its apparent size to predators. The first hypothesis may be useful to *C. spinosa* if it uses the flow of water to find its way through the streams. Neritid snails are thought to migrate, using a rheotactic response to find their way upstream by constantly moving against the

flow of water (Resh 1992). Spines may act in a sensory function by perceiving the direction of water around the snail. Destabilizing falls may be of importance to *C. spinosa*, not so much in falling down through the water column, but getting pulled downstream if it falls off of a rock. Both of these hypotheses are addressed in this study.

It is also possible that the spines cause large enough drag forces to keep those snails with the longest spines out of the highest velocity habitats in the streams. Lengths and numbers of spines in *C. spinosa* are variable intraspecifically due to breakage and continued shell growth without spine production. The shell sculpture of gastropods is created as the mantle secretes the shell in increments along the margin of the aperture. Spines, such as those found on *C. spinosa*, are created as discontinuous discrete elements when the mantle folds, such that a notch forms in the shell along the margin. As more shell is secreted, a spine forms as the notch folds in to form a hollow tube. The spines on *C. spinosa* form an evenly spaced row on the upper half of the whorl. These are produced from the time the snail is very small, about 3mm across the aperture. Variation in this even pattern due to mechanical breakage may alleviate the cost of drag in higher flow reaches of the stream and allow the snail to exist in higher elevations which typically have greater velocities.

To investigate the patterns of spine and shell morphology in *C. spinosa* as a function of stream flow, two streams were sampled in Moorea, French Polynesia. This was done to specifically ascertain the relationship between breakage of spines and habitat flow. The role of spines in sensing flow of water and destabilizing falls through water were also investigated within a laboratory setting.

Materials and Methods

Field survey

Patterns in spine and shell morphology, and how these patterns relate to habitat, were investigated by sampling one tributary each within the Opunohu and Afareaitu River catchments in Moorea, French Polynesia (Figure 1). These streams were similar morphologically in the lower reaches, but Afareaitu started to rise in elevation closer to the mouth

of the river than Opunohu. This rise in elevation was matched by an increase in substrate size and water turbulence. Whereas small to medium cobble and silt made up the majority of the substrate in downstream sites, large cobble and boulder predominate in Afareaitu upstream sites.

Each stream was sampled from the bottommost to topmost of *C. spinosa* distribution. Alternating riffle and run reaches were chosen so that homogeneous flow habitats which contained large numbers of snails were sampled. Ten minutes were spent at each site turning over rocks and collecting all *C. spinosa* found. Spine and shell measurements were taken in the field or lab using calipers. These included aperture width (which was used as an indication of snail size), the length of the last spine and the length of the second to last spine. The last spine was considered to be that fully developed spine which was closest to the margin of the aperture. Percent breakage of spines was estimated, taking scaling for animal size into account . A friction velocity index at each site was measured as the inverse of the average dissolving time of four cubes of sugar placed on the stream bed surface. This was used to indicate habitat flow. Regression plots were used to delineate relationships between the breakage of spines and friction velocity, as well as aperture width and distance travelled upstream.

Flow Tank

In order to look at the possibility that *C. spinosa* spines are used to detect flow, a circular flow tank was constructed out of a plastic tub. The radius of the tank was 22 cm and the water height was 13 cm. Holes were drilled around the perimeter of the tank to keep the water height level. Water was fed into the tank by a hose with a restrictor valve pointing in the counterclockwise direction at a height of 6 cm.

The first set of experiments (experiment set 1 hereafter) tested the effects of flow and intraspecific spine variation on snail orientation and activity. Sets of five snails with varying spine lengths were chosen for each trial and average spine length was measured with calipers. The snails were placed into the flow tank and allowed to equilibrate to the new environment for at least 15 minutes. The orientation and activity of each snail was
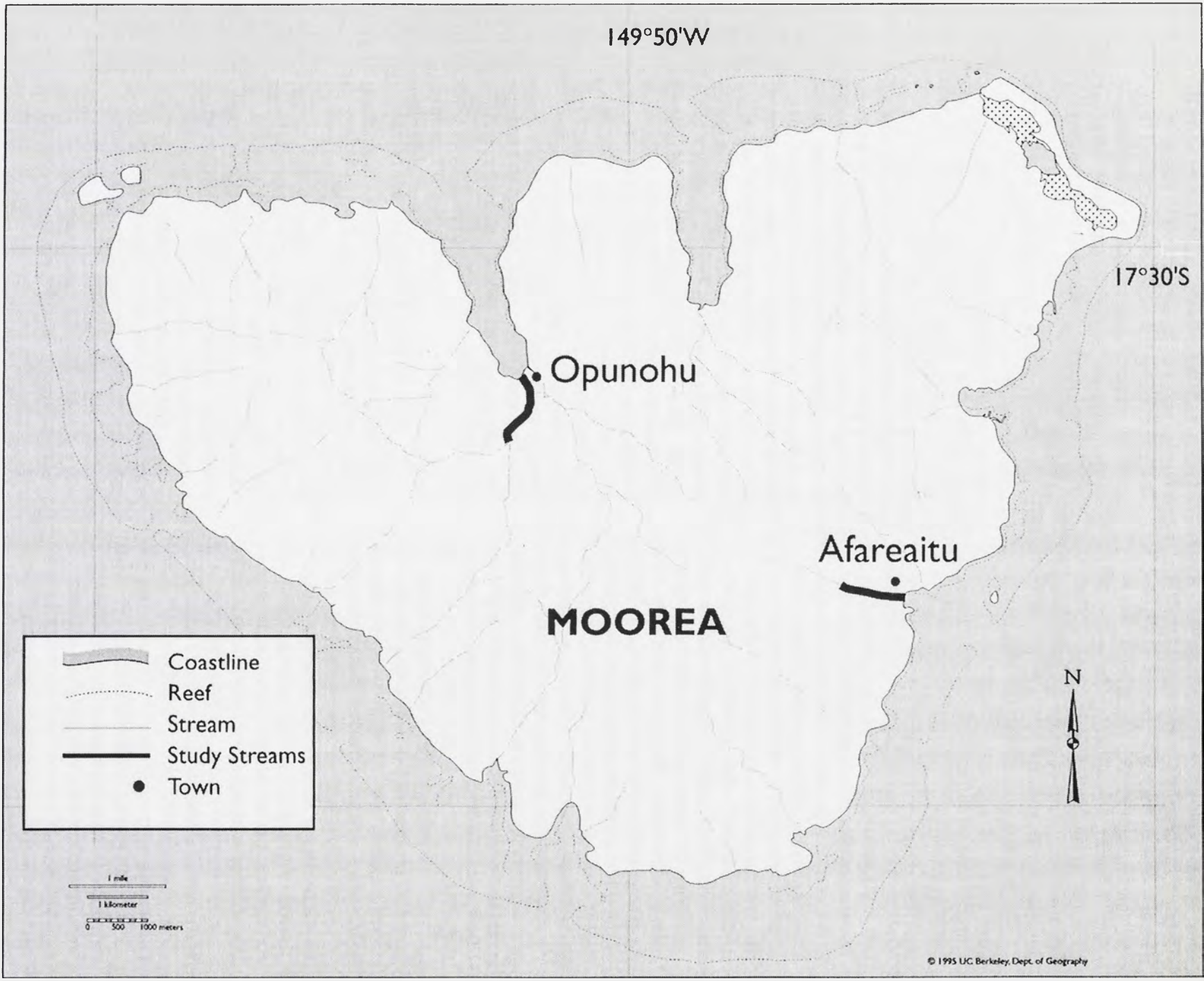
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Figure 1: Map of Moorea, French Polynesia, with streams sampled for *C. spinosa* in bold

noted as moving with the flow (upstream), moving against the flow (downstream), or not moving. This was noted every ten minutes for every snail for one hour. This test was run in flowing and still water.

A second set of experiments (experiment set 2 hereafter) tested the effects of spines on snail activity in moving water. Sets of six snails with relatively unbroken spines were measured for average spine length and placed in a flow tank trial for one hour under the same sampling regime. Half of the snails (experimental group) had their spines removed while the other six remained intact (control group). All six were placed back in the flow tank for another one hour trial. The activity of these snails was then compared with and without spines, using the intact spine snails as a control for the effects of trial.

For both sets of experiments, the number of times a snail faced in an upstream and downstream direction, and the number of times the snail was seen moving was pooled for the hour. For the experiment set 1, numbers were used to compare orientation preference with two tailed t-test, and movement in flowing and still water with a paired t-test. Orientation and movement were regressed onto average spine length to see the effects of natural spine length on activity. For the experiment set 2, a two way ANOVA was used to compare activity with and without spines, in control and experimental groups.

Destabilization tests

The tendency for snails to land upright (apertures flush to the substrate) with and without spines was tested using a glass jug filled with 17cm of water. The snails were held upright directly above the surface of the water and then dropped ten times each. The spines were removed with a wire cutter and smoothed down with sandpaper and the test was repeated. Paired t-tests were used to compare the number of times each snail fell upright with and without spines.

Results
Field survey

The length of the last spine varied between 0mm and 7mm (Figure 2A) while the length of the second to last spine varied between 0mm and 6mm (Figure 2B). Breakage of spines showed no relationship to the sheer

stress index (Figure 3). The mean aperture width did not correlate with site for Opunohu ($r2=0.01$, $p=0.67$) or Afareaitu ($r2=0.04$, $p=0.55$), where increasing site numbers corresponds to increasing elevation (Figure 4). The mean aperture width was significantly different between sites (two-tailed t-test: $t=7.19$, $df=308$, $P<0.001$).

