Environmental Science Policy and Management 107,
Geography 142, and Integrative Biology 158

# The Biology and Geomorphology of Tropical Islands

## Student Research Papers, Fall 1998


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

University of California, Berkeley

**Environmental Science Policy and Management 107, Geography 142, and Integrative Biology *158***



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**Above:** Cook's Bay, Moorea, from the Gump Biological Station.

**Book cover:** Map of Tahiti and Moorea drawn by Lieutenant James Cook in 1769. The title of the map is "A Plan on King George's Island or Otaheite, by Lieutenant J. Cook. Discovered by Cap Wallis the 19th June 1767". Moorea, to the left, is labeled "York Island called by the natives Imaio". Cook joined the Royal Navy at the age of 28, after having sailed merchant colliers (coal ships) along the coast of Britain. He was promoted to Lieutenant on 15 April 1768 and given command of *His Majesty's Bark Endeavour,* which he was instructed to sail to the Pacific to observe the Transit of Venus across the face of the Sun and to search for a great southern continent. Cook set up a fort at Point Venus in Matavai Bay, shown at the northern tip of Tahiti. Cook and Joseph Banks sailed entirely around Tahiti and produced a fairly accurate map. On June 2, a party including Banks rowed a small boat the 10 miles to Moorea. Cook notes in his Journal that the men "were well received by the Natives; that Island appear'd to them not to be very fruitfull". It shows in the very inaccurate map of Moorea. If only Cook had been with our 1998 Moorea Class he would have realized he passed up one of the jewels of the Pacific.

*From left to right: Back row (standing):* Dr. Jere Lipps (instructor), Dan Firestone, Eric Crandall, Miles Zajaczkowski, Kevin Cooney, Virginia Rich, Will Satterthwaite, Joe Talavera, Sarah Graber, Virginia Matzek (GSI), Dr. David Stoddart (instructor), Tegan Chrucher (GSI). *Third row (standing):* Laura Cossey, Audrey Bowers, Yoko Chavez. *Second row (kneeling):* Catarina Nerney, Peter Vallejo, Melanie McCutchan, Amy Lesen (GSI), Julio Gutierrez, Shannon Murphy, Sikina Jinnah, Heather Wright, Jessica Gelay. *Front row (sitting):* Kasha Parker, Kathleen Sims, Jamison Lipps, Rowan Roderick-Jones. Not pictured: Dr. David Lindberg and Dr. Vince Resh, instructors

*The clothesline at Cook's Bay*
**by Rown Alexi Roderick-Jones**

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# The Moorea Experience 1998

The Moorea Course is truly a special educational experience unmatched in most curricula any college or university. Its objective is to turn undergraduate students with an interest and background in natural science into research scientists. This is done by carefully selecting students who apply from any of the sciences, although most come from biology, geography, anthropology, and geology, to take part in a field research course taught mostly at the University of California, Berkeley's Richard P. Gump Research Station on Moorea, French Polynesia. The course has been immensely successful since its inception in 1991. Over 120 students have taken the course.

The Moorea Course combines many aspects of expeditionary research--scientific preparation, logistic planning, equipment and supply selection, and the development of an individual research problem on that tropical island. The course, given as Environmental Science Policy and Management 107, Geography 142 or Integrative Biology 158, starts with science background, logistics and supply at Berkeley for the first four weeks of the semester, then the entire group of 22 students, several faculty and three Graduate Student Instructors moves to Moorea to begin a week of scientific field trips on Moorea and Tahiti. With the Berkeley and field background, students then develop a scientific project of their own. Although science is important, safety, logistics, cost, equipment and supplies are important aspects of each project that requires detailed planning as well. For the next eight weeks, students pursue their own projects on Moorea, returning to Berkeley for final report preparation and oral participation in the annual Symposium on the Biology and Geomorphology of Tropical Islands.

This program is a complete exposure to scientific research, from detailed planning through the actual work to the final communication of results. In few ways does it differ from professional scientific activities. These students have attained apprenticeship as scientists and an excellent start on a science career. Indeed many students in past classes have gone on to graduate school in the sciences, to publishing the results of their Moorea work in scientific journals, to collaborations with scientists in other institutions from the California Academy of Sciences to the Smithsonian Institution and to many other Universities. The teaching staff is very much rewarded by this kind of success.

The 1998 Class was again very successful, as can be seen in the research papers in this volume. Everyone--students, GSIs and faculty--learned many new things, had new and different experiences, and had enjoyed most every minute. The projects varied from plants to animals, from the deep bays to the highlands, and from shallow waters to the truly pelagic offshore waters. One student worked on parasitic plants; another on parasitic animals. Others worked on fish, while still others studied sponges or water striders. The variety and achievement were enormous. Importantly some students have already had their work published!

The faculty and GSIs thank the class for good times, good camaraderie, and for sharing their excitement with us. A course of this complexity could not have taken place without a huge amount of effort from our colleagues at Berkeley and on Moorea. A number of other faculty and staff helped us by presenting lectures and workshops on a variety of topics. These people included Carole Hickman, Deborah Penry, Roy Caldwell, George Barlow (Integrative Biology), Pat Kirch (Anthropology), Cherie Northon (Geography), Norma Kobzina (Bioscience and Natural Resources Library), and Jim Hayward (UCB Diving Safety Officer). We especially thank Julie Myers and Dorothy Tabron (Integrative Biology), who kept the course going administratively, and Don Bain (Geography) and the Animal Use and Care Committee for advice, arrangements and assistance of various sorts. The staff of the University and Jepson Herbaria and the

Museum of Paleontology provided assistance with specimens. The students benefited from the help of the staff of the Visualization Center in Valley Life Sciences Building. The class field trip to the coast of Central California was made possible by the cooperation and efforts of Peter Conners and Lisa Valentine of the UC Davis Bodega Marine Laboratory.

We especially thank Debbie Woodward and John Boland, managers, as well as the rest of the staff of the UC Berkeley Gump Research Station on Moorea who kept the facilities operating so efficiently and who made our stay so very pleasant. Frank and Hinano Murphy of Moorea provided much assistance and interaction with Mooreans that enhanced our cultural experiences.

Without this help, our students would not have had the fantastic experience that they can remember for the rest of their lives. We changed them!

Jere H. Lipps, Professor, Integrative Biology
David R. Lindberg, Professor, Integrative Biology
Vincent Resh, Professor, ESPM
David Stoddart, Professor, Geography
Tegan Churcher, Graduate Student Assistant, Geography
Amy Lesen, Graduate Student Assistant, Integrative Biology
Virginia Matzek, Graduate Student Assistant, ESPM

PS: The faculty never make this course go by themselves. A very large part of the effort falls on the Graduate Student Assistants, who spend nine weeks of their lives living, teaching and learning with the students. The four professors especially thank our GSIs who did an outstanding job!

# Cavity-Dwelling Stomatopod Distribution and Indicators in Cook's Bay, Moorea

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ABSTRACT. In an effort to determine and characterize the distribution of a popular behavioral and physiological study organism, coral rubble gathered in Cook's Bay, Moorea, French Polynesia (149°50'W, 17°30'S), was examined for the presence of cavity-dwelling stomatopod crustaceans. Rubble characteristics and species partitioning were examined for five sites located among the patch reefs along the eastern side of the bay. Species composition was determined by the depth of the rubble, with *Gonodactylellus espinosa, Gonodactylus childii, Gonodactylellus affinis,* and *Chorisquilla excavata* inhabiting progressively deeper ranges. No stomatopods occur from 20-30 feet in depth. This apparent lack of habitation may be due to the sites' geography or extremely low abundance combined with sampling randomness. Stomatopod presence/absence in an individual piece of rubble is related to rubble volume, porosity, and cover type, factors indicative of the environment from which the rubble was gathered. Rubble with a minimum volume of 1600 $cm^3$ and an average cavity diameter size of 0.72 cm seems to be favored. Sponge and green algae are both good predictors of stomatopod presence. Sponges might offer protection as a by-product of self-preserving bioreactive compounds, while green algae might attract prey, increasing stomatopod feeding. Counter-indicators for stomatopod presence seem to be high sedimentation and tunicate presence. Brown algae, coralline algae, and encrusting coral presence/absence do not seem to matter.

## Introduction

*Purpose*

Stomatopods being favored research organisms for behavioral and physiological studies of their unique vision, chemoreceptivity, and ecology, the ability to predict specimen location based on habitat characteristics is of interest. Stomatopod distribution near the Richard Gump Biological Field Research Station in Cook's Bay, Moorea, French Polynesia, is of special note due to proximity to the station facilities. Examining stomatopod presence in coral rubble and ascertaining coinciding rubble characteristics allows for distribution mapping and characterization of the stomatopod habitat.

*Location*

This study focuses on cavity-dwelling species of stomatopods, which are found occupying coral rubble crevices. Coral rubble is readily produced by wave and storm action as well as structural undermining by burrowing organisms. It is associated spatially with living reefs.

The high volcanic island of Moorea, French Polynesia (149°50'W, 17°30'S), has well-developed reefs and is known, from previous collection of specimens, to have a diverse population of stomatopods.

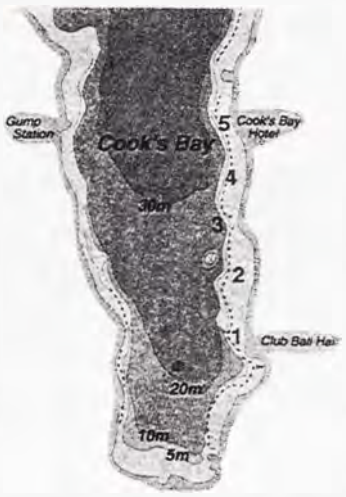



**Figure 1** – Bathymetric Contour of Cook's Bay showing depths and sampling sites.

The patch reefs extending along the eastern side of Cook's Bay, Moorea (see Figure 1), permit for rubble collection and examination along both depth and latitude gradients and were selected for this reason as the study area.

**Materials and Methods**

*Species*

Cavity-dwelling genera collected from Moorea as specimens include: *Chorisquilla* (1 sp.), *Echinosquilla* (1 sp.), *Gonodactylus* (2 spp.), *Gonodactylellus* (2 spp.), *Pseudosquilla* (1 sp.), *Raoulserenea* (4 spp.), and *Parvasquilla* (1 sp.) (Roy Caldwell, personal correspondence). Monographs and correspondence with Professor Caldwell about distinguishing physical characteristics helped delineate the four species found, representing 3 genera.

*Collection*

Collection occurred at five sites along the inner Cook's Bay patch reefs (see Figure and Table 1) and consisted of random in situ selection of available rubble from various depths along the vertical walls of the Bay's channel. Using SCUBA, rubble was collected from 5-40 feet, as constrained by the depth of the vertical wall at each site. Depth was determined by a Genesis Resource Dive Computer. Rubble was not standardized for depth or size, each being a variable of potential relevance to stomatopod habitation and impossible to regulate due to the chance nature of coral rubble production. A 15-piece sampling of each site was conducted over a two dive period following UC Berkeley Scientific Diving auspice stipulations and guidelines for safety. Each piece of rubble was individually marked with depth and site number and bagged for surfacing without specimen loss.

| Site | GPS Location |
|---|---|
| 1 | S 17'30.186" W 149'49.122" |
| 2 | S 17'29.851" W 149'49.076" |
| 3 | S 17'29.665" W 149'49.118" |
| 4 | S 17'29.250" W 149'49.123" |
| 5 | S 17'29.158" W 149'49.058" |

**Table 1** – Site Geographical Locations

*Measurements*

Data were collected as to rubble size, cover (sponges, coralline algae, brown algae, green algae, tunicates, encrusting corals), depth, site number, and number and species of stomatopod(s) associated with the rubble piece. Percent cover was noted, as was stomatopod size and sex, when determinate.

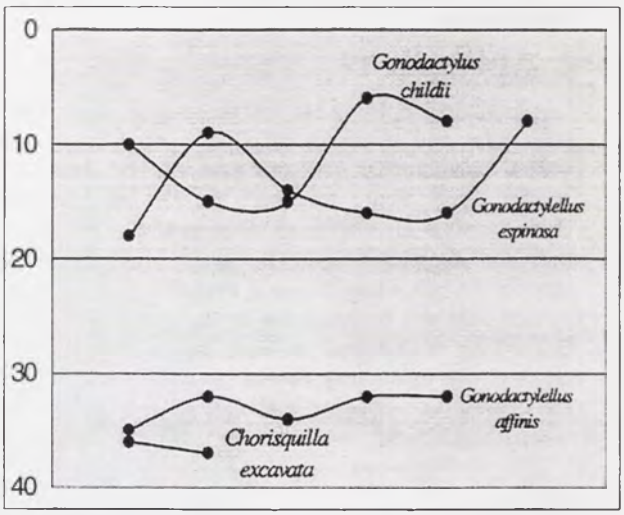
**Results and Discussion**

*Depth Correlation to Species Presence*

By plotting species depth distribution, gradients emerge. *Gonodactylellus espinosa, Gonodactylus childii, Gonodactylellus affinis,* and *Chorisquilla excavata* inhabit progressively deeper ranges, offering evidence for the presence of physiological range constraints. These constraints might be pressure or thermocline endurance, prey item selectivity with prey distribution being depth-dependent, or storm damage to shallower areas allowing more flexible/resilient stomatopod species with high fecundity to proliferate.