Flow tank

In experiment set 1, snails showed a greater mean number of observations per hour of movement in flow ($X=3.32$, $SD=2.44$) than still water ($X=4.82$, $SD=1.68$) (paired t-test: $df=48$, $p=0.007$). No difference was seen in mean observations per hour of upstream ($X=2.52$, $SD=2.42$) or downstream ($X=2.32$, $SD=1.9$) movement (two tailed t-test: $df=48$, $p=0.747$). The average spine length of snails did not correlate with the number of observations of movement ($r2=0.04$, $p=0.31$) or upstream orientation ($r2=0.06$, $p=0.21$) within
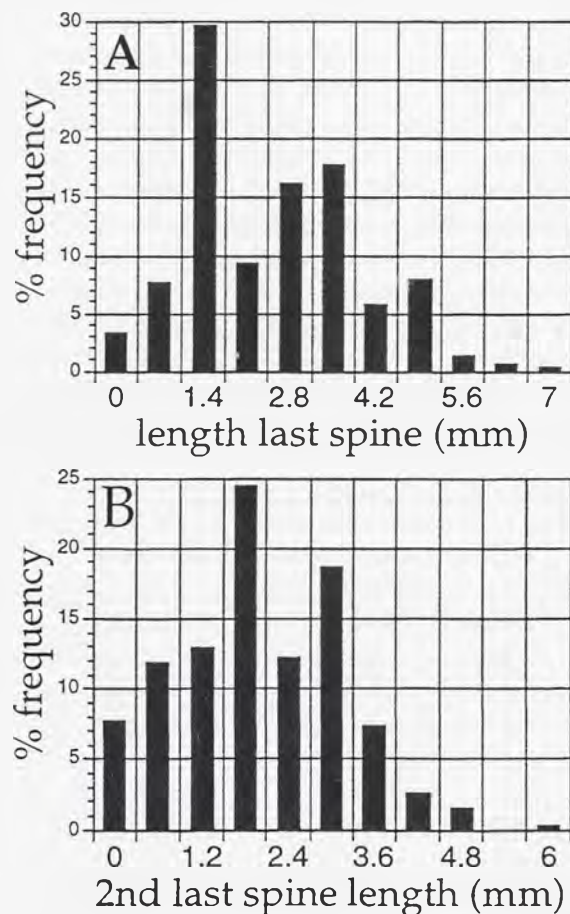

Figure 2. Frequency histograms of lengths of the (A) spine closest and (B)second closest to the margin of the aperture in *C. spinosa*.

one hour. In experiment set 2, both the experimental and the control group decreased in the number of observations per hour of movement and upstream orientation in the second trial. The experimental group which lost its spines, however, did not show any significant differance from this trend in reduction of movement (p=0.10) or upstream orientation (p=0.09).

Destabilization tests

Snails landed upright significantly more times with spines (*X*=3.05, SD=2.25) than without spines (*X*=1.25, SD=1.02) (paired t-test: df=19, P=0.006).

Discussion

Changing morphologies within benthic macroinvertebrates have long been tied to differences in habitat (Vogel 1981; Koehl 1984; Stazner and Holm 1989; Way et al. 1993). Most of these studies have investigated changes in body shape that are controlled genetically or physiologically rather than mechanically. The spines of *C. spinosa* show incredible variation (Figure 2A and 2B), spanning from lengths of 0 to 7mm in length (for animals averaging 12.38mm in width) caused mainly by mechanical breakage. Although *C. spinosa* inhabits reaches of stream which also vary greatly in friction velocity, its spine breakage does not correlate with these different flows (Figure 3). This implies that the spines of *C. spinosa* do not keep it from high flow habitats.

This lack of correlation, however, does not mean that the spines do not cause any mechanical drag on the snail because the snail could be dealing with these forces in ways other than spine morphology. The strength of the foot could be helping the snail stay attached to the substrate. Liu (1995) tested the tenacity of five species of Moorean neritid snails and found that *C. spinosa* was the second most tenacious. Therefore, the strength of the foot in *C. spinosa* could be making up for the forces which the *Neritina* spp. do not feel because of their smooth streamlined shells.

Because *C. spinosa* lives in high flow reaches, it was not surprising that they showed the greatest activity in moving water situations. Sampling within the streams showed that neither *C. spinosa*, nor any other neritid snail inhabit the deep pool sections. This could be true for several reasons. The substrates of these pools are composed of silt, as opposed to the rocks which cover riffle and run stream beds. Even within riffle and run reaches in which the rocks are covered in clay, silt, or fine particulate organic matter, snails were not found. These pools are also stagnant, receiving much less oxygen for respiration than the well mixed riffles and runs. Lastly, the pools are deep and turbid enough to exclude light, thereby limiting algae production. Since this is the main food source for neritid snails (Perchon 1968), this would greatly affect their distribution and, more importantly, their foraging behavior. Much of gastropod

Figure 3. Mean percent breakage of *C. spinosa* spines as a function of the friction velocity index (r2=0.01, p=0.62).

Figure 4. Mean aperture widths of *C. spinosa* from tributaries within the Afareaitu and Opunahu valley river basins. Error bars represent 1 SD.

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activity is associated with foraging, therefore, they are probably most likely to do so in the quasi-natural habitat of moving water within a flow tank.

Although *C. spinosa* is more active within moving water, it was not found to prefer an upstream or downstream direction. This implies that the snail does not exhibit a rheotactic response. Many neritid snails have been observed migrating upstream in long lines (Schneider and Frost 1986), but this has never been noted for *C. spinosa*. If it does migrate, it reaches much lower elevations than other Moorean snails. *N. canalis*, which is always found in the same reaches of stream as *C. spinosa*, reaches elevations of 122 m above sea level in Moorea (Resh 1992) while *C. spinosa* reaches only about 20 m above sea level. Resh (1992) showed that the average body size of *N. canalis* is greater with increasing elevations, indicating that older snails are farther upstream because of migration. *C. spinosa* showed no such pattern in body size (Figure 4), again indicating that it does not migrate upstream.

Upstream reaches of streams are generally associated with faster velocities and more turbulent flow, partly because of the larger boulders and cobbles which protrude from under the surface of the water. In Moorea, the transition to large substrate upstream reaches was well defined as the slope began to rise quickly at about 20 m above sea level. The upper limit of *C. spinosa* distribution in the Opunohu tributary seemed to match this transition zone, possibly due to an upper limit in drag forces that *C. spinosa* could not pass. *C. spinosa* distribution, however, stopped after this transition in Afareaitu. In this tributary the average aperture width of the snails was significantly smaller, indicating that body size is smaller than Opunohu snails. Even though the snail larvae move to the ocean to develop, they do not necessarily move beyond their prospective watersheds, leaving the opportunity for allopatric evolution between the two groups. Because body size is directly proportional to the drag of an organism, the decreased body size in Afareaitu snails could be allowing the snail to pass the transition zone between high elevation and low elevation reaches.

Although *C. spinosa* is found most often in high flow reaches, and is more active in

high flow situations, spines probably do not function in helping the animals find these habitats. Neither the natural variation in spine length nor the removal of spines had a significant effect on the movement or orientation of snails in moving water. Because *C. spinosa* does not move more often in either the upstream or downstream direction, it is not surprising that spines were found not to affect orientation. *C. spinosa* does move more often in flow situations, however, so the results show that spines probably are not used as sensory structures.

From this study, the most probable function of spines in *C. spinosa* is increasing the chances of landing upright after falls through the water. This could be advantageous to the animal for several reasons. By not going through normal righting behavior, the animal saves energy and looses the risks of having its foot exposed to predators. Landing directly on the aperture also decreases the amount of time it would take the animal to become attached to its substrate. In the highly variable streams of tropical islands, where stages rise and fall quickly during storm events, this could be the key to not getting washed downstream. Although *C. spinosa* are often found underneath rocks, they are also seen on top of large boulders and cobbles, and probably nocturnally forage for algae (Liu 1995). The question now arises as to whether this function is plausible for an organism which is not falling horizontally through the water column, but vertically into the flow of a stream channel. The flows within the riffles and runs are turbulent around those large rocks from which a snail may be pulled during a storm event, an environment much different than the still water in which the destabilization experiments were carried out. This implies that the function could be a remnant from an ancestor, especially one from a marine environment such as an island lagoon, where flows are much slower and certainly less turbulent.

Palmer (1977) showed the same function for shell varices on *Ceratostoma foliatum*, whose unequal weighting due to shell sculpture caused the animal to "flip flop" as it fell through the water, thereby increasing its chances of landing upright. *C. spinosa*, however, did not show this flopping action, but spiralled in an upright position through the

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water column around a dorsoventral axis as it fell. This spiralling did not occur once the animal lost its spines. Therefore, although the results are similar, the mechanics behind landing upright in the two gastropods are different, implying that the functions arose independently.

Whether or not the spines of *C. spinosa* are an ancestral or derived character is still under question and probably will not be answered until a phylogony becomes available through which the character itself can be traced. Although the marine *Clithon* sp. does not have spines, the type species of *Clithon* does, indicating that it is a central character around which species are placed into the genus. Therefore, it would seem most parsimonious that spines are a plesiomorphic character -- this matches the possibility that spines were a function for some marine ancestor. Spines certainly were not derived as sensory structures, and may not keeping *C. spinosa* from inhabiting the high flow reaches of low elevation streams. These factors combined point at the vestigial character of spines. Not all possible functions of spines in *C. spinosa* have been tested, however. Spines still have not been investigated as functioning in predator avoidance. Also, neritid snails are known to internally fertilize (Ford 1979), and *C. spinosa* has been noted to display a piggybacking behavior (pers. obs.) which may be related to this. In this case, spines may function in the positioning of the animals. Also, if spines are ancestral, the marine species would have lost them while the stream species did not. Not only are the stream species living in higher flows and a more variable environment, but they are lacking the great abundance of $CaCO_2$ which is found in the ocean. If the character was so easily lost from the marine group, it would seem that a vestigial character would not be maintained. Therefore, it seems most likely that the character is a functional marine character, possibly exapted for a new purpose.

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Distribution and ecology of freshwater shrimp (Decapoda) in the Opunohu river, Moorea, French Polynesia

Chris Feldman
Department of Integrative Biology
University of California, Berkeley 94720

ABSTRACT. Patterns in microhabitat and macroscale distribution as well as patterns in the community structure of freshwater shrimp occupying the ecotone between the mouth and head waters of a tropical river were revealed through an integrated study of microhabitat preference, macrohabitat distribution and feeding morphology and behavior. Microhabitat preference was quantified as abundance of organisms per microhabitat. Environmental variables were measured at each microhabitat and macrohabitat site and used to characterize sites and community structure responses over a local and large scale gradient. Large scale changes in macrohabitat such as elevation, canopy closure and salinity were important in determining community composition between sites while local gradients such as substrate and flow were important in segregating species at the microhabitat level. Functional feeding group, the classification of a stream invertebrate into a feeding category based on feeding morphology and behavior, was important in determining micro and macro scale distributions of freshwater shrimp. The Palaemonid shrimp *Macrobrachium* occurred in all reaches of the stream but was most abundant in the mid and low reaches. *Macrobrachium* preferred banks with rooted vegetation and other low flow areas. This species was considered a grazer or generalist. The two Atyid shrimp were seen only in the mid and high river reaches. *C. weberi* was seen in runs and pools of dense forest streams. This shrimp likely performs the role of stream shredder. *A. pilipes* on the other hand, was found only in fast flow riffles and leaf packs. Its filter feeding morphology dictate its microhabitat preference and macroscale occurrence. The shrimp composing the Opunohu catchment's macroinvertebrate community generally conform to the framework of the River Continuum Concept. This leads to questions of river ecosystem stability.

Introduction

The environmental and biological conditions surrounding an organism effect its physiology and ecology to limit its numbers and distribution. The distribution and abundance of organisms in natural communities thus depend upon a variety of abiotic and biotic factors. Stream ecosystems provide an array of changing physical conditions that influence benthic fauna. Some characteristics such as elevation, temperature and stream size change predictably along stream gradients and alter benthic community structure in regular ways (Grubaugh 1996). One framework for understanding riverine ecosystem dynamics is the River Continuum Concept (RCC), put forth by Vannote et al. (1980). The RCC proposes a longitudinal succession of organic matter processing, associated with changes in the functional feeding-group composition of the benthos. According to the RCC, leaf fall from terrestrial vegetation supports a community of shredders and collectors in head waters. Shredders use coarse particulate organic matter (CPOM >1mm) such as leaf litter, whereas collectors filter from seston, or gather from the sediments the fine particulate organic matter (FPOM 50um-1mm) (Vannote et al. 1980). Grazers, invertebrates adapted primarily for scraping and shearing attached algae from surfaces, are expected to be in low abundance in head waters streams because a dense canopy cover of riparian vegetation reduces the productivity of primary producers. As a stream increases in size, the influence of terrestrial vegetation on aquatic communities lessens. As riparian canopy cover decreases, leaf input diminishes and shading is reduced. This decrease in stream shading is paralleled by an increase in the productivity of primary producers (Minshall 1978). Thus, the RCC predicts a longitudinal shift in river ecosystems from a community of shredders and collectors to a community of grazers and

collectors. Finally, the lowest reaches of the river are dominated by a community of collectors which capitalize on the inefficiencies of upstream biota.

This regional view, or community level approach, is helpful and important in determining the coarse scale phenomena observed in riverine ecosystems. However, it is also necessary to consider patterns of distribution and abundance at the microhabitat level. Factors which govern the distribution and use of microhabitats of benthic macroinvertebrates include feeding morphology, substrate type (size) and stream flow (Resh et al. 1990; Cummins 1964; Statzner 1988). Feeding morphology is important in determining what an organism does and where it lives. Substrate is important as the medium on which an organism moves, rests, hides and feeds. It is important as shelter, a medium of adherence and in modifying the environment (Minshall 1984). Flow influences the metabolism, feeding and behavior of a benthic organism (Statzner 1988). It is the interplay of longitudinal and local physical characteristics which produce the distinct patterns in the structure of benthic communities along stream continua (Grubaugh et al. 1996).

This study attempts to bring together the broad scale factors considered in the RCC with microhabitat level factors in order to provide a more complete understanding of ecology and distribution of zoobenthos.

The streams of Moorea are numerically dominated by two families of freshwater shrimp (Resh et al. 1990). The family Palaemonidae is a successful, cosmopolitan family of marine and freshwater prawns. Species of this family are often aggressive, omnivorous and can osmoregulate well (Rollin 1994; Hobbs and Covich 1987). This family is represented on Moorea by several species of the genus *Macrobrachium*.. *Macrobrachium* is generally a grazer and bottom scavenger (Hobbs and Covich 1987; Resh et al. 1990). Members of this genus run the gamut of reproductive strategies. Some species are marine throughout all life stages. Others have become completely freshwater adapted and can reproduce there. Still others are diadramous, releasing eggs or larvae which wash out to sea (Resh et al. 1992).

Family Atyidae is represented on Moorea by *Atyoida pilipes* and *Caridina weberi*. This family contains only freshwater forms. The geographical range of Atyidae embraces the circumtropical regions of the world and parts of North America (Hobbs and Covich 1987). The genus *Atyoida* is restricted to Brazil, the Society Islands and the Hawaiian Islands. *Caridina* is nearly circumtropical in its distribution (Ortman 1894). Based on morphological characters, Ortman (1894) placed *Caridina*, *Atyoida* and *Atya* into an unnamed group above the genus level but below the subfamily level. No phylogenetic relationships were determined among this group. When feeding, members of the genus *Caridina* are known to scrape and sweep (Fryer 1960; 1977). Ortman considered the status of the genus *Atyoida* tenuous at best, but commented on its morphological similarities to *Caridina* and *Atya*. Several members of the genus *Atya* have been shown to passively filter feed in laboratory and field situations (Cowles 1915; Fryer 1977; Felgenhauer and Lawrence 1983; Covich 1988). Based on these studies and the similarity of the feeding appendages of *Atyoida* and *Atya*, Resh et al. postulated that *Atyoida pilipes* is a filter feeder. Other literature on *Atyoida* is lacking. Resh et al. (1992) also present evidence that both *Caridina weberi* and *Atyoida pilipes* are diadramous. A few studies (e.g. Fryer 1960,1977; Felgenhauer and Lawrence 1983) relate Atyid shrimp to specific microhabitats but no other studies focus on patterns of microhabitat distribution or attempt to understand patterns of shrimp abundance and distribution with respect to functional feeding groups and the RCC.

The purpose of this study is to discern the microhabitat and macroscale distribution among three species of freshwater shrimp and to ascertain the important physical and ecological characters associated with these microhabitat and macrohabitat patterns. The following questions will be addressed in this study: (1) Do well defined patterns of distribution and abundance occur among Atyid and Palaemonid shrimp with respect to microhabitat and macrohabitat (river reach). (2) To what local, longitudinal and morphological factors do these patters of distribution and abundance correspond? (3) Finally, how do these patterns compare to the

structure and function of benthic communities as postulated by the RCC?

Methods and Materials

Study Sites

     This study was carried out in the Opunohu Valley watershed on the north side of Moorea, French Polynesia (Figure 1; 17° 31' S, 149° 51' W). Field data were collected from 12 October to 17 November 1996, during austral spring (the wet season). Three low reach, mid reach and high reach sites were established along the tributaries and main stream of the Opunohu River. Sites were chosen on the basis of microhabitat heterogeneity, macrohabitat type, distance from river mouth and accessibility.
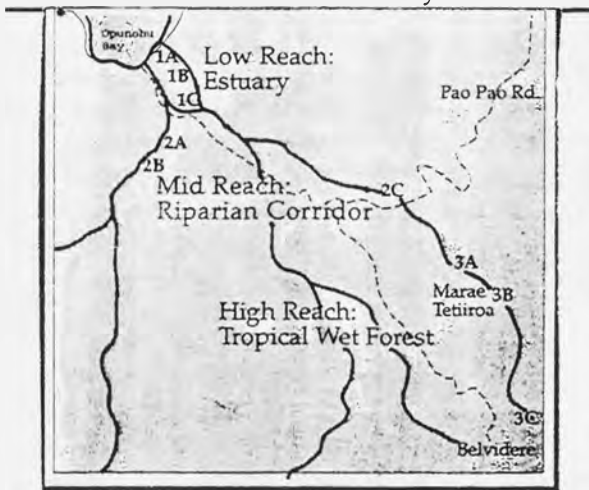
Low Reach: 1A, 1B, 1C
   at 0-2m
Mid Reach: 2A, 2B, 2C
   at 5-16m
High Reach: 3A, 3B, 3C
   at 120-245m
Fig. 1.: Map of Moorea and the study sites in the Opunohu Basin.

Macrohabitat Comparisons

     Low reach sites 1A, 1B, and 1C (figure 1)were located at the mouth of the Opunohu, at 0.25km and at 0.40km upstream, respectively. The mouth region is best described as an estuary (Caulpin 1986). Saline effluent from an adjacent shrimp-farm and bay water continually inundates the mouth area. As a result, conductivity, an indirect measure of salinity, is highest in the low reach (55-103uS). The low reach sites in this study are characterized by a sparse canopy cover and minimal leaf litter. Substrates are of small

size at the three low reach sites; mostly silt, gravel and small pebble. The vegetation along banks and pools is dominated by the mangrove fern *Acrosticrum aureum* , which often enters the water column.

     Sites 2A, 2B, and 2C (figure 1), the mid reach sites, were located further up the Opunohu basin, at 0.7km, 1.0km and 1.7km from the mouth, respectively. 2A and 2B were situated on the west fork of the Opunohu, above the first bridge of the Opunohu Valley Rd.. Distinguishing features of these two sites are the lack of canopy cover and the ubiquitous presence of the introduced macrophyte, *Wilkstroemia* sp. *Wilkstroemia* blankets banks and enters all stream microhabitats. Site 2C, positioned along the east fork of the Opunohu, below the Pao Pao Rd., differs from sites 2A and 2B by having a dense canopy composed of a thick *Inocarpus fagiferus* and *Hibiscus tiliaceus* overstory but only sparse mats of *Wilkstoemia* sp. All mid reach sites are bordered by pastures and/or farms. As a result, macrohabitat along this stretch of the Opunohu is characterized by a narrow band of riparian vegetation. This reach is not tidally influenced (conductivity=2uS). Leaf litter covers 30-50% of the floodplain. Typical substrates are pebble, cobble and boulder.

     High reach sites 3A, 3B and 3C (figure 1), were deepest in the Opunohu catchment at 2.8km, 3.0km and 3.6km from the river mouth. Sites 3A and 3B were near the Marae Tetiiroa, in tropical wet forest. Site 3C, behind the Belvidere lookout, was located in tropical cloud forest. Canopy closure is complete, with a dense *Inocarpus, Hibiscus* overstory and *Angiopteris* sp. understory. Leaf litter is plentiful, covering 50-90% of the floodplain area. Stream gradient is highest in this reach (slope=15-40%), and bank erosion high. The high reach sites were characterized by alternating riffle-pool microhabitats. This reach is also characterized by high flow rates and large substrates such as, pebble, cobble and boulder.

Physical characteristics of the study sites are presented in Appendix 1.

Microhabitat Comparisons

     Physical measurements were adopted to characterize microhabitats and to ascertain which microhabitat variables were important

in determining shrimp presence and abundance. Quantitative measures of water velocity, depth and width were attained for each microhabitat. Qualitative descriptions of substrate type, substrate embededness and benthos composition were also taken at each microhabitat. Using the Wentworth scale of substrate size, particle diameter was used to asses substrate type (Table 1; adopted from Cummins 1962). The benthos of each microhabitat was described in terms of percent rooted vegetation, leafy material and rock.