The apparent "dead zone" between 20 and 30 feet is predominantly a factor of the geography of the locations, with the most pronounced vertical face of the incline being at this depth. Because of this, any rubble collected from this depth was usually isolated on shelves, and highly sedimented. Under different physical conditions, I would expect to find a stomatopod species living at these depths, although a specimen might not be found due to extremely low abundance combined with sampling randomness.

**Species Depth Distribution**




**Graph 1** - Species Distribution with Depth

*Location in Bay Correlated to Species Presence*

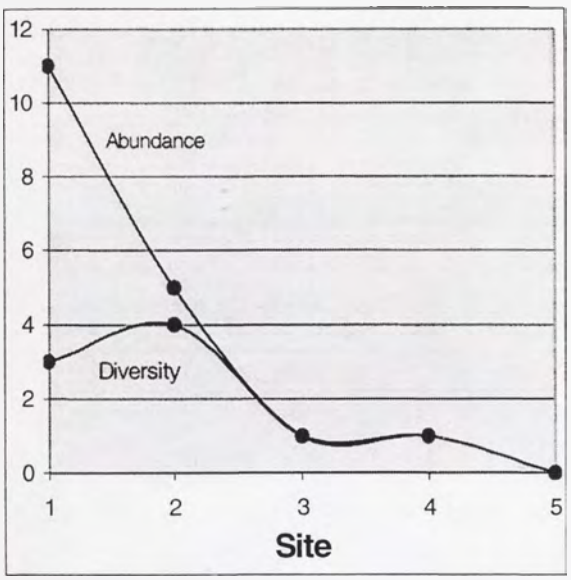
The stomatopod distribution with relation to location in Cook's Bay reflects the ecology of the reef environment in the area, rather than a physical difference in salinity, water temperature, or pH.

| Site | Pods ? | Green Algae | Sponge | Tunicate | Sediment | Cavity | Rubble |
|---|---|---|---|---|---|---|---|
| 1 | 0.47 | 0.87 | 0.6 | 0 | 0.07 | 0.93 | 4364.5 |
| 2 | 0.33 | 0.87 | 0.67 | 0 | 0.07 | 0.67 | 3151.2 |
| 3 | 0.07 | 0.53 | 0.6 | 0.07 | 0.13 | 0.58 | 3131.7 |
| 4 | 0.07 | 0.47 | 0.4 | 0.53 | 0 | 0.75 | 1703.8 |
| 5 | 0 | 0.4 | 0.2 | 0.33 | 0.07 | 0.60 | 1307.5 |
| all | 0.19 | 0.63 | 0.49 | 0.19 | 0.07 | 0.72 | 2896.4 |

**Table 2 -** Average Rubble Characteristics by Site

By analyzing all rubble, a set of "average" rubble characteristics, along with mean number of stomatopods per piece of rubble was attained. Actual stomatopod speciation exceeds the expected value for Sites 1 and 2, and falls short for Sites 3, 4, and 5 (see Table 2). The descending order of importance for contributing factors seems to be: green algae presence, cavity and rubble size, sponge presence, tunicate presence, and sedimentation.

Site abundance and diversity seem to have different criteria (see Table 3 and Graph 2). Although they converge for Sites 3, 4, and 5, Sites 1 and 2 show a disparity in species emphasis. While Site 1 has a much higher abundance, all 4 species found were at Site 2, including *Chorisquilla excavata*, found only at Site 2 at depths of 36-37 feet. This is due to Site 1 being shallower than Site 2, with bottom depths of 34 and 37 feet respectively, in conjunction with small sample size and accompanying stochasticity.




**Graph 2 -** Site Abundance and Diversity

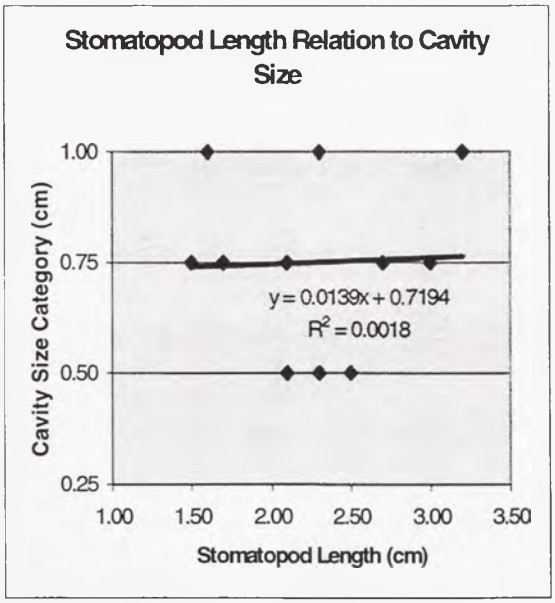
| Site | *Chorisquilla excavata* | *Gonodactyl-ellus affinis* | *G. espinosa* | *Gonodactylus childii* |
|---|---|---|---|---|
| 1 | 0 | 3 | 4 | 4 |
| 2 | 2 | 1 | 1 | 1 |
| 3 | 0 | 0 | 1 | 0 |
| 4 | 0 | 1 | 0 | 0 |
| 5 | 0 | 0 | 0 | 0 |

**Table 3 -** Species Abundance by Site

*Preferred Cavity Size*

Cavity-dwelling is a protective measure for adult stomatopods and their egg masses (young are planktonic), as well as a convenience for surprising prey (Basch, 1989). Protection during a molt is absolutely necessary when the shell is soft and vision is poor.

No stomatopod was found living in a piece of rubble with an average cavity diameter outside the range 0.5 - 1.0 cm, with the average being 0.72 for both the average piece of rubble found and inhabited. This similarity indicates a distribution of stomatopods within their preferred range, artificially resembling the randomization of coral rubble cavity size, which ranged from 0.25 - 2.0 cm.




**Graph 3 -** Relation of Stomatopod Length to Cavity Size

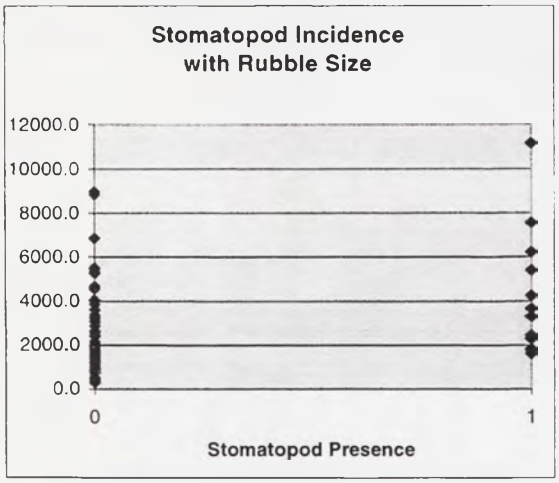
Unlike the results expected if stomatopods were selecting for a cavity diameter that would accommodate their body size specifically, there is no significant relationship between body length and cavity

entrance size (see Graph 3). This might have a basis in the Law of Diminishing Returns: additional cavity size is desirable until diameter approaches body length, making the cavity too hard to defend against homeless conspecifics and the risk of predation too high. The lower limit on acceptable burrow size would be the room required for an egg mass or turning maneuvers for cleaning and defense.

Upon examination, there was no species-specific gradient in cavity size, indicating that cavity selection is not based on predicted growth or other species-based characteristics.

*Rubble Volume*

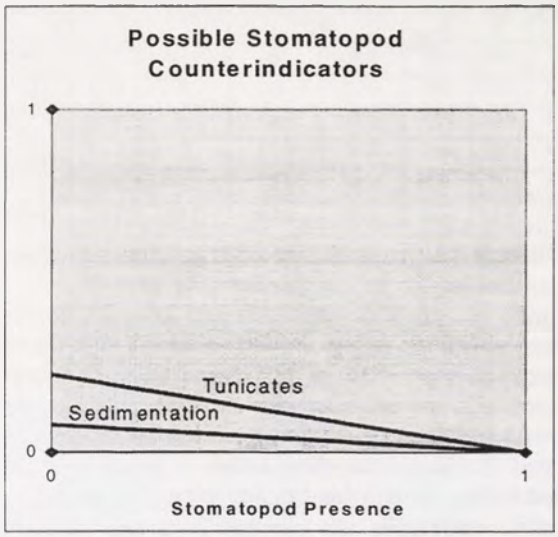
Safety in storms and tidal wash, number and length of cavities, and sheer chance in encountering a desirable burrow after settling out of the planktonic larval form seem to be the likely explanations for rubble size selectivity. No piece of rubble under 1600 $cm^3$ was inhabited and an upper volume limit was not encountered in the sample.




**Graph 4** - Rubble Size Correlation To Stomatopod Presence

*Sedimentation and Tunicates as Counter-Indicators*

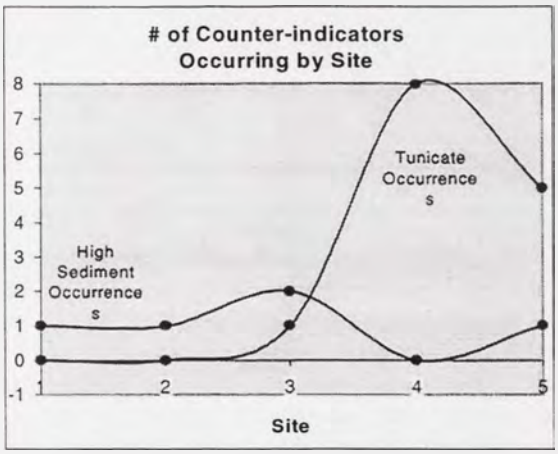
Sedimentation interferes with the respiration of both prey items (gills of small fish) and stomatopods, therefore consistently sedimented areas should not be expected to be populated by stomatopods. Empirical evidence shows the counter-indication of sedimentation for stomatopod presence (see Graph 5). In no case was a stomatopod found to be inhabiting a highly sedimented piece of rubble and abundance was low in areas with high incidence of highly sedimented rubble (see Graphs 2 and 6).




**Graph 5** - Stomatopod Presence with Tunicate and Sedimentation Presence

There is no literature support for the existence of chemical activity in tunicates that would discourage stomatopod habitation (Sings, 1996), but the similar form and lifestyle of tunicates and sponges might have led to niche partitioning to the extent that tunicates and sponges co-occurred only twice in the entire sample. In this case, the conditions desirable to stomatopods are also conducive to sponge growth.

Examination of Graphs 5 and 6 and the supporting evidence of no stomatopods inhabiting the same rubble as tunicates or high sedimentation lend credence to both being called "Counter-indicators" of stomatopod presence, since either excludes the presence of a stomatopod.

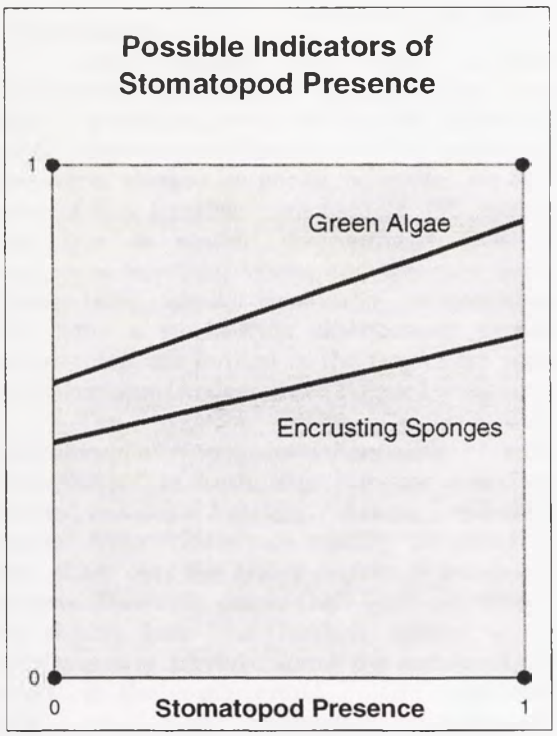



**Graph 6** - Tunicate and Sedimentation Occurrences by Site

*Green Algae and Sponges as Predictors*

Both green algae and sponges are possibly appealing food sources to potential stomatopod prey such as snails and small fish (Adjeroud, 1997; Koukouras, 1996).

Sponges, with their ability to increase water flow (Basch, 1989; Thacker, 1998) and chemical aggression (Marin, 1998), have a lot to offer a stomatopod in terms of predator safety and larvae protection. Planktonic sponge larvae are usually highly undesirable to fish as a food source due to their chemical profile and fish will even avoid areas where sponge spawn has been diluted and added by eye-dropper to the water over a usual feeding area (Beccero, 1997; Swearingen, 1998). If stomatopod larvae distribution and sponge spawning coincided, the stomatopod larvae would have decreased predation and higher chance of survival. Sponge predator deterrent for fish might not be exclusive to spongivorous fish and might reduce the threat of fish predation to the stomatopods, effectively increasing life span and total reproduction for the stomatopod.