SIZE CLASS	DIAMETERmm
Boulder	>256
Cobble	
Large	128-256
Small	64-128
Pebble	
Large	32-64
Small	16-32
Gravel	
Coarse	8-16
Medium	4-8
Fine	2-4
Sand	
Very Coarse	1-2
Coarse	.5-1
Medium	.25-.5
Fine	.125-.25
Very Fine	.063-.125
Silt	<.063

Table 1. Wentworth scale of particle size

Sampling methods

Six microhabitats were sampled: riffle, run, pool, leaf pack, bank with vegetation, bank without vegetation. However, leaf packs were absent from the deeper channeled estuarine sites (ie 1A, 1B, 1C) and banks with vegetation were lacking in the shaded high reach sites (ie 3A, 3B, 3C). Riffles are high-water velocity sections of a stream, defined by nonlaminar flow. In this study, riffles always had a water velocity between 20m/min and 60m/min. Runs are shallow troughs that generally have smooth, laminar flows of slow to moderate velocity (Cauplin 1986). Runs always had water velocities below 20m/min. Pools were classified as static portions of the stream with

a water velocity of 0m/min. Leaf packs are small (0.3-1.5m) bundles of leaves caught against boulders or large debris. They are usually associated with riffles but sometimes occur in pools. Stream embankments in which terrestrial macrophytes such as *Acrosticum* and *Wilkstroemia* enter the water and cover >50% of the submerged bank are considered banks with vegetation. Banks without vegetation were defined as areas barren of any vegetation.

Shrimp were collected with an aquatic D-frame net with a 500um mesh. Fifteen dips with the D-net were made for each microhabitat. Leaf pack collections were made by scooping entire packs into the net. *Atyoida pilipes* and *Caridina weberi* were identified by differences in cheliped setae, rostral spines and shape, and scaphocerite morphology (pers obser.). While species of the genus *Macrobrachium* were easily distinguished from Atyids, they were difficult to distinguish from each other. In this study, different species of the genus *Macrobrachium* were treated as a single group alled *Macrobrachium* sp. To measure microhabitat preference among these shrimp, each species was identified and tallied for every microhabitat. Six replicates were obtained for each microhabitat at every site. Type specimens were collected from mid reach and high reach sites on the 30th of October. They were preserved in 90% ethanol and shipped to the UCMP at Univ. Calif. Berkeley.

Finally, a pairwise correlation test was run on relative shrimp abundance and important habitat variables using JMP stat package. Habitat factors included: surface velocity (m/min), conductivity (uS), elevation (m), distance from mouth (km), substrate type (Wentworth particle size), percent rooted vegetation, and percent leafy material. Correlations are reported in appendix II.

Functional Feeding Group Analysis

Studies that support, dispute or rely on RCC predictions as an appropriate description of lotic ecosystems are based on functional feeding group composition (Grubaugh et al. 1996). It was necessary then, to establish the functional role, or guild, of each shrimp species and speak of this guild in terms of shredder, collector or grazer.

Shred Test

Atyoida pilipes, Caridina weberi and *Macrobrachium* sp were collected from the three reaches of the Opunohu river and separated into 8oz plastic containers. Water was changed daily for treatment and control groups. Shrimp were starved for 4-7days until their guts had cleared. Shrimp were then presented with 7 cut 3cm discs of stream caught Hibiscus and Inocarpus leaves. Each disc was unmoistened with a paper towel and weighed. Dry weight was not taken because leaf periphyton would have been damaged in the process. After 10 days the status of shrimp was evaluated based on characters such as foregut and hindgut empty or full and gravid females still gravid or eggs resorbed. Leaves were checked for physical damage and reweighed. Treatment and control group leaves were compared using ANOVA.

Collector Test

Eight *A. pilipes* and 15 *C. weberi* were collected from high reach and mid reach sites. These were placed separately into a flow tank and observed for 30 minutes. The flow tank resembled the bottom half of a plastic trash can and was approximately 25gal in volume. A hose was attached and kept flush up against one side. At full force the hose created a circular flow. One stone was placed into the tank to provide refuge and substrate to the shrimp. Detritis was added to elicit filter feeding, or collector behavior.

Results

Macrohabitat Comparison

A total of 2,681 shrimp were sampled along the Opunohu catchment. *Macrobrachium* sp. was numerically dominant in this study, representing 49% (1314 individuals) of Opunohu shrimp. *C. weberi* was slightly less numerous, composing 39% (1048 individuals) of Opunohu shrimp. *A. pilipes* was least abundant, consisting of only 12% (319 individuals) of the shrimp found in the Opunohu. Shrimp were found at all locations, from 0m to 245m in elevation.

The low reach sites (1A, 1B, 1C) consisted singly of the Palaemonid shrimp, *Macrobrachium*. Both Atyid species were completely absent from this estuarine area

(figure 2;). 43% (563) of *Macrobrachium* were collected here.

Mid reach sites (2A, 2B, 2C) contained all three shrimp species. These sites were numerically dominated by *Macrobrachium* and *A.pilipes* while only scant numbers of *C.weberi* were observed (figure 2). Community structure of benthic macroinvertebrates at the mid reach sites consisted of 63% *Macrobrachium*, 30% *A.pilipes* and 7% *C. weberi* . Slightly more *Macrobrachium* were found at the mid reach sites (571) than at the low reach sites. However, the percent of *Macrobrachium* collected in the Opunohu was the same at this reach as it was in the lower reach (43%). 81% (261) of *A. pilipes* were obtained at the three mid reach sites. Only 6% of Opunohu *C. weberi* were found at the mid reach sites.

The three high reach sites (3A, 3B, 3C) were dominated numerically by *C.weberi* . *Macrobrachium* and *A.pilipes*, on the other hand, were much less abundant (figure 2). The results of the macrohabitat comparison show that the numbers of *C. weberi* rise dramatically in high reach sites while numbers of *A. pilipes* and *Macrobrachium* fall in high reach sites. In fact *C.weberi* composes 80% of the high reach macroinvertebrate community. The formerly dominant *Macrobrachium* and *A. pilipes* compose only 15% and 5%,respectively, of this high elevation benthic community. 94% (981) of *C. weberi* occur in this reach of the Opunohu. But only 15% (182) of *Macrobrachium* and 19% (58) of *A. pilipes* sampled in the Opunohu were collected at the high reach sites.

Microhabitat Comparison

The results of the microhabitat sampling show associations between shrimp species and certain microhabitats (figure 3).

Macrobrachium is seen most often in banks with vegetation, pools and runs (figure 3). It is not associated with riffles or leaf packs and occurs only infrequently in banks without vegetation. Of the 1314 sampled *Macrobrachium*, 436 came from banks with vegetation, 381 from pools, 244 from runs, 116 from banks without vegetation, and only 34 from riffles and 30 from leaf packs. Statistical analysis correlating shrimp abundance to microhabitat variables shows that *Macrobrachium* is positively correlated with rooted macrophyte vegetation

(r=0.5397;appendix II). *Macrobrachium* is also negatively correlated with high water velocity (r=-0.3103).

A. *pilipes* occurs in only two microhabitats: riffles and leaf packs (figure 3). Figure 3 shows that *A. pilipes* is not associated with any other microhabitat. Of the 319 *A. pilipes* gathered from the Opunohu, 222 were found in leaf packs, 86 in riffles, 7 in runs, 4 in pools, 0 in banks with vegetation and 0 in banks without vegetation. It should be noted that all the leaf packs from which *A. pilipes* were taken, were located in high flow riffles. In fact, correlation analysis reveals that *A. pilipes* is positively correlated with only one microhabitat variable, surface velocity (r=0.4459; Appendix II).

C. *weberi* occurs in all microhabitats but is distributed most abundantly in runs and pools (figure 3). 1048 *C. weberi* were collected from the Opunohu catchment. 474 were found in runs, 326 in pools, 104 in leaf packs, 91 in banks without vegetation, 30 in riffles and 23 in banks with vegetation. No distinct correlation between *C. weberi* abundance and microhabitat variables were detected.

However, correlations betwen *C. weberi* and macroscale gradients such as elevation and distance to mouth were made (elev, r=0.6206; dist, r=0.5892)

Functional Feeding Group Analysis
  Shred Test
    Hibiscus leaves kept with *Macrobrachium* and *C. weberi* display visible physical damage as well as significant weight loss in comparison to control leaves (p=0.0005). *Hibiscus* leaves kept with *A. pilipes* show only minor external damage and no significant weight loss.

Hibiscus leaves kept with *Macrobrachium* decreased in weight by 65%. Two leaves were eaten fully while one was left untouched. Leaves were chewed from the periphery inward. Foreguts and hindguts were generally full and gravid females remained gravid.

Hibiscus leaves kept with *C. weberi* lost 72% of their initial weight. Every leaf kept with *C. weberi* decreased in weight and revealed physical damage. Leaves appeared scrapped and bored from the inside out. Only
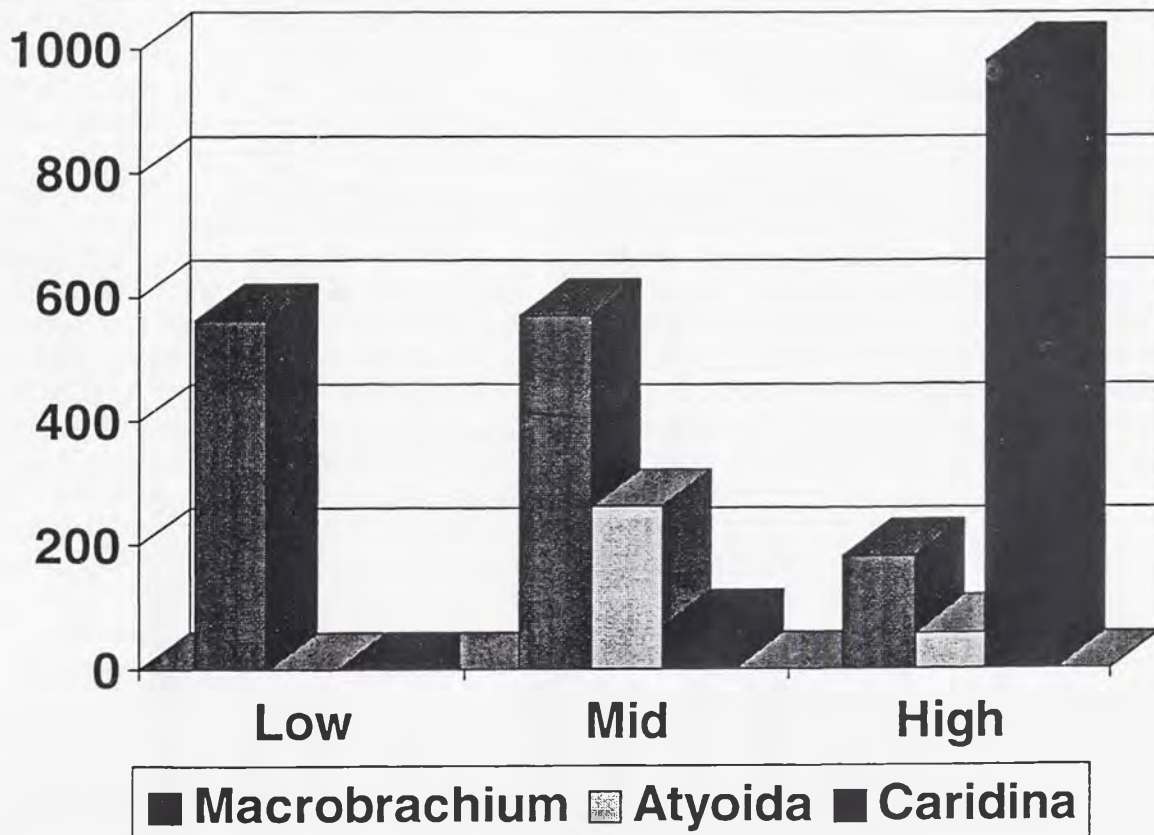

Figure 2. Relative abundance of Opunohu shrimp.

"leaf skeletons" of lignified viens remained. *C. weberi* guts were full and gravid females remained gravid.

    Hibiscus leaves kept with *A. pilipes* lost only 34% of their initial weight. This amount of weight loss was not significantly different from the fluctuation in weight of the control leaves which gained in weight by 13%. The leaves did, however, show some visible damage. Their surfaces looked slightly gleamed or grazed, as if a fine top layer had been removed. Other evidence of leaf consumption by *A. pilipes* in the laboratory includes partly full fore guts and hind guts as well as ovigerous females.

    Inocarpus leaves kept with *Macrobrachium* and *C. weberi* showed only slight physical damage and did not drop in weight appreciably. Treatment leaves decreased in weight by only 5% for both *Macrobrachium* and *C. weberi* . Furthermore, control *Inocarpus* leaves gained in weight by nearly 3%. ANOVA showed the difference between control and treatment leaves to be insignificant (p=0.49). Thus, weight lost by treatment leaves is not necessarily explained by shrimp detritivory but may lie within the natural weight fluctuations of decaying leaves. (*A. pilipes* was not used in this experiment because of a lack of suitable specimens).

Collector Test

    After 30 minutes of constant water flow, two of the eight *A. pilipes* and 0 of the 15*C. weberi* were observed filter feeding. Both species would generally orient perpendicular to the current. *A. pilipes* made quick, alternating side to side sweeps with its chelipeds while remaining stationary.

C. weberi was also seen making similar chelipeds sweeps. However, only *A. pilipes* filter fed. Both pairs of chelipeds were used. The chelipeds were held forward and extended far to the side, facing the current. Chelipeds were opened and setae extended. Chelipeds were quickly and intermittently closed and brought to the mouth then rapidly repositioned against the current.

Discussion

Functional Feeding Groups and Microhabitat preference

    Atyid shrimp are a dominant faunal component in many tropical streams (Pringle and Blake 1994). Yet little is known of the function of these Atyid shrimp (Covich 1988b). By classifying the freshwater shrimp of the Opunohu catchment into functional feeding groups based on behavioral modes of feeding and morphologies of the food acquisition system, we can gain insight on the capacity of these stream invertebrates to consume available food resources (Cummins and Klug 1979; Grubaugh et al. 1996). The patchiness of these preferred resources as well as the predictable longitudinal distribution of organic material will then determine the microhabitat and macroscale distributional patterns of these benthic shrimp (Sites and Willig 1991; Vannote et al. 1980).

    The described feeding morphology and observed feeding behavior of *A. pilipes* suggest it is a filter feeder. The filter feeding behavior of *A. pilipes* in the laboratory is consistent with field and lab observations on the filter feeding behaviors of the related*Atya* sp. (Cowles 1915; Fryer 1977; Felgenhauer and
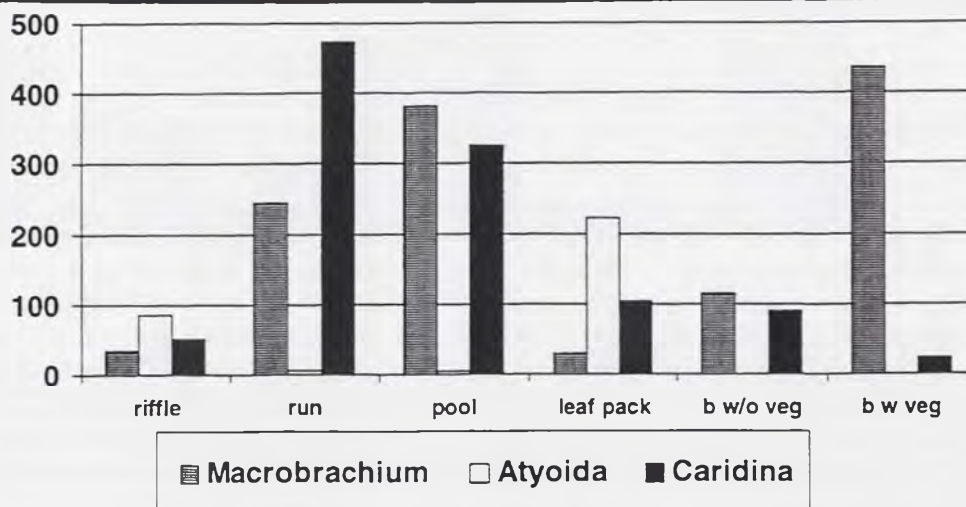

Figure 3. Microhabitat preference of Opunohu shrimp.

Lawrence 1983; Covich 1988b). The morphological similarities in cheliped structure and setae between the two genera further strengthen the idea that *A. pilipes* is a collector (Resh et al. 1992). If *A. pilipes* is described as a collector then its well defined microhabitat distribution is explained. *A. pilipes* is associated only with riffles and leaf packs. Investigating further, I found that *A. pilipes* occurred only in leaf packs that were located in "riffle" flow areas. Correlation analysis suggested that high *A. pilipes* abundance and high surface velocity were linked. Fryer (1977) and Covich (1988) hold that choice of microhabitat among filter feeding Atyids is primarily related to flow rate.

The feeding morphology and behavior of *C. weberi* suggest it is a detritivore, able to consume CPOM, and thus a shredder. (Cowles 1915; Fryer 1960, 1977). Laboratory results suggest it can scrape and masticate large leaf litter. Weight lost by *Hibiscus* presented to *C. weberi* (72%) was greater than weight lost by a temperate leaf presented to a known shredder for a similar length of time (40%)(Cummins and Petersen 1973). However, *C. weberi* was not associated with leaf packs nor correlated with leafy material. This can be explained by the tiny mouth parts of members of the Atyidae which prevent them from masticating or shredding the larger leafy material in leaf packs (Fryer 1960, 1977). Instead *C. weberi* is associated with slower flow microhabitats such as runs and pools which accrue CPOM.

Macrobrachium has been described as a generalist and an algal grazer (Thorp and Covich 1991;Wong 1996). Feeding behaviors in the lab also suggest it is an opportunist. Field dissections confirm its role as a grazer, however. *Macrobrachium* is most commonly associated with rooted vegetation. Terrestrial macrophytes may provide food or stabilize organic matter entering the system (Schiemer and Zalewski 1992). *Macrobrachium* seems to avoid high flows, and rooted vegetation provides a good buffer from rapid water.

RCC Comparison

Covich (1988a) points out that neotropical streams differ from temperate streams in age, geology, nutrients, temperature, biogeography and constancy. He holds that these differences make temperate and tropical streams difficult to compare. Yet macroscale distributional patterns of Palaemonid and Atyid shrimp make sense in the light of their respective functional feeding groups and the RCC. Figure 4 highlights the similarities between the RCC predictions and the macroinvertebrate communities of the Opunohu catchment. In the head waters, leaf litter input is highest. Leaf retention in the high reach streams is also highest as is leaf decomposition (Khandwala pers. comm.). Canopy is dense in the high reach, keeping algal productivity low. The RCC predicts a community of macroinvertebrates dominated by shredders with some collectors and few grazers. In the Opunohu we see a pattern similar to the one predicted by the RCC. *C. weberi* dominates the high reach, closed canopy sites while *Macrobrachium* numbers are at their lowest here. *A. pilipes* is also seen here in fair proportions (with respect to its total sample size). As canopy opens up and nutrients spiral downstream, we expect a community of grazers and collectors. The Opunohu shows exactly that. *Macrobrchium* and *A. pilipes* dominate the mid reach sites, each partitioned into its own microhabitat. With a lack of allochthanous input, *C.weberi* numbers are low in the mid reach sites. At the mouth, we expect a community run singly by collectors. The mouth of the Opunohu, however, is dominated by *Macrobrachium*, an opportunistic grazer. Why is the collector absent.? Where is *A. pilipes*?Perhaps salinity, predation by Pacific fish, substrate or lack of suitable riffle microhabitats excludes colonization by these Atyids. Over the entire Opunohu ecotone, however, it can be seen that the invertebrate functional communities have arranged themselves in a manner similar to the one proposed by the RCC.

Conclusions

Microhabitat and macroscale distributions among three species of shrimp were determined. Important local and longitudinal characters were flow velocity, elevation and canopy closure. Patterns of community structure and function are similar to those predicted by the RCC.