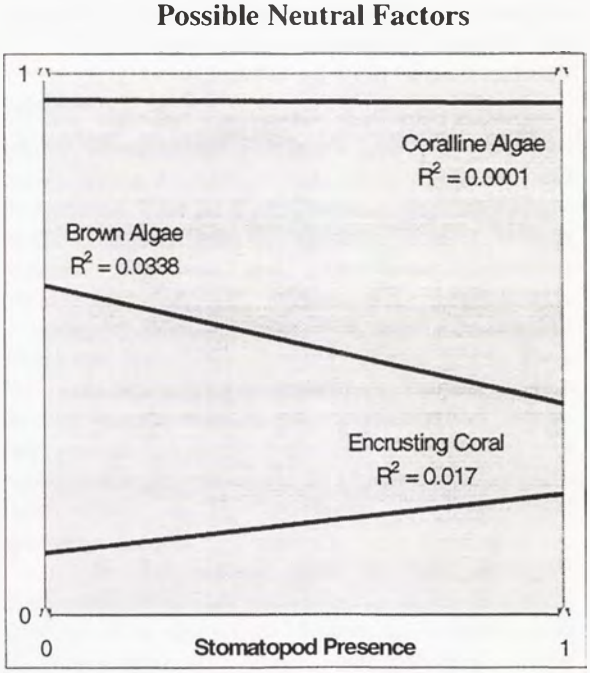



**Graph 7** – Demonstration of High Correlation Between Stomatopod Presence and Potential Indicator Species

The presence of either green algae or sponges corresponds to two-fold increase in the probability that a given piece of rubble is inhabited by a stomatopod. This finding and the pragmatism of the hypotheses of increased food source, water-flow, and predator protection, contribute to the suggestion of green algae and encrusting sponges as an indicator of stomatopod presence.

*Coralline & Brown Algae and Encrusting Coral Presence as Neutral Factors*

Ubiquitous in distribution, the high abundance and tolerance of the algae make them poor indicators for stomatopod presence – they are not as discriminating as the stomatopods in habitat. The sampling of encrusting coral presence is far too low to be of statistical value (4 occurrences) and a glance at Graph 8 shows extremely low $R^2$ values, reflective of minimal correlation.




**Graph 8** – Neutral Factors' Relevance

**Conclusions**

This paper serves as the groundwork for further research into stomatopod environmental ecology and intraspecific interactions.

Of personal and scientific fascination are the possible interactions between sponges and stomatopods. To get a better understanding of the ecology of stomatopod inhabitation, a number of factors could be measured: the bioactivity of the

specific sponges associated with the stomatopods, the timing of spawn/larval release, and the water-flow-inducing capabilities of the sponges involved.

**Acknowledgments**

I would like to thank the teaching staff (professors and, most especially, Amy, Tegan, and Virginia) for all their patience and help. I would also like to thank Richard Gump for his contribution to field biology at UCBerkeley and Hinano for her perspective on another culture. To all the Gumpees: I will never be the same – thank you.

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# The Semiaquatic Gerromorpha (order Hemiptera) of Moorea, French Polynesia: Classification, Distribution, Ecology and Behavior

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ABSTRACT. Semiaquatic Gerromorpha were collected during October and November 1998 on the island of Moorea, Society Islands, in marine and freshwater habitats. Five species were collected, representing five genera in three families. The family Gerridae had the most representation, with three species; *Limnogonus luctuosus, Trepobates* sp., and *Halobates hawaiiensis* were all fairly well represented. The family Hermatobatidae was represented by just a single species, *Hermatobates* sp., and the family Veliidae was also represented by a single species, *Rhagovelia* sp. Three of these species are newly described to Moorea, although no adults were found in two of the three undescribed species. All species were measured and a simplified key was made and provided for quick identification. Characters found useful in classifying these species included: interocular width of head, head color markings, length of first antennal segment, length of the middle femur, mesotibio-tarsal hair fringe and structure of the male genitalia. In addition, their distribution was recorded and mapped. A sex ratio analysis determined that males and females coexisted in the same proportions in freshwater *L. luctuosus* and marine *H. hawaiiensis*. Results of laboratory experiments with *L. luctuosus* and *H. hawaiiensis* showed that *L. luctuosus* preferred shaded habitat, while *H. hawaiiensis* preferred sunlit habitats which is congruent with the environments in which both species were found. T-test anaylsis was used to compare mosquito larvae predation rate between *L. luctuosus* and *H. hawaiiensis*. However, the data did not support a significant difference in mosquito larvae predation. Furthermore, other feeding behaviors and stridulatory mechanisms in the field and in the lab were visually observed and noted.

## 1. Introduction

The majority of water striders (Hemiptera, infraorder Gerromorpha) are highly specialized for a life on the surface of water. Most waterstriders inhabit the surfaces of freshwater streams or ponds, however, we now know of four families composed of 150 species that live in marine environments such as mangroves, intertidal zones, and the open ocean (Cheng 1985). Unlike freshwater waterstriders that have a world-wide distribution, marine waterstriders are limited to the tropics for some unknownreason (Anderson and Poinar 1998).

The common name "waterstrider" (Gerromorpha) is interchangeable with "pondskaters" in freshwater habitats and "sea skaters" in marine habitats. Among freshwater insects, waterstriders are readily observed as they skate over the water surface of ponds and streams. However, due to their grey pubescence, sea skaters look like whitish specks or air bubbles as they traverse across the surface of the ocean. In the south-central Pacific, specialist field work on freshwater semiaquatic gerromorphans has been confined to Tahiti, Raiatea, Tahaa, and Borabora (Anderson 1975) while marine field work has been confined to Tahiti, the Tuamotus and the Marquesas (Herring, 1961). More extensive surveys in the Pacific have been conducted in Australia, New Guinea, Samoa, Fiji, Japan and the Hawaiian island. Most of the literature about the Moorea insect fauna focuses on the orders Diptera and Psocoptera. The only semiaquatic gerromorphans so far recorded from the Society Islands, which includes Moorea, are *Limnogonus luctuosus* (Anderson 1975), *Halobates hawaiiensis* (Cheesman 1925, Johnson 1934, and Zimmerman 1934), *and Halobates sericeus* (Cheng 1996). Thus the semiaquatic gerromorphan fauna of the Society Islands remains poorly understood. In the first part of the study, I attempted to catalog the semiaquatic gerromorpha in Moorea and provide information on the habitats of individual species.

In the second part of this study, I conducted laboratory experiments on the two most cosmopolitan species on Moorea, *L. luctuosus* and *H. hawaiiensis*. These waterstriders occupy varied habitats, including high mountain streams like the Opunohu River, man-made ditches, estuaries, marshes, coastal shores, and open ocean. Their ability to thrive in a wide variety of niches is expressed in their diverse morphological forms. One important adaptation for marine life is attributable to a high UV tolerance by the cuticle of *Halobates* sp. (Cheng 1978). I discuss the adaptive significance of ultraviolet radiation protection, particularly

with respect to habitat preferences of *L. luctuosus* and *H. hawaiiensis*.

Waterstriders are predators or scavengers. The capture of prey by waterstriders has interested many entomologists. Waterstriders locate potential prey by the different ripples created by their weak movements (Murphy 1971; Wilcox 1972; in Cheng 1976). Many authors have noted food preferences for *Halobates* spp. in the field and in the laboratory (Tizard et al, 1885; Usinger and Herring 1957; Cheng 1974 in Cheng 1976). Four species of waterstrider have been documented as predators of mosquito larvae (Jenkins, 1964). Moreover, the Veliidae and Gerridae have been frequently reported as predators of the early larval instars of mosquitos (Hungerford 1917, Bragina 1931, and Frick 1949 in Collins and Washino 1985). Yet, little is known about how the waterstriders obtain the mosquito larvae that must float up from below or how often they need to eat for survival.

## 2. Materials and Methods

### 2.1 *Sites:*

The volcanic island of Moorea (17° 30′ and 149° 50′W) is the second youngest island in the Society Archipelago. The Society Islands are an isolated group of islands situated in the south-central Pacific Ocean. In total, 10 study sites were chosen on Moorea, in freshwater and marine localities. Collections of freshwater gerromorphans took place at five sites in the main stream and tributaries of the Opunohu River (Fig. 1). Sightings and smaller collections of freshwater gerromorphans occurred in three separate locations: 1) a pond adjacent to the Pao Pao River, 2) the Afareaitu River, and 3) the brackish salt marsh adjacent to the Beachcomber Hotel on the western peninsula. Study sites are described in descending order from the upper catchment of the stream to downstream, numbered River 1 - 5 (Fig. 1).

River 1 is the upstream most that lies adjacent to the Pao Pao-Marae-Belvedere Road. It is located on the south-facing slope of Mt. Rotui, which peaks at 899 m. Water enters through an elevated double pipe culvert and then trickles down a cascade of large, basalt boulders and interspersed cobbles. Pools containing waterstriders are located on the periphery of the stream. Tahitian chesnut (Legumenoceae, *Inocarpus fagiferus*) and native hibiscus (Malvaceae, *Hibiscus teliaceus*) dominate the riparian vegetation and create a closed canopy over the stream. The average depth of pools is 6 cm and they are composed of silty substrate. Two out of six pools dried uo and disappeared before the end of the study.

River 2 is surrounded by agricultural practices (eg. Coffee grown upstream and taro production downstream). A small, road bridge with overhanging vegetation is built of wood and concrete and allows free stream flow underneath. Tahitian chesnut is sparse, although the stream banks are lined with abundant herbs.

River 3 lies parallel to the road. Cattle and sheep farming influence water quality at this site. By visual inspection, the substrate has a fairly black, anoxic appearance and the water is turbid and discolored. Tahitian chesnut provides a dense canopy cover.

River 4 is a fourth-order stream that drains the north-east facing slope of Mt. Mouaroa. This site was sampled along the banks beneath the road bridge. It has an open canopy, although hibiscus and Tahitian chesnut are growing immediately downstream. The stream bed is composed of small cobbles and pebbles.

River 5 is a drainage ditch along side a paved road, just before water enters the base of Opunohu Bay. The depth of the water in the 2ft. wide channel ranges from 0.1 to 10 cm. Cultivated mango, hibiscus, and *Mimosa pudica* line the southern side of the channel. Dense stream vegetation proliferated in the concrete channel and several detrital hibiscus flowers floated on the water surface.

Marine gerromorphan collections took place at five sites on the Northern coast of Moorea: 1) the lagoon between the two coralline islands, Motu Fareone and Motu Tiahura, 2) the peninsula between Opunohu Bay and Cook's Bay, and 3) three sites in Cook's Bay. Study sites are ordered from west to east, numerically Ocean 1 - 5 (Fig. 1).

Ocean 1 lies between the two motus, and striders were obtained in the lagoon between the depths of 2 and 4 m. On the surface, the water flow does not appear as turbulent as the fast moving current below. The water has a clear appearance and floating, dead algae is prevalent in very low abundance.

Ocean 2 is located at the tip of the peninsula between the two bays. The private beach adjacent to this site is characterized by many coconut trees and fine sand. None of the

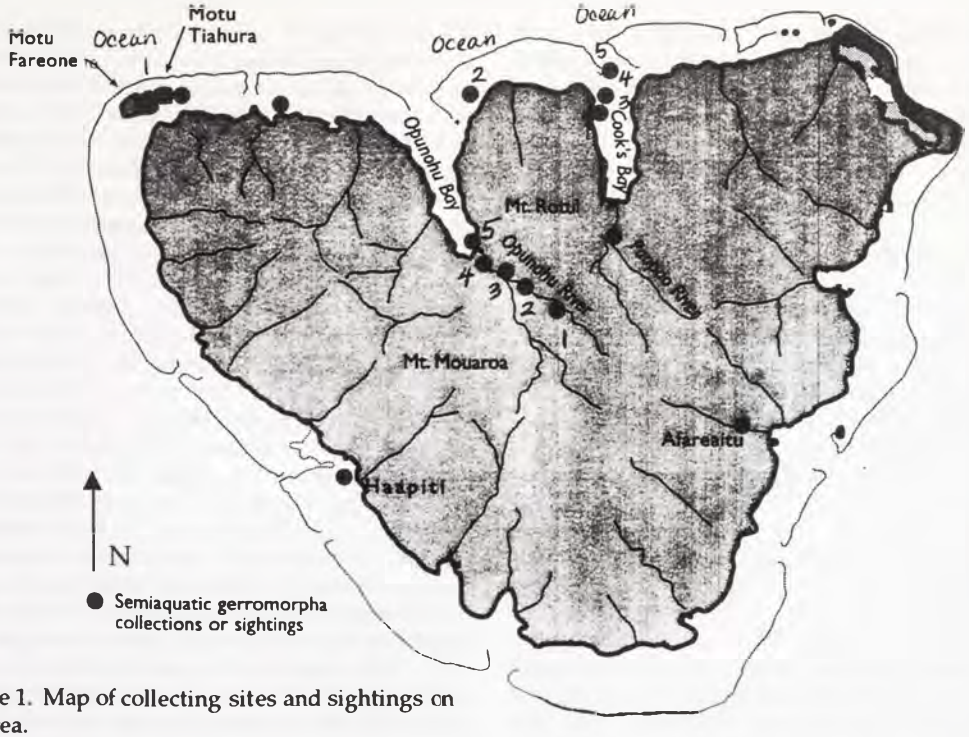



Figure 1. Map of collecting sites and sightings on Moorea.

coral heads below prenetrated the surface of the water.

Ocean 3 is located off the dock of the Richard B. Gump Station. Individuals of *H. hawaiiensis* were strongly attracted to the dock lights at night. This phototactic behavior was induced two hours after the lights were turned on. The nearby coastal vegetation mainly consists of *Casuarina equisetefolia, Thespesia populnea,* and *Mimosa pudica.* The presense of rocky coral heads above the water level was quite permanent and was not dependent on the tidal level.

Ocean 4 is located directly across from the dormitory bungalows of the Richard B. Gump Station. Waterstriders were obtained about 200 m from shore. Dense, floating algae occasionally clumped together, forming algal mats that varied in size.