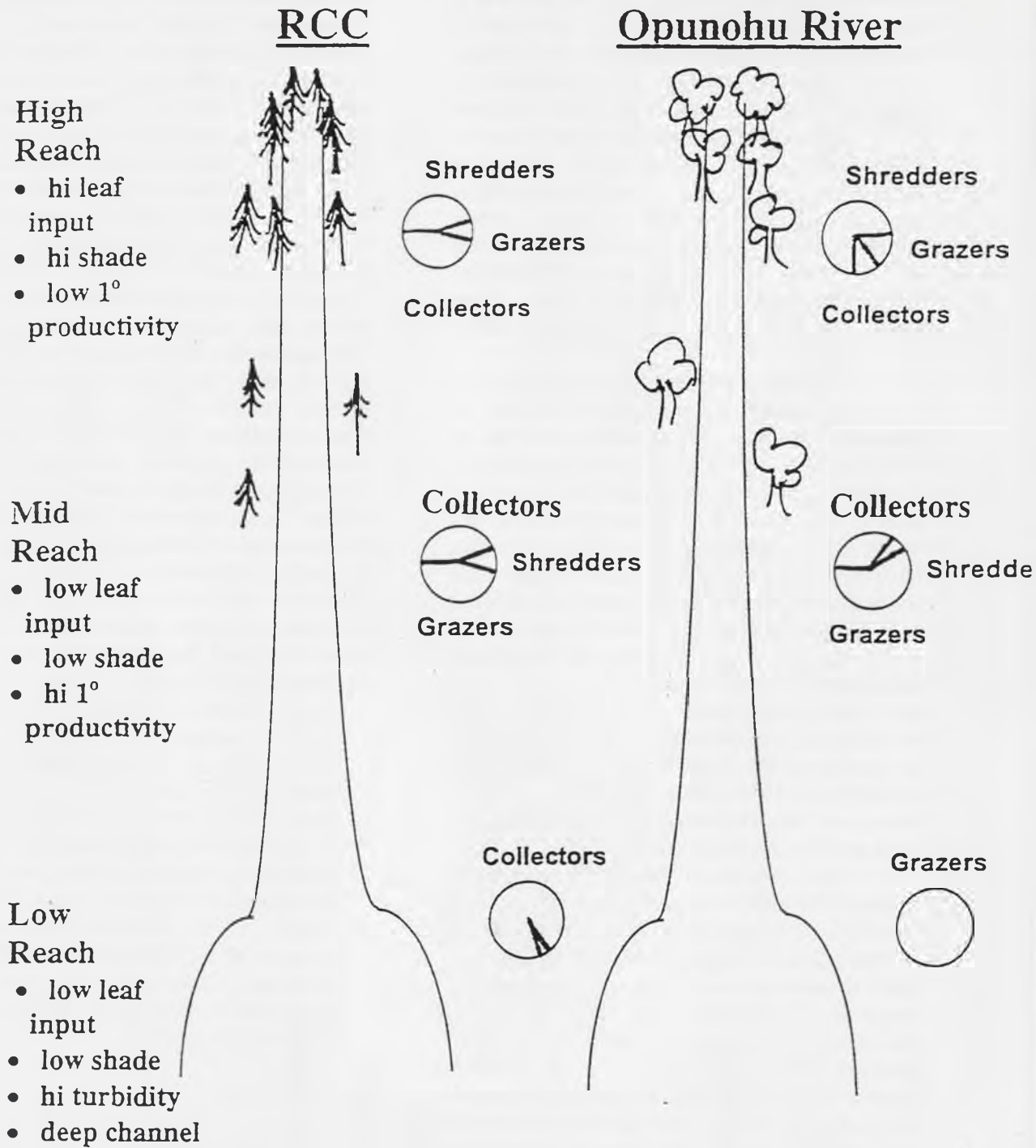The Society Islands are only 0.3-4.3 millon years old. Thus the community

Figure 4. Comparison between the RCC and measured community structure in the Opunohu catchment.

structure in the Opunohu catchment has been established in a relatively short amount of time. This leads to questions of stability over time, both phylogenetically and functionally.

Will riverine ecosystems always establish themselves in patterns similar to the RCC regardless of the taxa involved?

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Appendix I: Physical Characteristics of sites

site	locale	macrohabitat	bank errosion	catchment litter	floodnplain litter	canopy cover	turbidity	dom. veg	Algae	condct (uS)	slope (%)	elev (m)	dist from mouth (km)
1A	Mouth of Opunohu	Estuary	Low	Low	Low	Low	Turbid	Hibiscus / Acrosticum	Yes	103	<5	0	
1A	Mouth of Opunohu	Estuary	Low	Low	Low	Low	Turbid	Hibiscus / Acrosticum	Yes	103	<5	0	0
1B	250m up from Opunoh	Estuary	High	Low	Low	Low	Turbidity	Hibiscus / Acrosticum	Yes	68	<5	0	0
1C	Confluence of Opunoh	Estuary	High	Low	Low	Moderate	Turbidity	Hibiscus / Acrosticum	Yes	55	<5	2	0.25
2A	W. Fork of Opunohu; 1	Riparian Corric	Low	Low	Moderate	Low	Clear	Wilkstroemia / Hibiblscus	Yes	2	<5	5	0.4
2B	W. Fork of Opunohu; 1	Riparian Corric	Low	Low	Moderate	Low	Turbid	Wilkstroemia / Hibiblscus	Yes	1	<5	10	0.7
2C	E. Fork of Opunohu; 1	Riparian Corric	Low	Dense	Moderate	Dense	Clear	Wilkstroemia / Hibiblscus	Yes	2	<5	16	1
3A	Below Marae Tetiiroa	Tropical Wet F	High	Dense	Dense	Dense	Clear	Inocarpus / Hibiscus / An	Yes	2	15	120	1.7
3B	Marae Tetiiroa	Tropical Wet F	High	Dense	Dense	Dense	Clear	Inocarpus / Hibiscus / An	Yes	2	15	140	2.8
3C	Belvidere	Tropical Cloud	High	Dense	Moderate	Dense	Clear	Inocarpus / Hibiscus / An	Yes	2	40	245	3.6

Appendix II: Pairwise Correlation Analysis for Important Microhabitat variables

Correlations

Variable	Conductivity (microS)	Elevation (m)	Dist. from Mouth (km)	Atyoida pilipes	Caridina weberi	Macrobrachium sp.	Surface Vel. (m/min)	% Rooted Veg	Leafy material	Substrate Type 1
Conductivity (microS)	1.0000	-0.4385	-0.6718	-0.1684	-0.2818	0.2360	-0.2950	0.0417	-0.3942	-0.5652
Elevation (m)	-0.4385	1.0000	0.9255	-0.0583	0.6206	-0.3162	0.0468	-0.0622	0.1744	0.4059
Dist. from Mouth (km)	-0.6718	0.9255	1.0000	-0.0177	0.5891	-0.3595	0.1653	-0.1158	0.2882	0.5640
Atyoida pilipes	-0.1684	-0.0583	-0.0177	1.0000	-0.0794	-0.1025	0.4459	-0.0993	0.3692	0.2043
Caridina weberi	-0.2818	0.6206	0.5891	-0.0794	1.0000	-0.1405	-0.1787	0.0096	0.1419	0.1341
Macrobrachium sp.	0.2360	-0.3162	-0.3595	-0.1025	-0.1405	1.0000	-0.3103	0.5397	-0.2635	-0.3311
Surface Vel. (m/min)	-0.2950	0.0468	0.1653	0.4459	-0.1787	-0.3103	1.0000	-0.1344	0.1765	0.4499
% Rooted Veg	0.0417	-0.0622	-0.1158	-0.0993	0.0096	0.5397	-0.1344	1.0000	-0.3050	-0.1915
% Leafy material	-0.3942	0.1744	0.2882	0.3692	0.1419	-0.2635	0.1755	-0.3050	1.0000	0.4113
Substrate Type 1	-0.5652	0.4059	0.5640	0.2043	0.1341	-0.3311	0.4499	-0.1915	0.4113	1.0000

5 rows not used due to missing values.

A Behavioral and Ecological Phylogeny of the Freshwater *Neritidae* on Moorea

Jennifer Rose Conners
Department of Environmental Science, Policy and Management
University of California, Berkeley 94720

ABSTRACT. Five species of freshwater Neritid snails were observed in the field and in the laboratory to designate characters upon which a phylogeny could be based. The 12 resulting characters were either of a behavioral or ecological nature. Using a marine outgroup for polarity, 105 trees were analyzed. The most parsimonious tree (length=22) was selected for comparison with a phylogeny based on Neritid radula morphology. Although differences were apparent, significant patterns were observed between the two trees indicating that the use of behavioral and ecological characters may be appropriate for determining phylogenetic relatedness.

Introduction

The family Neritidae contains approximately 200 living species in 5 main genera: *Nerita, Neritilia, Neritina, Smaragdia* and *Theodoxus* (Moore 1960). These snails occur in both marine and freshwater environments. On the island of Moorea, French Polynesia, five species of fresh water Neritidae have been identified: *Neritina auriculata, Neritina canalis, Neritina turrita, Septaria porcellana,* and *Clithon spinosa* (Resh et al. 1990 and 1992). (Appendix A)

Freshwater Neritids are thought to be descendants of marine *Neritidae* which colonized stream habitats (Ford and Kinzie 1982). This idea is supported by the natural history of the freshwater species which are diadromous, dependent on the marine environment for part of their life cycle (Haynes 1988). Adult Neritids migrate upstream to lay their eggs. After the eggs hatch, the veligers travel downstream to complete their larval developmental metamorphosis in brackish or full marine environments.

A recent phylogenetic study using morphological characters has indicated that the only true *Neritina* on Moorea is *Septaria porcellana* and that the genera names for *Neritina auriculata, Neritina canalis,* and *Neritina turrita* may be incorrect (Unabia, pers. com.).

A phylogeny can be constructed using a variety of different characters. Traditionally, morphological or molecular characters have been accepted by the scientific community (Ax 1987). However, the use of behavioral, functional and ecological characters is gaining support (DeQueiroz and Wimberger 1991; Hickman 1991 and 1996).

Assuming that the five freshwater species are monophyletic with respect to a marine outgroup, I intend to evaluate phylogenetic relatedness using ecological and behavioral characters. For purposes of this study, behavior of a snail is defined as any observable action or response and ecology is defined as the interaction between the organism and its environment (Lincoln 1982).

Materials and Methods

Survey and collection

Initial field observations were made at four sites on Moorea: the Opunohu river catchment (17 31'S, 149 S 50'W) and the Vairemu, Vainae and Uufau streams near Haapiti (figure 1). In addition to field observations, two surveys were conducted to document distribution of the Neritids, one at the Opunohu stream and the other at Uufau. Each survey began at the estruarine environment and continued at 40 meter intervals along the length of the stream. A five minute timed search was conducted at each site.

Figure 1. Study sites on Moorea.

Individuals of each species for use in laboratory experiments were collected from the Opunohu river catchment and the Vairemu stream, with the exception of *N. auriculata*. The smaller populations of *N. auriculata* necessitated the collection of individuals at all four sites to minimize the impact on each population.

Character designation

In studying the evolution from a marine environment to a freshwater environment, it is important to consider the action of natural selection on an organism's ecology (Baum and Larson 1991). However, Lewontin (1984) warns against the idea that an environment can be simplified into discrete problems for an organism to solve through adaptation. Because the evolution of a character can be influenced by several environmental factors together, it is important to consider character utility and historical genesis (Greene 1986a).

There are several guidelines for defining independent and useful characters. Characters must be able to be coded into two or more discrete states with differences between the taxa (Pimentel and Riggins 1987). The coding of character states should reflect proportional differences between taxa and remain unchanged through the addition of new taxa or improved sampling (Chappill 1989).

Using these character definition criteria and observations from field studies,

13 characters were proposed with corresponding character states. After assigning character states to each species, those states which involved percentages or other distinct categories were not analyzed statistically, unless there appeared to be variation within categories. Analysis of variance tests were run on several data sets using SYSTAT version 5.2 (Wilkinson et al. 1992) to delineate between character states when necessary.

Character analysis

Ecological characters

1. Substrate preference. O=prefers rocks, 1=no distinct preference. Species were tested separately to eliminate the possibility of competitive influence on substrate choice. Two individuals were placed in each of six compartments in an aquarium with flowing freshwater. Two compartments contained rocks, two contained leaves, and two contained a sand/dirt mixture, all collected from the Opunohu stream (figure 2). The compartments were arranged so that each substrate type was accessible from every starting point and free movement between compartments was allowed. Observations were made every twelve hours for six days to record the position of individuals in the tank. Rock preference was defined by the presence of individuals on rocks or the hard surface of the tank walls more than 75% of the time.

rock	leaf	sand
sand	rock	leaf

Figure 2. Substrate preference tank arrangement.

2. Flow preference. 0=highest flow preferred, 1=medium flow preferred. Flow preference was tested using a flow tank and a hose. 15 individuals of a species were placed on the bottom of the tank at random and allowed to crawl for a minute to establish a hold. The water was then turned

on as high as possible and the resulting movement of snails was observed. The bottom of the tank was divided into bands of equal width from the outside (highest flow) to the center (no flow). The position of the snails was recorded every five minutes for an hour. Flow preference was defined as the zone where each species was found more than 50% of the time.

3. Salinity tolerance. 0=intolerant, 1=tolerant. Five tanks of increasing salinity were created: 100%, 75%, 50%, 25%, and 0% salt water. Five individuals of a species were placed in each tank and observed after 2 hours to determine their status: alive or dead. Death, for all experiments, was determined to be the lack of response to a stimulus. Observations were recorded every 12 hours thereafter, for a total of 62 hours. Based on initial studies, a "tolerant" individual was defined as one which survived >24 hours in a 50% salt water solution. "Intolerant" individuals were those which did not survive 24 hours in the same solution.

4. Juvenile salinity tolerance. 0=tolerant, 1=intolerant. This test was intended to compare the adult salinity tolerance with that of a juvenile to see if tolerance changes with age. The testing was run the same way as the tests for adult salinity tolerance. Juveniles were classified by size, being smaller than 2mm in width.

5. Resistance to desiccation. 0=survives <72 hours without water, 1=survives>72 hours without water. 14 individuals of each species were placed in a tank and deprived of water. Observations were made every 12 hours to determine the number of live and dead snails. A species' limit with respect to desiccation was defined as the time when >50% of tested individuals were dead.

Behavioral characters

6. Period of activity. 0=nocturnal, 1=no distinct period of activity. Period of activity observations were coupled with substrate preference tests. At each observation time, the number of individuals grazing or otherwise moving around the tank was recorded as the number active. For purposes of this study, a species was defined as nocturnal if the number of active individuals at night was more than twice the number of active individuals in the morning. A species did not have a distinct pattern of activity if the number active at night and in the morning were similar.

7. Orientation to flow. 0=orient toward flow, 1=orient away from flow. Orientation toward or away from the direction of flow was recorded as flow preference observations were made. Each of the 15 individuals were observed every five minutes for an hour.

8. Detachment behavior. 0=falls off the rock <5% of the time, 1=falls off the rock >25% of the time, 2=falls off the rock >50% of the time. Rocks were turned over in the Opunohu stream and the Uufau stream at Haapiti. As the rock was lifted, the number and species of snails which fell off within two seconds were recorded along with the number and species which remained attached. A total of 100 individuals of each species were counted.

9. Righting behavior. 0=<1 minute, 1=1-7 minutes, 2=fewer than 50% righted themselves. 15 individuals of each species were placed on their backs on a wet concrete surface. The number of individuals which had turned themselves over onto their foot were recorded every minute for the first ten minutes. After this period, observations were made at 15, 20, 30 and 45 minutes. Righting speed was defined as the time by which more than 50% of tested individuals had completely righted themselves.

10. Behavior in standing water. 0=crawls up and/or away from standing water, 1=remains in place. 12 individuals of each species were placed in a rectangular container filled halfway with fresh water, except in the *Nerita plicata* test, where salt water was used. Snail position with respect to four zones was recorded every 2 hours of a 6 hour period. (Figure 3). The area on the bottom of the container, the starting point for the snails, was designated Zone I. Zone II described both sides of the container. Zone III described the area 15cm from the container, and Zone IV referred to any area beyond these zones. If the majority of a species' representatives remained in zones I and II, a character state of 0 was assigned. If

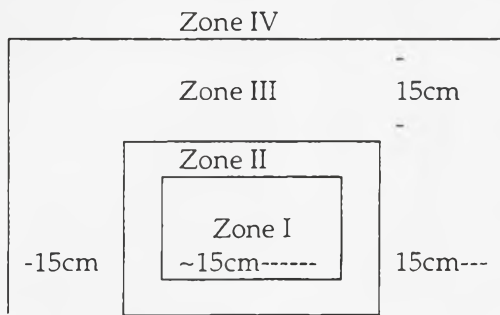the majority were found in zones III or IV, a character state of 1 was assigned.

Zone IV

Zone III   15cm

Zone II

Zone I

-15cm   ~15cm------   15cm---

Figure 3. Arrangement of zones for standing water behavior characterization.

11. Crawling speed. 0=fast, 1=medium, 2=slow. 20 individuals of each species were allowed to crawl on 30cm x 45cm sheet of wet glass. Measurements were taken one snail at a time, beginning with the first movement of the snail. The length of the path traveled over 1 minute was measured and average speed values calculated for each species. "Fast" was determined to be 16 cm/minute or faster, "medium" was 10-15.9 cm/minute, and "slow" was 0-9.9 cm/minute.

12. Community formation. 0=found in groups, 1=scattered. Two surveys were done in the field to record the distribution of species in the streams. Sampling sites were spaced 40 meters apart and five minutes were spent looking for snails at each site.

13. Grazing pattern. 0=grazed only on the slide, 1=grazed over an extended

area. Microscope slides were left in the Opunohu river catchment for two weeks, allowing a film of epiphytic algae to form. Five snails of each species were prevented from grazing for two days and then given the opportunity to graze on a slide in a tray of water. A "0" character state indicates the species grazed on the slide only, changing direction upon reaching the edge of the slide. A "1" character state indicates the species grazed over a wider area, and moved past the slide and onto the dish before returning to the slide.

Phylogenetic analysis

Results from character analysis tests were entered into MacClade version 3.0 (Maddison and Maddison 1992) for establishment of a matrix. The matrix was then analyzed by P.A.U.P. version 3.1.1 (Swofford 1993) for possible phylogenies based on the character states of each species. *Nerita plicata* was designated as the outgroup and used to polarize the phylogeny. *N. plicata* is thought to be the closest marine relative of the freshwater Neritids (Govindan and Natarjan 1972). Use of this species as an outgroup allowed for the assumption that the freshwater species are monophyletic.

Results

Character results

Character states were assigned for all of the characters except character 13, grazing pattern. (Table 1)

Table 1. Matrix of character states for 5 *Neritidae* species and the outgroup, *N. plicata*.

Character #	N. auriculata	N. canalis	N. turrita	S. porcellana	C. spinosa	N. plicata
1	0	0	1	0	0	0
2	0	1	0	1	0	0
3	0	1	1	1	0	?
4	0	0	1	0	1	?
5	1	1	0	1	1	0
6	1	1	0	1	0	?
7	1	0	1	1	0	0
8	0	2	1	0	0	?
9	2	2	1	2	2	0
10	1	1	0	1	1	0
11	2	1	1	2	0	0
12	0	1	0	1	1	0

1. Substrate preference. (Table 2) Substrate preference results showed that all species preferred rocks or hard surfaces to leaves and sand, with the exception of *N. turrita*, which was found on rocks only 2/3 of the time.

species	rock	sand	leaf
N. auriculata	87%	12%	1%
N. canalis	98%	0%	2%
N. turrita	62%	20%	18%
S. porcellana	96%	3%	1%
C. spinosa	98%	1%	1%

Table 2. Frequency of species on each substrate.

2. Flow preference. (Table 3) Flow preference was originally established with three character states, but after analyzing the final results, only high and medium flow preferences were assigned as states. *N. auriculata* and *C. spinosa* preferred high flow, and the other three species preferred medium flow.

	high flow	medium flow	low flow
N. turrita	20	66	26
N. auriculata	103	9	0
N. canalis	8	98	6
S. porcellana	14	90	8
C. spinosa	96	13	3

Table 3. Individuals found in each flow area.

3. Salinity tolerance. (Table 4) The results of salinity tolerance studies indicate a negative correlation between the concentration of salinity and the length of time an individual can survive in that environment. *N. turrita, C. spinosa* and *N. plicata* were most tolerant to salinity.

	100%	75%	50%	25%	0%
turrita	36	0	0	0	0
canalis	12	12	36	0	0
auric.	2	24	36	0	0
porc.	2	12	36	0	0
spin.	12	36	0	0	0
plicata	0	0	0	60	48

Table 4. Number of hours after which all individuals were dead. A "0" value means that after 62 hours, live individuals remained.

4. Juvenile salinity tolerance. (Table 5) *N. turrita* and *C. spinosa* juveniles were found to be most tolerant to salinity, which differs from the results of the adult salinity tolerance study.

	100%	75%	50%	25%	0%
turrita	0	0	0	0	0
canalis	2	2	24	0	0
auric.	12	12	24	36	0
porc.	2	2	2	0	0
spin.	0	0	0	0	0

Table 5. Number of hours after which all juveniles of a species were dead. "0" value means that after 62 hours, live individuals remained.