Ocean 5 centered around the barrier reef. Waterstriders were spotted on both sides, but only caught from the back reef due to the shallow and calm quality of the water.

2.2 *Collecting methods:*

Collections were made using an insect net with a diameter of 35 cm and depth of 50 cm and an aquarium dip net. All freshwater and marine waterstriders were prevented from escaping by securing mosquito netting over the mouth of the container with a rubber band. After lab experimentation, specimens were sorted and stored in 70% alcohol. In preparation for classification, 65 specimens were examined with a dissecting microscope, ranging from 10X to 13X power magnification. Body dimensions of nymphs and adults were measured in millimeters with an ocular micrometer. Adult males and females of *L. luctuosus, and H. hawaiiensis* were safely distinguished by comparisons of the genitalia. Specimens without matured genitalia were placed in nymphal instars (I - V) by using a combination of total body lengths and mid femur measurements. The total length is not quite reliable in itself since the membranes between the abdominal segments can enlarge (Andersen, 1994). The interocular width ratio, a way to determine coastal species from truly oceanic species (Herring, 1961), was calculated by dividing the width between eyes ("1" in Figure 8)

by the width of one eye ("2" in Figure 8). Due to a time constraint, for most *H. hawaiiensis* juveniles, I only took the measurements that were most important in separating nymphal instars (Appendix 5 - 7). Furthermore, I used a T-test to determine whether *l. luctuosus* and *H. hawaiiensis* differed in their sex ratio.

2.3 *Experiments:*

For the shade and sunlight habitat preferences experiment, 36 randomly selected adults and juveniles of *Limnogonus luctuosus* and *Halobates hawaiiensis* were contained in two, blue plastic tubs (44 x 15 cm). A piece of cardboard covered one half of the plastic tub, allowing sun light to shine on the other half. This experiment was replicated 5 times for the 12 individuals of *L. luctuosus* and 7 times for the 24 individuals of *H. hawaiiensis.* In each replication, the cardboard was shifted to the other half of the tank to eliminate waterstider bias towards favoring one side of the tank for some unknown reason. During the five minutes of rest period between trials, the waterstriders dispersed themselves evenly in the tank. I investigated whether *L. luctuosus* and *H. hawaiiensis* would demonstrate habitat preferences with regard to shade and sunlight. I tested the hypothesis that the two species differ in their shade and sunlight preferences. In addition, I used a chi-square test to determine if the proportion of individuals on each side of the tub differed from a random expectation of 50 percent.

For the feeding experiment, six *L. luctuosus* adults and seven *H. Hawaiiensis* adults were contained in 10 cm diameter cups filled with 120 ml of water for seven days. Each adult was kept alone so that the feeding behavior of one waterstrider did not affect the feeding behavior of another waterstrider. Each waterstrider was fed 10 mosquito larvae on the first day of the seven-day experiment. The plastic containers were checked twice daily for signs of predation on mosquito larvae. Statistical tests for both sun and shade experiments and mosquito larvae predation experiments were performed using JMP Start Statistics (Sall and Lehman 1996).

## 3. Results

### 3.1 Classification

All waterstriders are grouped in the infra-order Gerromorpha, Heteroptera as defined by Stys and Kerzhner (1975). Gerromorphs consist of 8 families, about 106 genera, and approximately 1200 species (Cheng 1985). So far, very little is known about which waterstriders inhabit Moorea freshwater and marine localities. This paper classifies five species of waterstriders found in Moorea, French Polynesia. Two species previously documented in the Society Islands are redescribed. Three genera are newly described for the island of Moorea. Two freshwater species, *Trepobates* sp. and *Rhagovelia* sp. and one marine species, *Hermatobates* sp. is newly described. The averages and standard deviations of total body length, interocular width ratio, first antennal segment and middle femur segment from freshwater *L. luctuosus , Trepobates* sp., *and Rhagovelia* sp. are recorded as well as each instar and adult males and females *of* marine *H. hawaiiensis* (Table 3). To separate *L. luctuosus,* and *H. Hawaiiensis* into their respective nymphal instars, I used total body lengths and middle femur lengths as a guide. Total body lengths rarely overlap in the different stages.

The generic and subgeneric classification of the order hemiptera, found in Moorea, is presented in a taxonomic checklist below (Table 1).

### 3.2 *External Morphology*

General features of semiaquatic gerromorpha, like head coloration, length of antennal segments, tarsal length, wing polymorphism, are used by most hemipterists (Herring 1961). The following are general descriptive notes of the six gerromorphans that I found in Moorea.

The head, thorax, and abdomen of waterstriders are well defined. The eyes are

**Table 1. Semiaquatic Insects of Moorea**

| Order | Family | Subfamily | Genus | Species |
|---|---|---|---|---|
| Order Hemiptera | | | | |
| Suborder Gerromorpha | | | | |
| | Family Veliidae | | | |
| | | | Genus *Rhagovelia sp.* | |
| | Family Gerridae | | | |
| | | Subfamily Gerrinae | | |
| | | | Genus *Limnogonus* Stal | |
| | | | | Species *luctuosus* |
| | | Subfamily Trepobatinae | | |
| | | Tribe Trepobatini | | |
| | | | Genus *Trepobates sp.* | |
| | | Subfamily Halobatinae | | |
| | | | Genus *Halobates* Eschscholtz | |
| | | | | Species *hawaiiensis* |
| | Family Hermatobatidae | | | |
| | | | Genus *Hermatobates sp.* | |

prominent and the color varies from deep red to brown to black. All species have four segmented antennae and the total length of the antennae surpasses the length of the head. The sucking mouth-part, the rostrum, varies in length from 0.3 mm to 2.8 mm for the five species. Larvae have one-segmented tarsi while adults always have two tarsal segments. The thorax is comprised of three segments that bear the legs of all five species and the wings of certain, winged *L. luctuosus*. Wing polymorphism is a common phenomen (Polhemus) but in all collections of *Halobates hawaiiensis*, I have failed to find any individual with wings. The abdomen bears the genitalia which was not distinguishable in any of the nymphal instars of *Halobates hawaiiensis*. All five species are hemimetabolous and *Halobates hawaiiensis* juveniles resemble the adults although the body proportions are different. For example, head to body ratio in juveniles is 0.08 (Appendix 5 - 7) while in adults is 0.11 on average (Appendix 1). The instars also have uniquebanding coloration.

Unfortunately, I have not had the opportunity to classify any of the formerly undescribed species into species names. However, I have sketched certain features of each of the formerly undescribed species (Figure 2 - 8) and I have loaned specimens to Dr. Cheng, who has kindly examined them. Several instar representatives of *Halobates hawaiiensis* and the one representative of *Hermatobates* sp. have been confirmed.

DESCRIPTION OF SPECIES FOUND:

For quick identification, refer below to Table 2.

**Rhagovelia** sp. China and Usinger, 1949

*(newly described)*

External Morphology: Length 0.83 mm to 1.75 mm (Appendix 8). Great degree of sexual dimorphism. Juveniles with fairly short antennae, approximately 0.15 mm (Table 2). Preapical claws. Middle tarsus contains a plumose fan of hairs which can be folded into the cleft. Distribution elsewhere: North America (Merrit and Cummins 1996).

**LimnogonusLuctuosus** Montrousier, 1865

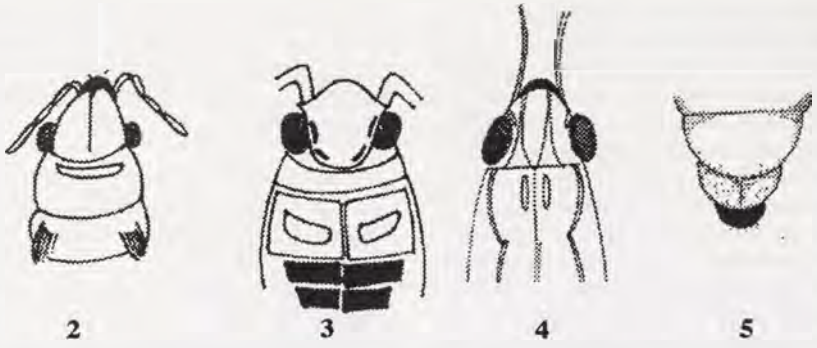
*(redescribed)*

External Morphology: Male length 6.8 mm - 8.72 mm and female length 6.56 mm - 9.12 mm (Appendix 4). Body coloration is dark brown to black. Sublateral stripes on head never quite reaching anterior most part of the head. Fairly long first antennal segments for both sexes, pronotum to mesopleuron. Paired spots on either side of medial stripe. Abdominal dorsum with a

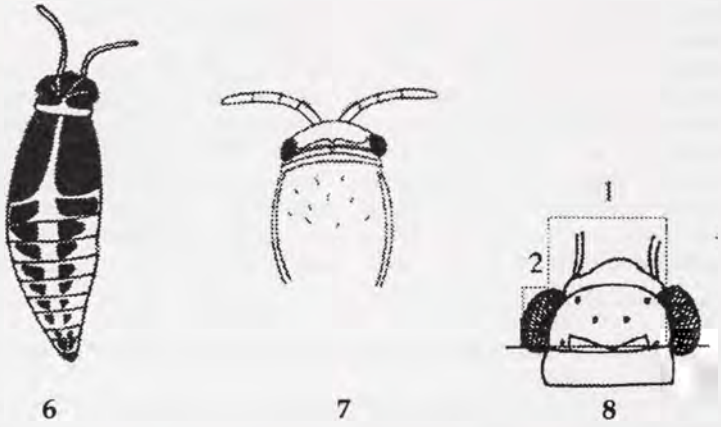
Table 2.

KEY TO THE SPECIES OF SEMIAQUATIC GERROMORPHA OCCURRING IN MOOREA AND NEARBY MOTUS

1. Small, oval shaped body. Hind femur short, not exceeding apex of abdomen. Dorsum of head with median longitudinal sulcus.....(Veliidae) 2
1'. Hind femur distally exceeding apex of abdomen. Dorsum of head without median longitudinal sulcus. Mid legs inserted closer to hind legs than fore legs.....3
2. Coloration dark brown. Abdomen relatively slender and raised. Pair of hair patches on mesothorax (fig. 1).....male *Rhagovelia* sp.
2'. Coloration light brown. Mesothorax with unique banding pattern (fig. 2).....female *Rhagovelia* sp.
3. Elongate, oval body. Stout and short legs. Head is widened and pronotum compressed. First antennal segment with hair fringe and sparse hairs on dorsal thorax region (fig. 6).....*Hermatobates* sp.
3'. Elongated, oval body. Legs rather long. Thoracic region long..... .....(Gerridae) 4
4. Smooth, glossy appearance. Wings or wingpads may or may not be present.....5
4'. Body covered with silvery-gray pubescence. Rostrum short and stout (0.6 mm - 1.0 mm).....6
5. Body comparatively long and narrow.....*Limnogonus luctuosus*
5'. Body comparatively short and broad. Two paired spots on the pronotum (fig 3).....*Trepobates* sp.
6. Head coloration with a yellow "V" shaped design. Three paired markings on the dorsum of head (fig 7) Meso-tibial tarsal hair fringe present..... .....adult *Halobates hawaiiensis*
6'. Head coloration with four yellow lines originating at the dorsal base of the head and radiating outward. Segmented abdomen with paired banding pattern (fig. 5).....juvenile *Halobates hawaiiensis*




Figures 2 - 5. Freshwater gerromorpha: 1. *Rhagovelia* sp. Male head, pronotum, and mesothorax, dorsal view. 2. *Rhagovelia* sp. Female head, pronotum, and mesothorax, dorsal view. 3. *Trepobates* sp. Female head and pronotum. 4. *Trepobates* sp. Female terminalia, ventral vew. (Not drawn to scale.)




Figures 6 - 8. Marine gerromorpha: 5. Juvenile *Halobates hawaiiensis*, dorsal view. 6. *Hermatobates* sp. Juvenile head and thorax, dorsal view. 7. *Halobates hawaiiensis*. Female head,dorsal view, with calculations for measuring interocular width ratio. (Not drawn to scale).

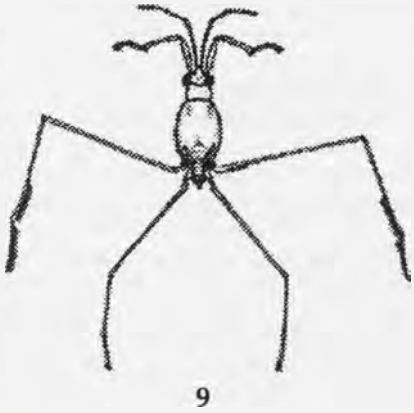



Figure 9. *Halobates hawaiiensis*. Male body, dorsal view. (Ed Tarvyd illustration, not drawn to scale.)

median row of pale, elongate spots. Head width is 1.58 mm across eyes in males and 1.56 mm in females (Appendix 8). Macropterous and apterous forms. The frequency of winged species is considerably less than the frequency of individuals with reduced flight organs (proportion ~ 1:20). Distribution elswhere: Australia, Soloman Islands, New Hebrides, Fiji, Samoa Islands, Tahiti, Taiatea, Tahaa, and Borabora (Andersen 1975).

**Trepobates sp.** Matsuda, 1960

*(newly described)*

External Morphology: Male length 4.9 mm and female lenth 6.2 mm(Appendix 2). Wingpads are dark brown. Female genitalia is black with row of hair tufts at the tip (Figure 5). Distribution elswhere: Singapore, Australia, Soloman Islands, Phillipines, Moluccas, New Guinea (Polhemus and Polhemus 1996).

**Halobates hawaiiensis** Usinger, 1938

*(redescribed)*

External Morphology: Male length 3.7 mm - 5.44 mmand female lenth 3.76 mm - 5.2 mm. Juveniles: Apterous. Head coloration is black with four elongate, yellowish stripes. Pronotum with two distinct halves. Average maximum body width of adults is 1.8 mmfor males and 1.77 mm females (Table 3). Mesotibial tarsal hair fringe present. Adults: Large, silvery gray with apical 4 antennal segments. Dense stiff black bristles on acetabula. Yellow marking on head has a shape of a wide letter "V". Maximum body width of females is slightly larger compared with males. Besides transformation of three abdominal segments into male phallus, the general body structure does not greatly differ between sexes. Distribution elswhere: Hawaii, Marquesas, Society Islands: Tahiti, Tuamotu (Cheng 1985)

**Hermatobates sp.**

*(newly described)*

External Morphology: Length 0.83 mm. Average interocular eye ratio is 3.33 for males and 3.48 for females. Trochanters beige, leg segments brown, and ventral abdomen with stacked pair of brown spots. Claws apical. Tarsal hair fringe on mid and hind leg. Distribution elswhere: One species occurs in the Caribbean and the remaining nine species occur in the Indo Pacific (Anderson 1998).

3.3 *Distribution*

The waterstriders of the order Hemiptera were found in both freshwater and marine habitats of Moorea, French Polynesia. I found five species of waterstriders: two exclusively inhabiting freshwater localities, one species invading both freshwater and a brackish salt marsh, and two exclusively inhabiting marine localities.

*Limnogonus Luctuosus* was the most widely distributed species in the Opunohu River. I rarely saw less than three together and I typically saw patches of 10 to 12 individuals. In the combined freshwater study sites, *L. luctuosus* ranged in length from 6.56 mm to 9.36 mm (Appendix 4), suggesting a univoltine cohort pattern. *L. luctuosus* adults were usually found in the more open areas, whereas the nymphs seem to prefer shallow waters among the roots of riparian vegetation or in the small crevices of rocks and pebbles. The finding of *L. luctuosus* is consistent with previous published reports. Anderson (1975) suggests that *L. luctuosus is* widely distributed in the southeastern Pacific.

**Table 3.** Means and Standard Deviations of measurements (mm) of total body lengths, interocular eye ratio, first antennal segment, and midfemur lengths of aquatic hemiptera from Moorea.

| Species | Sex | N | Total Body Length | Maximum Width | Interocular Width Ratio | 1st Antennal Segment | Middle Femur |
|---|---|---|---|---|---|---|---|
| *Rhagovelia sp.* | - | 6 | 1.29 ± 0.65 | 0.45 | 3.0 ± 1.41 | 0.15 ± 0.07 | 0.35 ± 0.21 |
| *Trepobates sp.* | M | 1 | 4.9 | 1.8 | 2.9 | 1.4 | 4.1 |
| *Trepobates sp.* | F | 1 | 8.2 | 2.5 | 2.3 | 1.4 | 4.4 |
| *H. hawaiiensis* | | | | | | | |
| first instar | - | 6 | 1.33 ± 0.13 | 0.7 | 4.08 ± 0.69 | 0.3 | 1.23 ± 0.15 |
| secondinstar | - | 16 | 1.80 ± 0.14 | 1.0 | 3.48 ± 0.45 | 0.5 | 1.65 ± 0.64 |
| third instar | - | 7 | 2.24 ± 0.15 | 1.2 | 3.88 ± 1.10 | 0.5 | 2.25 ± 0.64 |
| fourth instar | - | 4 | 2.77 ± 0.19 | * | 3.75 | * | 2.30 ± 0.44 |
| fifth instar | - | 3 | 3.28 ± 0.24 | * | * | * | 2.53 ± 0.23 |
| adult | M | 8 | 4.74 ± 0.55 | 1.93 ± 0.08 | 3.33 ± 0.87 | 1.44 ± 0.32 | 5.44 ± 0.72 |
| adult | F | 7 | 4.32 ± 0.51 | 2.62 ± 0.72 | 3.48 ± 0.82 | 1.13 ± 0.18 | 4.98 ± 0.44 |
| *Hermatobates sp.* | - | 1 | 0.83 | 0.48 | 4.0 | 0.18 | 0.3 |
| *L. luctuosus* | M | 5 | 7.82 ± 1.30 | 2.46 ± 0.11 | 1.66 ± 0.44 | 1.82 ± 0.04 | 5.76 ± 0.17 |
| *L. luctuosus* | F | 7 | 7.85 ± 0.66 | 2.33 ± 0.16 | 2.47 ± 0.98 | 1.83 ± 0.14 | 5.54 ± 0.42 |

*No data available

*Rhagovelia* sp. and *Trepobates* sp. occured in fewer numbers, but nevertheless shared the same stream habitat as the the more abundant *L. Luctuosus*.

*Halobates hawaiiensis* was found in all three major marine study sites. *H. hawaiiensis* dominated the coastal areas and were spotted alone, in mating pairs, and aggregated in dense patches. Most species of the marine waterstriders, genus *Halobates* Eschscholtz, are found in sheltered coastal waters, typically in the fringing reef and lagoon (Herring 1961, Cheng 1985). However the habitat range for the coastal species of *H. hawaiiensis* was found to extend at least 200 meters beyond the barrier reef.

Juveniles of *Halobates hawaiiensis* were always found inhabiting the fringing reef and the lagoon between the two motus. They usually maintained densely aggregated patches. At any given site, individuals of *Stenobates sp.* ranged in length from 1.27 mm to 4.32 mm (Appendix 1, 5 - 7), suggesting year-round mating and a multiple cohort pattern. Juveniles of *Halobates hawaiiensis* remained close to the beach on the fringing reef and in the sheltered waters of Cook's Bay. One representative of *Hermatobates* was found in the lagoon, east of the Motu Tiahura. No adults were found representing *Hermatobates* sp. or *Rhagovelia* sp. (Table 3).

Although males comprised almost 50 percent of the *H. hawaiiensis* population, and *L. luctuosus* males comprised only about 40 percent of the total population, a Chi-square analysis showed that the data did not support a difference in the sex ratio between *L. luctuosus* and *H. Hawaiiensis* although it doesn't exlude the fact there could be a difference. ($\chi^2 = 1.37$, DF = 1, $0.25>p>0.1$)

The distribution and habitat preferences of Hemiptera species in an ideal transect from river to ocean shows disjunct populations between freshwater and marine habitats (Figure 10). After three days of intensive surveying in daylight hours, no waterstriders were found in the introduced mangrove (*Rhiziphora stylosa*) adjacent to the Beachcomber Hotel nor at the beach in Haapiti. However, these boundaries are subject to change in various types of weather and so it is impractical to determine exact boundaries since the populations tend to have different ranges depending on the environmental conditions. For example, open ocean species, like *Halobates sericeus* are commonly blown onshore by heavy winds (Herring 1961). In addition, the ocean provides a medium for movement, so it is difficult to determine boundaries because they ultimately prove to be more widely distributed.
Evidence of salt marsh invasion by *L. luctuosus* could reflect the wing polymorphism of this species. Ephemeral streams like the one located east of the Beachcomber Hotel disappeared in the dry season leaving individuals of *L. luctuosus* trapped in the brackish water of the salt marsh (personal observation). Since the stream bed adjacent to the salt marsh had entirely dried up, I predict that *L. luctuosus* would appear in the winged form, as seen in one representative (personal observation). The ability to fly to the nearest pool of water would give the winged forms a great survival advantage. According to Remane (1976), many freshwater gerromorpha are known to extend their habitat ranges into

**Table 4.** Total number of insects caught at each site and number of individuals at each developmental stage

| Site No. | Species | Total | I | II | III | IV | V | Adult(M) | Adult (F) |
|---|---|---|---|---|---|---|---|---|---|
| River 1 | *L. luctuosus* | 12 | - | - | - | - | - | 5 | 7 |
| River 2 | *L. luctuosus* | 2 | - | - | - | - | - | 1 | 1 |
| River 3 | *L. luctuosus* | 10 | - | 3 | - | - | - | 2 | 5 |
| River 3 | *Rhagovelia* sp. | 5* | | | | | | | |
| River 4 | *L. luctuosus* | 21 | - | - | 3 | - | 1 | 5 | 12 |
| River 4 | *Trepobatinae* sp. | 10* | | | | | | | |
| River 4 | *Rhagovelia* sp. | 3* | | | | | | | |
| River 5 | *L. luctuosus* | 30 | - | - | - | 2 | 10 | 8 | 10 |
| River 5 | *Trepobatinae* | 6* | | | | | | | |
| Ocean 1 | *H. hawaiiensis* | 37 | 4 | 13 | 6 | 4 | 6 | 1 | 3 |
| Ocean 1 | *Hermatobates* sp. | 1* | | | | | | | |
| Ocean 2 | *H. hawaiiensis* | 26 | - | 6 | 15 | - | 2 | 1 | 2 |
| Ocean 3 | *H. hawaiiensis* | 51 | 6 | 16 | 7 | 4 | 3 | 8 | 7 |
| Ocean 4 | *H. hawaiiensis* | 4 | - | - | - | - | - | 2 | 2 |
| Ocean 5 | *H. hawaiiensis* | 10 | - | - | - | - | - | 5 | 5 |

* Could not determine stage of development

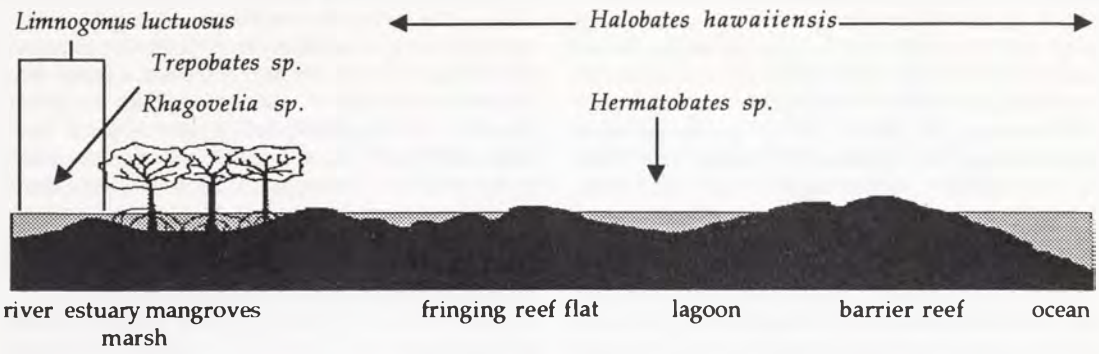



Fig. 10. Idealized transect of aquatic habitats, from river to ocean, showing habitat preferences of Moorean waterstriders indicated by family, genus, or species names. (After Anderson, 1994)

saline waters, such as *Gerris thoracicus*, a close relative of *L. luctuosus*. Perhaps the ability of salt marsh invasion, reflects a euryhaline tolerance. Although, individuals of *L. luctuosus* that were transplanted onsea water, did not live longer than a week in the laboratory (personal observation).

Although *H. hawaiiensis* from Tahiti and Hawaii are morphologically alike, Cheng (1985) points out that the two amphi-tropical populations may differ genetically. Herring (1961) proposes that the wide distribution of the near-shore species of *H. hawaiiensis* is due to surface skating and passive drifting alongs coasts.

**4. Experiments**

*4.1 Shade vs. sunlight*

*Limnogonus luctuosus* and *Halobates hawaiiensis* differed significantly in their shade and sunlight preferences. 80 percent of *L. luctuosus* individuals preferred shade (n = 60) while only 35 percent of *H. hawaiiensis* individuals preferred shade (n = 84). *L. luctuosus* showed a significant preference for shade ($\chi^2$ = 23.1, P < 0.0001). Meanwhile, *H. hawaiiensis* showed a significant preference for sunlight ($\chi^2$ = 8.2, P = 0.0042).

*4.2 Mosquito larvae predation rate*

Several instances of predation were observed for *Limnogonus luctuosus* and *Halobates hawaiiensis*. They were fiercely predaceous and cannabilistic and attacked everything that was tossed onto the water surface (eg. dried leaves, sticks, ants, and dead insects). The feeding periods of both *L. luctuosus and H. hawaiiensis* varied greatly and waterstriders were still mobile even with food attached to their sucking rostrum.

I never witnessed waterstrider predation on mosquito larvae, however, I could ascertain the quantity of mosquitolarvae eaten in one week for one freshwater species *L. Luctuosus* and one marine species *H. Hawaiiensis* . During the experimental period, some mosquito larvae had beeneaten and only their head and skin remained floating at the top. Due to the mosquito netting, I have discounted the possibility that the mosquitolarvae had simply pupated into adults, leaving the larval skin behind. On average, *L. luctuosus and H. hawaiiensis* ate about the same numberof mosquito larvae in 7 days (*L. luctuousus* = 5, SD = 2.53, n = 6; *H. hawaiiensis* = 6.14, SD = 1.95, n = 7). The experiment failed to show a significant difference among the two species (t-test = 0.920, DF = 11, and 0.25>p>0.1).