5. Resistance to desiccation. (Table 6) The most resistant species were *S. porcellana, N. turrita* and *N. auriculata*. *C. spinosa*, the least tolerant, survived less than 36 hours without water.

hrs.	aur.	can-alis	turr	plic ata	porc	spin.
12	1	0	0	0	0	0
24	1	0	3	0	0	1
36	2	5	3	1	0	14
48	2	8	6	1	0	14
60	3	14	6	11	0	14
72	3	14	7	14	0	14
84	14	14	10	14	0	14
96	14	14	14	14	0	14

Table 6. Total number of individuals dead

6. Period of activity. (Table 7) Period of activity data showed that four species, *N. auriculata*, *N. turrita*, *C. spinosa* and *N. plicata*, displayed nocturnal behavior. *N. canalis* and *S. porcellana* did not exhibit a marked pattern of activity.

	aur.	*can.*	*turr.*	*porc.*	*spin.*	*plic.*
a m	25%	58%	25%	42%	25%	8.3%
p m	67%	50%	83%	42%	92%	67%

Table 7. Percent of individuals active in the morning and at night.

7. Orientation to flow. (Table 8) Orientation to flow results show that *N. turrita* and *C. spinosa* oriented themselves away from the direction of flow the majority of time. *N. auriculata*, *N. canalis*, and *S. porcellana* oriented themselves towards the flow.

|	away	towards	neither
N. turrita	62	25	25
N. auric.	8	101	3
N. canal.	22	79	12
S. porc.	18	86	8
C. spin.	103	8	1

Table 8. Individual orientation.

8. Detachment behavior. (Table 9) *N.canalis* exhibited the detachment behavior with the highest frequency. *N. turrita* also exhibited the behavior, but not with the same frequency as *N. canalis*. *S. porcellana* and *C. spinosa* did not fall off rocks often, and *N. auriculata* never fell off a rock when turned over. (Figure 4)

species	yes	no
N. auriculata	0	100
N. canalis	61	49
N. turrita	26	74
S. porcellana	2	98
C. spinosa	27	73

Table 9. Number of individuals which did and did not exhibit the detachment behavior.

Exhibited behavior?
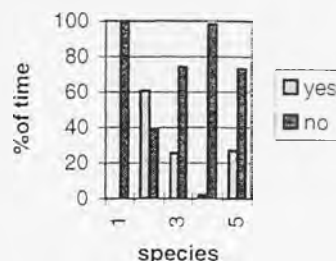
1=auriculata, 2=canalis, 3=turrita, 4=porcellana, 5=spinosa.
Figure 4. Detachment behavior results.

9. Righting behavior. (Table 10) Righting speed results showed that *N. plicata* could right themselves quickly. *N. turrita* were able to right themselves, but not as quickly. *N. canalis, S. porcellana*, and *C. spinosa* were not adept at righting themselves. Values in the table refer to the percentage of individuals which righted themselves in the specified time category.

species	<1min	<10 min.	<45 min.
auriculata	0%	0%	13.3
canalis	0%	26.6%	26.6%
turrita	13.3%	93.2%	100%
plicata	73.3%	100%	100%
porcellana	0%	0%	0%
spinosa	0%	26.6%	26.6%

Table 10. Righting speed.

10. Behavior in standing water. (Table 11) Only two species, *N. turrita* and *N. plicata*, moved out of the container. The other species remained in the water.

species	ave. # in zones I/II	ave. # in zones III/IV
N. auriculata	12	0
N. canalis	12	0
N. turrita	3.5	8.5
N. plicata	1.5	10.5
S. porcellana	12	0
C. spinosa	12	0

Table 11. Behavior in standing water.

11. Crawling speed. (Table 12) Crawling speed values were averaged for determination of character states. *N. plicata* was the fastest, followed by *N. turrita*. *S. porcellana* crawled the slowest.

An analysis of variance test indicated that significant differences existed between species (P<.05). A post hoc Tukey test showed no significant difference between *N. auriculata* and *S. porcellana* (P=.334), *N. canalis* and *N. turrita* (P=.105), and *N. plicata* and *C. spinosa* (P=.99), but significant differences between each of the three pairs.

Species	ave. speed (cm/min.)
N. auriculata	6.6
N. canalis	10.9
N. plicata	16.5
S. porcellana	8.1
C. spinosa	16
N. turrita	12.9

Table 12. Average crawling speeds.

12. Community formation. Community formation results were based on results of the distribution survey. Data did not lend itself to a statistical analysis, but patterns are easily observed by looking at the data table. *N. canalis* and *C. spinosa* were observed to be widely distributed along the length of the streams. The same pattern existed with *S. porcellana*, but with less density. *N. auriculata* and *N. turrita* exhibited group formation, occurring in distinct bands within the stream. (Appendix B)

13. Grazing pattern. (Table 13) Grazing pattern data indicated that two discrete character states may exist, however with only 4 replicates, data was insufficient to support the assignment of character states to each species.

species	yes	no
auriculata	4	1
canalis	4	1
turrita	0	5
porcellana	5	0
spinosa	1	4

Table 13. Specific grazing behavior.

Phylogenetic analysis

Analysis of the matrix with PAUP resulted in 105 trees evaluated, the longest with a length of 30 and the shortest with a length of 22. The most parsimonious tree is shown below. (Figure 3)
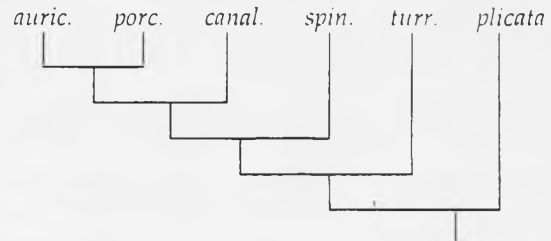

Figure 5. The phylogeny of freshwater *Neritidae* with *plicata* as the out-group.

Discussion

The results of the character studies are generally consistent with expected results formed from initial field observations. One exception is *S. porcellana*'s resistance to desiccation. This is surprising because of all five species, *porcellana* is the only one without an operculum, a protective structure which can be used to shield the soft body of the snail from the environment or predators. It would seem that without an operculum, *porcellana* would be vulnerable to changing environmental conditions. The data, however, did not reflect any vulnerability: *S. porcellana* exhibited the greatest resistance to desiccation. This can be explained by the way *porcellana* was observed adhering tightly to the rocks and glass wall of the dry tank. A seal was created which appears to serve the same function as an operculum, perhaps even more effectively.

This example brings into question the role that morphology plays in behavior and ecology. In looking over the list of characters, it is evident that shell morphology may have a significant influence over the interaction between a snail and the stream environment. For example, *auriculata* and *porcellana* both have flat shell shapes which could affect their migration upstream. Although their shell shapes are the result of convergent evolution, an ecological phylogeny might interpret their similarities as

synapomorphies. This idea underscores the importance of choosing characters which are independent of other influences.

Looking at the phylogeny itself, we are able to infer what Bigelow (1958) terms "the relative recency of common ancestry." This phylogeny indicates that *N. auriculata* and *S. porcellana* are the most derived taxa, followed by *N. canalis, C. spinosa* and then *N. turrita*, the least derived species.

Although this phylogeny is the most parsimonious given our matrix data, it is not the best tree. Theoretically the most parsimonious phylogeny, the most simple explanation of evolutionary relatedness, would only have a length representative of the number of adaptations which have occurred.

To examine the integrity of the phylogeny, it is important to look at the characters used to separate the species. The role of behavioral and ecological characters is still being disputed, but becoming more accepted for organisms whose behavior and function may have strong genetic underpinnings (Hickman 1991).

A comparison between the behavioral and ecological phylogeny and an obtained phylogeny based on radula morphology shows differences between the arrangement of species on the tree (C. Unabia pers.com.). However, patterns of similarity do exist between the two trees: Both trees show *N. auriculata, C. spinosa* and *S. porcellana* as consistently occurring at the most derived end of the tree. Also, both trees indicate that *N. turrita* is most closely related to the outgroup, *N. plicata*.

The problem with a direct comparison between the two trees is that the morphology-based tree takes into account 16 species, some of which affect the placement of the 5 shared species on the tree. Also, the phylogeny used for comparison is actually a 50% majority-rule consensus of 13 trees, so it is possible that more similarities or differences would result if the behavioral and ecological phylogeny was compared to each of the 13 most parsimonious morphological trees.

Conclusion

It can be concluded that important similarities exist between the behavioral and ecological phylogeny and the phylogeny based on radula morphology. Further study with a greater number of characters might result in a more definitive and parsimonious phylogeny. If carefully analyzed to ensure independence from other factors, ecological and behavioral characters may be an effective way to elucidate the nature of phylogenetic relatedness.

Acknowledgments

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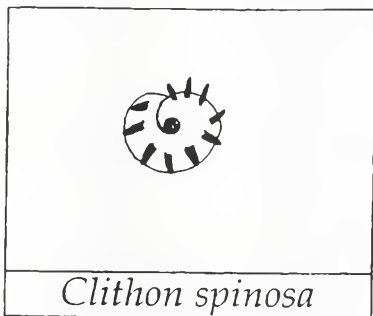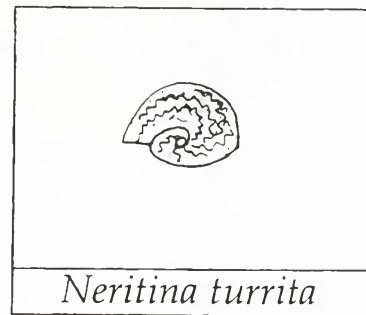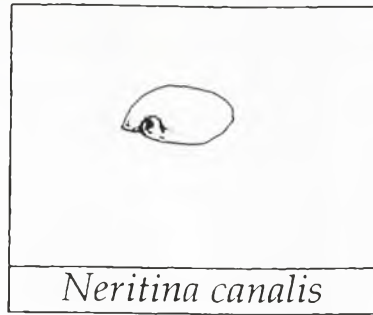
Appendix A. The five freshwater gastropods on Moorea, and *N. plicata*, the marine outgroup.

Appendix B. Individuals found during two surveys at Opunohu and Vairemu Rivers.

site	N. auriculata	N. canalis	N. turrita	S. porcellana	C. spinosa
1	32			25	
2		5	5		1
3		6	6		
4		39	13	4	
5		19	16	2	
6		5	25	6	
7		25	5	5	1
8		23			
9		7		2	1
10		17			3
11		9		1	2
12		8		1	1
13		11			2
14		6			2
15		7			2

1	27				
2	30				
3	6	30			19
4		7		1	9
5		5			13

6		10		2	29
7		1		1	11
8		5			6
9		5	12	1	4
10		4	18		9
11			26	1	4
12		3	7	1	2
13				3	3
14		16			5
15		3		2	
16		4		1	3
17		5		4	2
18		2		1	7

3