**5. Discussion**

*5.1 Shade vs. sunlight*

From the shade preference by *L. luctuosus*, I was able to draw two possible explanations. Firstly, preferences for shade may be attributed to how closely the laboratory envionment resembled the natural habitat. The cardboard shading may simulate the forest canopy shading in the upstream environments. Therefore, we may expect to see a difference in behavior among those waterstriders that reside in the

downstream sites with less canopy coverage. However, at closer inspection of the downstream ranges of the stream, waterstriders are rarely found in the middle of the stream with faster current and greater insolation, but are located underneath groundcover vegetation on the banks of the stream. The broad leaves of stream bank vegetation provide a shaded microhabitat for the waterstriders. Exploring the same reasoning, *H. hawaiiensis* would prefer the sunlit portion of the tub because it simulates their natural environment.

Alternatively, preferences for sunlight may bear some relation to the physiology of the marine species. In laboratory experimentation, marine *Halobates* demonstrated high absorption of UV light by the cuticle (Cheng 1978). Without any tree canopy cover and low-growing, coastal vegetation in the middle of the bay, *H. hawaiiensis* receives constant insolation.

*5.2 Mosquito larvae predation rate*

Although the results did not show a significant difference between the food consumption of *L. luctuosus* and *H. hawaiiensis*, I cannot exclude the possibility that there might be a difference that a larger sample size would show. The fact that *L. luctuosus* and *H. hawaiiensis* actually fed on mosquito larvae, contributed more valuable information to our present knowledge of food consumption. However, I do not believe that mosquito larvae serve as a primary food source for waterstriders since three out of 13 insects died by the end of the experiment, likely due to malnutrition.

*5.3 General behavior observations*

Whereas Cheng (1985) reported that adults of *Halobates* spp. had never been observed to feed on one another, I saw several tension contacts and roughly 10 instances of cannibalism on adults, even in the presense of younger nymphs. In addition, both freshwater and marine waterstriders demonstrated two different stridulatory mechanims. Their wettable claws that penetrate the surface tension are responsible for giving them traction as they traverse on the water surface. This skating movement utilized only the middle and hind legs, as fore legs are only used for grasping food and other insects. Both species also had the ability to jump straight up and down, but did not repeat this activity more than two or three times in a row. The intention of this behavior was fairly unclear, however, sudden experimenter disturbance seemed to induce this behavior.

On several occasions, I saw male individuals of *L. luctuosus* drop their abdomens on the surface of the water and vibrate the water for approximately three seconds. This activity created concentric rings of ripples around the male and usually elicited an escape response from a conspecific. During a 10 minute observation period, I saw males exhibit this behavior five times, on average. This observation should instigate further studies on intraspecific communication in male *L. luctuosus*.

**6. Conclusion**

The current research points the entomological community in four new directions. First, we should make hypotheses on why Moorea has a low representation of gerromorphans. Secondly, what is the evolutionary history of the species on the islands? Thirdly, how did the present species arrive and inhabit the island? Finally, with respect to applied research, can gerromorphans on Moorea provide a means of biological control?

The gerromorphan fauna of Moorea is now known fairly more than before. Diagnostic details of one veliid, one hermatobatid, and four gerrids and, where possible habitat preferences, sexual ratios, and mosquito larvae predation were studied.

This paper contributes to our knowledge of the extent to which the semiaquatic species of Gerromorpha have radiated in the Society Islands. Very few genera of freshwater gerromorpha have immigrated into the Pacific area. Overall, the semiaquatic gerromorphan species richness of the Opunohu River is rather small compared with other tropical, isolated island streams. Perhaps isolation of the Society Islands, short life span, and weak flying-ability are accountable for low stream colonization by insects (Resh et al. 1990) However, it is unclear whether the present species have a primary role in discriminating colonization of new species. Perhaps more species of gerromorphans occur in Moorea which haven't yet been discovered, or perhaps only six species exist and some other mechanisms prevent the introduction of new species, or caused the rapid extinction of other species. Future collections in stream and marine localities and further research on interspecific competition, food availability such as mosquito

larvae, and dispersal mechanisms will help to answer this question.

A future evolutionary and phylogenetic analysis based on the preserved specimens can give insight into the origination of the present species. Compared with continental coastal areas where marine insects are typically derived from ancestral terrestrial or freshwater linneages, freshwater species of Hawaiian streams are thought to have been derived from marine ancestors (Howard and Polhemus 1991). A similar trend is possible for the island of Moorea.

Six species are known so far form the Society Islands, but it is unlikely that the present collection includes all of the semiaquatic hemipteran fauna that exist in the Society Islands. In comparison with another tropical archipelago, Hawaii has a total of 320 Heteroptera, a suborder of Hemiptera which inludes the Gerromorpha (Nishida 1994). As future collections pursue, further studies may investigate whether these species are nonindigenous and they do not naturally occur in Moorea, but have arrived accidentally or intentionally, indigenous and naturally occur in Moorea, but also naturally occur elsewhere, or endemic and found exclusively in Moorea.

Until the last decade, knowledge about the biology and ecology of sea skaters was generally quite sparse (Cheng 1985). Entomologists have directed considerable attention toward the study of aquatic hemiptera as biological control agents. Evidence of insect predation may give additional economic importance to some species of semiaquatic gerromorpha.

**Acknowledgments**

I am grateful to the University of California, Berkeley, for providing the Gump Research Station on Moorea. I would like to thank station managers John Boland and Debbie Woodward; Dr. Jere Lipps, Dr. David Lindberg, Dr. Vince Resh, and Dr. David Stoddart for their endless support and guidance; and the entire Moorea class of 1998. Special thanks to Amy Lesen, Tegan Churcher, Virginia Matzek for all their patience. Additional thanks to Dr. Wai P. Chan and Dr. Cherie Northon for necessary computer tutorials. I am indebted to my parents, Javier and Kazue Chavez for their moral and financial support. Final thanks to Dr. Lanna Cheng of the Scripps Institute of Oceanography for her helpful advice and aid in identifications.

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Appendix 1. Diagnostic characteristics of adult *Halobates hawaiiensis* on Moorea.

| Male or Female | M | M | M | M | M | M | F | F | F | F | F |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Total Body Length | 4.86 | 4.70 | 5.0 | 4.90 | 5.12 | 5.44 | 4.10 | 4.72 | 5.20 | 4.48 | 3.76 |
| Head-Body ratio | 0.17 | 0.15 | 0.15 | 0.15 | 0.15 | 0.16 | 0.15 | 0.18 | 0.14 | 0.17 | 0.19 |
| Interocular width ratio | 3.0 | 3.7 | 1.6 | 3.1 | 3.6 | 3.1 | 2.1 | 4.5 | 3.7 | 2.8 | 4.2 |
| First antennal segment | 1.4 | 1.7 | 1.6 | 1.6 | 1.7 | 1.6 | 1.3 | 1.3 | - | 1.3 | 0.9 |
| Second antennal segment | 0.6 | 0.6 | 0.5 | 0.6 | 0.5 | 0.9 | 0.4 | 0.5 | - | 0.5 | 0.4 |
| Third antennal segment | 0.3 | 0.4 | 0.4 | 0.3 | 0.4 | 0.5 | 0.3 | 0.4 | - | 0.4 | 0.4 |
| Fourth antennal segment | 0.6 | 0.4 | 0.4 | 0.5 | 0.4 | - | 0.4 | 0.5 | - | 0.4 | 0.4 |
| Head length | 0.7 | 0.6 | 0.6 | 0.7 | 0.8 | 0.8 | 0.6 | 0.7 | 0.7 | 0.8 | 0.6 |
| Head width | 1.5 | 1.4 | 1.5 | 1.5 | 1.5 | 1.5 | 1.4 | 1.5 | 1.4 | 1.5 | 13 |
| Eye length | 0.5 | 0.5 | 0.5 | 0.5 | 0.5 | 0.5 | 0.5 | 0.5 | 0.5 | 0.5 | 0.5 |
| Rostrum length | 1.1 | 1.0 | 0.9 | 0.9 | 1.0 | 1.0 | 0.9 | 1.0 | 1.1 | 1.2 | 0.9 |
| Pronotum length | 0.4 | 0.4 | 0.4 | 0.5 | 0.5 | 0.4 | 0.5 | 0.5 | 0.4 | 0.5 | 0.4 |
| Pronotum width | 1.4 | 1.2 | 1.2 | 1.3 | 1.2 | 1.3 | 1.3 | 1.3 | 1.4 | 1.2 | 1.1 |
| Thorax length | 2.3 | 2.2 | 2.3 | 2.4 | 4.4 | 2.0 | 2.5 | 2.6 | 2.3 | 2.1 | 3.7 |
| Thorax width | 2.0 | 1.8 | 1.9 | 2.0 | 1.9 | 2.0 | 2.3 | 2.3 | 2.4 | 2.2 | 3.9 |
| Fore coxae length | - | - | 0.6 | - | 0.5 | 0.6 | 0.7 | - | 0.4 | 0.7 | 0.2 |
| Fore femur length | 1.8 | 1.8 | - | 0.7 | 1.6 | 1.6 | 1.9 | 1.8 | 1.6 | 1.8 | 0.5 |
| Fore femur width | 0.3 | 0.4 | 0.4 | .11 | 0.3 | 0.4 | 0.2 | - | 0.3 | 0.2 | 0.2 |
| Mid coxae length | - | - | 0.6 | - | 0.8 | 0.6 | 0.8 | 0.8 | 0.9 | 0.9 | 1.0 |
| Mid femur length | 5.6 | 5.6 | 5.6 | 5.3 | 5.7 | 6.7 | 5.0 | 5.6 | - | 5.4 | 4.7 |
| Mesotibial length | 4.0 | 4.2 | 3.8 | 4.2 | 4.0 | 4.2 | 1.6 | 4.4 | - | 4.0 | 3.4 |
| Mesotarsal length | 2.6 | 2.5 | 0.6 | 2.5 | 2.6 | 2.6 | 2.7 | 2.7 | - | 2.6 | 2.3 |
| Abdomen length | 1.8 | 1.9 | 1.7 | 1.8 | 2.8 | 1.2 | 1.0 | 1.4 | 1.3 | 1.0 | 2.0 |
| Abdomen width | 0.8 | 0.8 | 0.9 | 2.0 | 2.2 | 1.0 | 2.3 | 1.9 | 1.1 | 1.0 | 1.7 |
| Terminalia length | - | - | - | - | 1.9 | 0.8 | - | 1.0 | 0.3 | 0.2 | 0.3 |
| Terminalia width | - | - | 0.4 | 0.5 | 1.5 | 0.6 | - | 0.5 | 0.3 | 0.2 | 0.3 |

Appendix 2. Diagnostic characteristics of adult *Halobates hawaiiensis* on Moorea (cont.).

| Male or Female | F | F | F | M | M |
|---|---|---|---|---|---|
| Total Body Length | 4.32 | 3.90 | 4.08 | 3.70 | 4.16 |
| Head-Body ratio | 0.09 | 0.15 | 0.21 | 0.10 | 0.13 |
| Interocular width ratio | 4.0 | 3.7 | 2.8 | 4.4 | 4.2 |
| First antennal segment | 1.1 | 0.9 | 1.1 | 1.0 | 0.9 |
| Second antennal segment | 0.5 | 0.4 | 0.4 | 0.4 | 0.4 |
| Third antennal segment | 0.4 | 0.4 | 0.4 | 0.4 | 0.3 |
| Fourth antennal segment | 0.4 | 0.4 | 0.6 | 0.4 | 0.4 |
| Head length | 0.6 | 1.5 | 1.3 | 0.3 | 0.5 |
| Head width | 3.0 | 0.3 | 0.5 | 1.3 | 1.4 |
| Eye length | 0.5 | 0.4 | 0.9 | 0.4 | 0.5 |
| Rostrum length | 0.8 | 0.9 | 0.4 | 0.9 | 1.0 |
| Pronotum length | 0.5 | 0.4 | 1.1 | 0.4 | 0.4 |
| Pronotum width | 1.1 | 1.0 | 1.1 | 1.2 | 1.4 |
| Thorax length | 1.8 | 2.1 | 1.8 | 2.0 | 1.8 |
| Thorax width (maximum) | 1.8 | 1.7 | 1.8 | 1.8 | 1.8 |
| Fore coxae length | - | 0.6 | 0.7 | 0.6 | 0.5 |
| Fore femur length | 1.5 | 1.3 | 3.6 | 1.6 | 1.2 |
| Fore femur width | 0.2 | 0.2 | 0.4 | 0.2 | 0.3 |
| Mid coxae length | 0.4 | 0.9 | 1.8 | 0.9 | 0.6 |
| Mid femur length | 4.6 | 4.5 | 4.7 | 4.7 | 4.3 |
| Mesotibial length | 3.5 | 3.6 | 3.5 | 3.4 | 3.3 |
| Mesotarsal length | 2.2 | 2.5 | 2.4 | 2.4 | 2.3 |
| Abdomen length | 2.3 | 0.9 | 1.1 | 0.8 | 1.8 |
| Abdomen width | 0.9 | 0.8 | 0.9 | 0.9 | 1.8 |
| Terminalia length | - | 0.1 | 1.2 | 0.6 | 0.6 |
| Terminalia width | - | 0.3 | 1.1 | 0.6 | 0.5 |

Appendix 3. Diagnostic characteristics of adult *Trepobates* sp. on Moorea

| Male or Female | F | M |
|---|---|---|
| Total Body Length | 6.2 | 4.9 |
| Head-Body ratio | 0.17 | 0.21 |
| Interocular width ratio | 2.3 | 2.9 |
| First antennal segment | 1.4 | 1.4 |
| Second antennal segment | 0.9 | 1.0 |
| Third antennal segment | 1.0 | 1.0 |
| Fourth antennal segment | 1.4 | 1.4 |
| Head length | 0.9 | 0.8 |
| Head width | 1.4 | 1.4 |
| Eye length | 0.6 | 0.5 |
| Rostrum length | 2.0 | 2.0 |
| Pronotum length | 0.6 | 0.7 |
| Pronotum width | 1.3 | 1.0 |
| Wingpads length | 1.8 | 2.6 |
| Wingpads width | 1.1 | 1.3 |
| Thorax length | 2.7 | 2.1 |
| Thorax width (maximum) | 2.5 | 1.8 |
| Fore coxae length | - | 0.7 |
| Fore femur length | 1.8 | 2.1 |
| Fore femur width | 0.2 | 0.3 |
| Mid coxae length | - | 0.4 |
| Mid femur length | 4.4 | 4.1 |
| Mesotibial length | 4.2 | 3.9 |
| Mesotarsal length | 2.4 | 0.3 |
| Abdomen length | 2.6 | 2.0 |
| Abdomen width | 1.5 | 0.8 |

Appendix 4. Diagnostic characteristics of *Limnogonus luctuosus* on Moorea

| Male or Female | M | M | M | M | F | F | F | M | F | F | F | F |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Total Body Length | 7.92 | 8.72 | 6.8 | 6.88 | 9.12 | 9.36 | 6.96 | 7.92 | 7.68 | 8.2 | 6.56 | 7.92 |
| Head-Body ratio | 0.18 | 0.16 | 0.21 | 0.2 | 0.20 | 0.17 | 0.23 | 0.16 | 0.14 | 0.17 | 0.17 | 0.18 |
| Interocular width ratio | 1.4 | 1.8 | 1.8 | 1.8 | 1.0 | 2.2 | 1.5 | 2.2 | 4.0 | 2.0 | 3.7 | 2.2 |
| First antennal segment | 2.1 | 1.7 | 1.8 | 1.8 | 1.8 | 1.9 | 1.8 | - | 1.8 | 1.8 | 1.8 | 1.8 |
| Second antennal segment | 1.3 | 1.4 | 1.3 | 1.3 | 1.3 | 1.2 | 1.4 | - | 1.3 | 1.2 | 1.3 | 1.3 |
| Third antennal segment | 1.2 | 1.1 | 1.1 | 1.1 | 1.0 | 1.2 | 1.1 | - | 1.1 | 1.1 | 1.0 | 1.1 |
| Fourth antennal segment | 1.0 | 1.3 | 1.5 | 1.2 | 1.5 | 1.5 | 1.4 | - | 1.3 | 1.5 | 1.4 | 1.4 |
| Head length | 1.2 | 1.2 | 1.3 | 1.2 | 1.5 | 1.4 | 1.3 | 1.1 | 1.0 | 1.2 | 1.0 | 1.2 |
| Head width | 1.5 | 1.7 | 1.6 | 1.5 | 1.5 | 1.6 | 1.6 | 1.6 | 1.6 | 1.5 | 1.6 | 1.5 |
| Eye length | 0.6 | 0.7 | 0.6 | 0.6 | 0.6 | 0.6 | 0.6 | 0.7 | 0.6 | 0.6 | 0.6 | 0.6 |
| Rostrum length | 1.7 | 2.6 | 2.5 | 2.8 | 2.5 | 1.9 | 2.6 | 2.4 | 2.4 | 2.4 | 2.4 | 2.5 |
| Pronotum length | 0.5 | 0.7 | 0.7 | 0.7 | 0.7 | 0.6 | 0.6 | 0.6 | 0.4 | 0.7 | 0.6 | 0.6 |
| Pronotum width | 1.4 | 1.6 | 1.4 | 1.4 | 1.4 | 1.4 | 1.5 | 1.4 | 1.4 | 1.3 | 1.3 | 1.4 |
| Wingpads length | 2.6 | 3.0 | 2.7 | 2.8 | 2.8 | 2.9 | 2.8 | 2.8 | 2.6 | 2.5 | 2.5 | 2.7 |
| Wingpads width | 1.0 | 1.4 | 1.3 | 1.2 | 1.2 | 1.3 | 1.3 | 1.4 | 1.2 | 1.1 | 1.1 | 1.2 |
| Thorax length | 2.4 | 2.6 | 2.2 | 2.4 | 2.1 | 2.2 | 2.4 | 2.4 | 2.5 | 1.9 | 2.3 | 1.4 |
| Thorax width (maximum) | 2.5 | 2.2 | 2.3 | 2.5 | 2.5 | 2.6 | 2.4 | 2.6 | 2.2 | 2.3 | 2.2 | 2.3 |
| Fore coxae length | 0.8 | 0.6 | 0.6 | 0.7 | 0.7 | 0.7 | 0.6 | 0.6 | 0.6 | 0.6 | 0.7 | - |
| Fore femur length | 2.4 | 2.4 | 2.2 | 2.6 | 2.2 | 2.6 | 2.6 | 2.6 | 2.3 | 2.3 | 2.4 | 2.2 |
| Fore femur width | 0.3 | 0.3 | 0.4 | 0.4 | 0.3 | 0.3 | 0.4 | 0.2 | 0.3 | 0.3 | 0.4 | 0.3 |
| Mid coxae length | 1.0 | 0.9 | 1.0 | 0.8 | 0.8 | 0.8 | 0.8 | 1.0 | 0.8 | 0.8 | 0.8 | 0.8 |
| Mid femur length | 5.9 | 6.3 | 5.6 | 5.8 | 5.6 | 6.0 | 5.8 | 5.6 | 5.2 | 5.2 | 5.2 | 5.4 |
| Mesotibial length | 5.5 | 5.4 | 5.1 | 5.7 | 5.3 | 5.6 | 5.4 | 5.6 | 5.1 | 5.0 | 5.4 | 5.1 |
| Mesotarsal length | 3.0 | 2.8 | 2.6 | 2.7 | 2.9 | 2.9 | 2.4 | 3.0 | 2.7 | 2.8 | 2.8 | 2.7 |
| Abdomen length | 3.7 | 4.2 | 2.8 | 2.8 | 4.0 | 4.0 | 3.0 | 3.8 | 2.6 | 3.7 | 2.8 | 3.6 |
| Abdomen width | 1.6 | 1.7 | 1.6 | 1.6 | 1.8 | 1.6 | 1.4 | 1.5 | 1.4 | 1.8 | 1.4 | 1.6 |
| Terminalia length | 0.2 | 0.4 | 2.4 | 2.6 | 0.4 | 1.2 | 1.6 | 0.4 | 1.2 | 0.8 | 2.4 | 0.5 |
| Terminalia width | 0.2 | 0.2 | 0.6 | 0.8 | 0.4 | 0.4 | 0.8 | 0.6 | 0.8 | 0.7 | 0.7 | 0.7 |

Appendix 5. Diagnostic characteristics of juvenile *Halobates hawaiiensis* on Moorea.

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Total Body Length | 1.27 | 1.92 | 2.32 | 2.96 | 3.52 | 2.96 | 3.28 | 2.56 | 3.04 | 2.4 | 1.92 | 1.28 |
| Head-Body ratio | 0.08 | 0.22 | 0.19 | - | - | - | - | - | - | - | - | - |
| Interocular width ratio | 4.0 | 3.8 | 5.7 | - | - | - | - | - | - | - | - | - |
| First antennal segment | 0.3 | 0.5 | 0.5 | - | - | - | - | - | - | - | - | - |
| Second antennal segment | 0.2 | 0.3 | 0.2 | - | - | - | - | - | - | - | - | - |
| Third antennal segment | 0.1 | - | 0.3 | - | - | - | - | - | - | - | - | - |
| Fourth antennal segment | 0.3 | - | 0.3 | - | - | - | - | - | - | - | - | - |
| Head length | 0.1 | 0.4 | 0.4 | - | - | - | - | - | - | - | - | - |
| Head width | 0.5 | 0.8 | 0.9 | - | - | - | - | - | - | - | - | - |
| Eye length | 0.2 | 0.3 | 0.3 | - | - | - | - | - | - | - | - | - |
| Rostrum length | 0.4 | 0.6 | 0.5 | 0.6 | 0.8 | 0.6 | 0.6 | 0.6 | 0.6 | 0.5 | 0.3 | 0.4 |
| Pronotum length | 0.1 | 0.4 | 0.2 | - | - | - | - | - | - | - | - | - |
| Pronotum width | 0.6 | 0.7 | 0.8 | - | - | - | - | - | - | - | - | - |
| Thorax length | 0.8 | 0.9 | - | - | - | - | - | - | - | - | - | - |
| Thorax width (maximum) | 0.7 | 1.0 | 1.2 | - | - | - | - | - | - | - | - | - |
| Fore coxae length | 0.2 | 0.4 | 0.3 | - | - | - | - | - | - | - | - | - |
| Fore femur length | 0.3 | 1.0 | 0.9 | - | - | - | - | - | - | - | - | - |
| Fore femur width | 0.1 | 0.1 | 0.1 | - | - | - | - | - | - | - | - | - |
| Mid coxae length | 0.3 | 0.3 | 0.5 | - | - | - | - | - | - | - | - | - |
| Mid femur length | 0.5 | 2.6 | 2.7 | 2.6 | 2.8 | 2.5 | 2.4 | 1.8 | 2.4 | 1.8 | 1.4 | 1.4 |
| Mesotibial length | 0.3 | - | 2.1 | - | - | - | - | - | - | - | - | - |
| Mesotarsal length | - | - | 2.1 | - | - | - | - | - | - | - | - | - |
| Abdomen length | 0.3 | 0.5 | 0.5 | - | - | - | - | - | - | - | - | - |
| Abdomen width | 0.5 | 1.0 | 1.2 | - | - | - | - | - | - | - | - | - |
| Terminalia length | 0.07 | - | - | - | - | - | - | - | - | - | - | - |
| Terminalia width | 0.07 | - | - | - | - | - | - | - | - | - | - | - |

Appendix 6. Diagnostic characteristics of juvenile *Halobates hawaiiensis* on Moorea (cont.).

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Total Body Length | 1.84 | 2.0 | 1.44 | 1.76 | 2.8 | 1.92 | 2.4 | 2.16 | 2.24 | 1.52 | 1.76 | 1.44 |
| Head-Body ratio | - | - | - | | 0.16 | 0.12 | 0.13 | 0.13 | 0.13 | 0.14 | 0.14 | 0.11 |
| Interocular eye ratio | - | - | - | - | 3.75 | 3.33 | 3.0 | 3.71 | 4.0 | 3.67 | 3.0 | 4.0 |

Appendix 7. Diagnostic characteristics of juvenile *Halobates hawaiiensis* on Moorea (cont.).

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Total Body Length | 1.44 | 2.16 | 1.52 | 1.44 | 1.76 | 1.92 | 1.84 | 1.76 | 1.92 | 1.92 | - |
| Head-Body ratio | 0.11 | 0.13 | 0.13 | 0.14 | 0.21 | 0.15 | 0.13 | 0.13 | 0.12 | 0.15 | 0.2 |
| Interocular eye ratio | 5.0 | 3.0 | 4.4 | 3.33 | 3.43 | 4.0 | 3.0 | 3.0 | 3.25 | 3.43 | 4.0 |

Appendix 8. Diagnostic characteristics of *Rhagovelia* sp.

| | | |
|---|---|---|
| Total Body Length | 1.75 | 0.83 |
| Head-Body ratio | 0.26 | 0.36 |
| Interocular width ratio | 4.0 | - |
| First antennal segment | 0.2 | 0.05 |
| Second antennal segment | 0.2 | - |
| Third antennal segment | 0.2 | - |
| Fourth antennal segment | 0.4 | - |
| Head length | 0.4 | 0.3 |
| Head width | 0.5 | - |
| Eye length | 0.1 | - |
| Rostrum length | 0.5 | - |
| Pronotum length | 0.4 | - |
| Pronotum width | 0.7 | - |
| Thorax length | - | - |
| Thorax width (maximum) | - | 0.45 |
| Fore coxae length | - | - |
| Fore femur length | 0.4 | - |
| Fore femur width | 0.1 | - |
| Mid coxae length | - | - |
| Mid femur length | 0.5 | 0.15 |
| Mesotibial length | 0.4 | - |
| Mesotarsal length | 0.4 | - |
| Abdomen length | 0.1 | - |
| Abdomen width | - | - |

Appendix 9. Diagnostic characteristics of *Hermatobates* sp.

| | |
|---|---|
| Total Body Length | 0.83 |
| Head-Body ratio | - |
| Interocular width ratio | 4.0 |
| First antennal segment | 0.18 |
| Second antennal segment | - |
| Third antennal segment | - |
| Fourth antennal segment | - |
| Head length | - |
| Head width | - |
| Eye length | - |
| Rostrum length | - |
| Pronotum length | - |
| Pronotum width | - |
| Thorax length | - |
| Thorax width (maximum) | 0.48 |
| Fore coxae length | - |
| Fore femur length | - |
| Fore femur width | - |
| Mid coxae length | - |
| Mid femur length | 0.3 |
| Mesotibial length | - |
| Mesotarsal length | - |
| Abdomen length | - |
| Abdomen width | - |

Appendix 10. Number of mosquito larvae eaten per day.

| | DAY | | | | | | |
|---|---|---|---|---|---|---|---|
| SPECIES | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| *L. luctuosus* | 0 | 0 | 0 | 1 | 2 | 1 | 1 |
| *L. luctuosus* | 0 | 0 | 1 | 2 | 0 | 1 | 0 |
| *L. luctuosus* | 0 | 1 | 1 | 0 | 1 | 1 | 2 |
| *L. luctuosus* | 0 | 0 | 1 | 1 | 0 | 0* | |
| *L. luctuosus* | 0 | 0 | 1 | 1 | 1 | 0 | 0* |
| *L. luctuosus* | 1 | 1 | 2 | 1 | 2 | 2 | 0* |
| *H. hawaiiensis* | 0 | 2 | 3 | 1 | 1 | 0 | 0 |
| *H. hawaiiensis* | 0 | 0 | 1 | 0 | 1 | 0 | 2 |
| *H. hawaiiensis* | 0 | 2 | 2 | 2 | 1 | 1 | 0 |
| *H. hawaiiensis* | 0 | 1 | 1 | 0 | 0 | 3 | 0 |
| *H. hawaiiensis* | 0 | 1 | 1 | 1 | 1 | 0* | |
| *H. hawaiiensis* | 1 | 1 | 2 | 1 | 2 | 2 | 0 |
| *H. hawaiiensis* | 1 | 0 | 1 | 2 | 1 | 0 | 1 |

* Found dead

# A Correlation between Changes in Depth and Changes in Algal Density in *Porites lutea*

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ABSTRACT. Zooxanthellae density in the hermatypic coral *Porites lutea* decreased significantly when hosts were elevated to 1m from 5m in depth. The experiment was conducted over a period of 5 weeks on the island of Moorea, French Polynesia. This change is consistent with previous observations of greater algal densities at increasing depth in reef corals on Moorea (Linville 1994). All corals tested were removed from the lagoon and placed at 1m on either the barrier reef or the fringing reef and put under Ultraviolet radiation (UVR) blocking panels, UVR transmitting panels, or left exposed (ambient) as a control on panel effects. No significant differences were found between those corals protected from and those exposed to increased UVR on the barrier reef. Coral hosts left exposed and those protected by UVR blocking panels on the fringing reef had significantly lower density than those under UVR transmitting panels, suggesting sedimentation contributed to decline in the lagoon. Because corals at both sites, regardless of treatment had significantly lower zooxanthellae density at 1m than at 5m, a 1°C elevation in temperature is suggested as an alternative cause for the decline.

## Introduction

In addition to feeding modes available to deep sea dwelling corals (carnivory, filter feeding and osmosis of dissolved organic material), hermatypic, or reef-building , corals in the photic zone receive sugars and amino acids from between one and five million cysts per cm( of one species of symbiotic algae (zooxanthellae) residing in their tissue, *Symbiodinium microadriaticum*(Figure 1). As much as 98% of the carbon fixed by *S. microadriaticum* is transferred to the coral, an association that aids in the construction of calcium carbonate reefs. Zooxanthellae benefit from nitrate and phosphate waste cast off from the animal host, especially important in nutrient poor tropical waters (Veron 1986).

Hermatypic corals obtain their color from the symbiotic algae. In the absence of the olive-brown symbiont or its pigments, the white calcium carbonate "skeleton" shows through the colorless coral polyps. Regulation of dividing cells can be controlled by the host by expulsion and digestion (Hoegh-Guldberg 1996). In their motile phase, *S. microadriaticum* are able to leave one species of coral and infect hosts of entirely different cnidarian and molluscan taxa (Schoenberg and Trench 1980). Expulsion of the zooxanthellae, whether initiated by the symbiont or the host, is thought to be a physiological response to environmental stress, providing opportunities for new combinations of hosts and endosymbiont (Buddemeir 1993). Hermatypic corals can recover their symbiont population from low levels, but prolonged "bleaching," whether due to changes in salinity, temperature, irradiance, increased sedimentation, pollution or disease leads to the death of coral host.

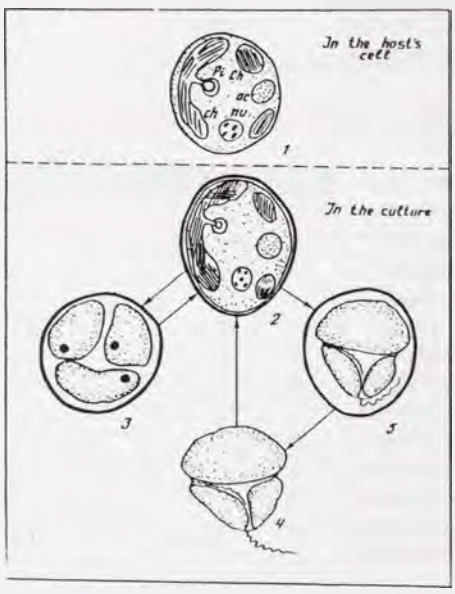



**Figure 1.** Life cycle of the dinoflagellate, *S. microadriaticum*.

In recent years, frequent and severe mass bleaching events have affected coral reef systems around the world. Many of the mass bleachings have occurred during El Nino years (Glynn 1993a), prompting researchers to look for correlations with global warming. Ultraviolet radiation (UVR) flux, alone or synergistically with elevated temperature is also suspected. Shallow water reef communities have been particularly impacted, raising the possibility of UVR penetrating the calm seas associated with El Nino in the tropics (Fisk 1985). The ozone layer is thinner near the equator and the zenith angle of the sun is lower, and because of the relative lack of suspended matter, the increased UVR penetrates more deeply in tropical waters (Gleason 1993a). While the connection between bleaching and elevated seawater temperature is well established in the field (Brown & Suharsono 1990, Hoegh-Guldberg & Salvat 1995) and in the lab (Glynn & D'Croz 1990), the effect of UVR is more controversial (Stimson 1997). UVR stress alone has been shown to cause coral bleaching both through loss of pigment (Hoegh-Guldberg and Smith 1989) and loss of zooxanthellae (Gleason and Wellington 1993b).
In this study, specimens of Porites lutea were removed from a depth of 5m and deposited 1m below the surface to test whether a strong increase in UVR would cause bleaching in reef building corals at Moorea.

**Materials and Methods**

The experiment was performed at the Gump Biological Research Station on Moorea, French Polynesia (17° 30' S, 149° 50' W). Previous research has indicated that UVR in the Moorea lagoon has limited biological effect at 5m (Dunne and Brown 1996). On October 6 and 7 1998, Porites lutea were collected along the west slope of the fringing reef in Cook's Bay at a depth of > 5m by snorkel and SCUBA. Because the ability to tolerate UVR stress may depend on higher water flow and PAR (Jokiel 1997), sites were chosen within a turbid lagoon for comparison with a barrier reef where currents are relatively swift and clear. The specimens were immediately transplanted to a depth of 1m on the fringing and barrier reef flats. At both locations, three corals were placed under a UVR blocking panel, three were left exposed to ambient conditions, and three were placed under a UVR transmitting panel as a control on the possible effects of using panels. There were two replicate treatments on each reef, and *Porites lutea* were haphazardly assigned to a treatment regime as they were gathered. On October 10, as a control on the physical stress of uprooting and moving the specimens, an additional six corals were collected at 5m and transplanted to another location within the lagoon at 5m

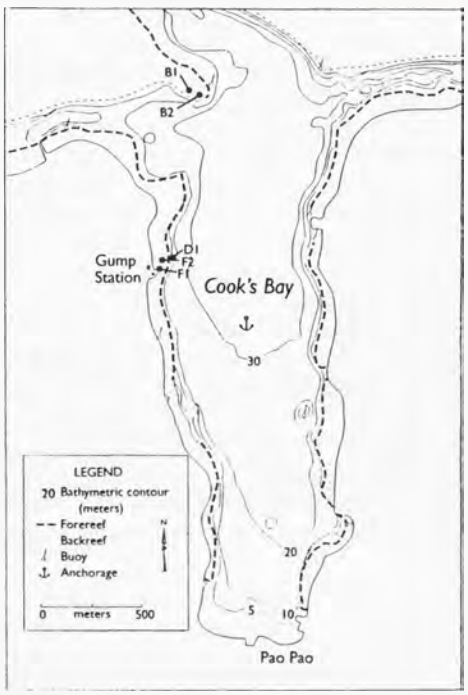



**Figure 2.** Study sites on Moorea, French Polynesia

Following Gleason's method (1993a), plastic panels measuring 38x38x0.3 cm. were secured to stainless steel rods, 15-20 cm above the corals. UVR blocking panels were made of op-3 acrylic (92% transparent to wavelengths >400 nm) and the UVR transmitting panels were made of op-1 acrylic (92% transparent to all wavelengths) [CYRO Industries]. All panels collected a layer of sediment and corraline algae, which required that they be wiped clean everyday.

The barrier reef sites were ~100m from the surf in shallows on the reef flat, where they were continually flushed by tides. The lagoon is much less diverse in coral genera than the barrier reef, and it should be noted that the fringing reef sites were near a pineapple juice factory discharging

effluents into the bay. A Secchi disc held horizontally was visible at 10 m on the barrier reef, 6 m at the fringing reef, and 3 m at the deep site. Salinity was 35% at all sites. There was no difference in temperature at either reef, but it was 0.5-1° C cooler at the deep site.

The corals were retrieved 35 days later, and the algal densities were measured. Corals from 5m and 1m freshly collected from the lagoon were analyzed for comparison with the transplanted corals. Zooxanthellae were separated from their hosts by heating the corals in glass jars containing seawater over an open flame. The temperature was maintained between 35° and 40° C for three hours. While this procedure did not lead to a complete "bleaching", a sufficient number were expelled for estimation of the relative densities of the corals. After cooling for three hours, a 10mm sample was centrifuged to separate the mucus; the pellet was then resuspended in tap water and the zooxanthellae were counted in a hemacytometer at 400x magnification (Gleason 1993a). The number of cells per $cm^2$ were estimated by extrapolating the hemacytometer volume to the jar volume and dividing by the surface area of the coral. Surface area of the coral was derived by weighing the amount of tin foil it took to cover the coral.

**Results**

The Wilcoxon Two-sample Test was used to analyze all results. Corals at 5m, whether moved or not, had significantly higher densities of zooxanthellae than those freshly collected (stable) at 1m and corals that had been transplanted to 1m for 5 weeks ($p=0.005$), both on the fringing and barrier reefs. The loss of zooxanthellae was due to the increase in elevation, not to stress from being moved ($p=0.1$) (Figure 3).

A two-tailed test of the ambient corals on the fringing and barrier reefs indicates that the corals moved to the barrier reef had a significantly higher ($p=0.025$) algal density, which would suggest that they were under less stress. The presence of a panel or UVR block made no significant difference ($p=0.1$) on the barrier reef, indicating that some other factor was responsible for the decline observed in all treatments.

On the fringing reef, two-tail tests indicate that corals protected by a panel had significantly higher algal density($p=0.025$) than those without one. Zooxanthellae densities were not significantly different ($p=0.025$) between corals under the UVR- (blocking) and UVR+ (transmitting) panels, suggesting some other effect of the panel is responsible. Panels at all sites collected sediment, but it may be that the terrestrial sediment running into the lagoon accounts for the lower density in ambient corals on the fringing reef compared to the barrier reef (Figure 4).

| Environment | Treatment | Avg. Cells/$cm^2$ | Std. Dev. |
|---|---|---|---|
| Barrier Reef | UVR- | 82022 | 336616 |
| | UVR+ | 156040 | 116709 |
| | Ambient | 105624 | 61868 |
| Fringing Reef | UVR- | 88271 | 6292 |
| | UVR+ | 189766 | 75166 |
| | Ambient | 40896 | 26773 |
| | Controls (Stable) | 35737 | 17164 |
| Lagoon (5m) | Ambient | 292697 | 176597 |
| | Controls (Stable) | 375139 | 271688 |

**Table 1.** Average cells/$cm^2$ and standard deviation of samples, n=6.

**Discussion**

Algal density and pigmentation are known to vary with available light. Despite high phenotypic variability within each sample, algal density decreased with elevation to higher depths. A correlation between increased algal density and increased depth is consistent with a previous survey of *Porites* on Moorea (Linville 1994), and studies of nearly all hermatypic corals elsewhere, but not all experiments have shown change in density with change in depth (Stimson 1997). The reason corals have fewer algae at 1m than 5m is not known, and it may not necessarily be a sign of ill health. *Porites* spp. have low growth rates and low metabolisms (Glynn 1993b), have strongly resisted bleaching in Moorea (Gleason 1993c, Hoegh-Guldberg & Salvat 1995), and are by far the most common genus on the fringing reef.

Marine animals such as corals, clams, zooanthids, and sponges that depend on symbiotic relations with zooxanthellae require compounds to protect themselves from over exposure to sunlight. These compounds have been identified as Microsporine-like amino acids (MAA) whose production has been shown to be a response to UVR stress (Dunlap & Chalker 1986). The ability of the corals to make the compounds appears to be highly variable, even within a species. UVR is known to damage zooxanthellae resulting in oxygen toxicity (Lesser and Shick 1989), but experimental studies of UVR stress alone have produced contradictory results. Kinzie (1993) found that colonies of *Montastrea verrucosa* exposed to increased UVR and PAR had significantly less algae than colonies exposed to PAR alone. Stimson examined the algal density of *Pocillopora damicornis* over a year and found a correlation between increased UVR and PAR and decreased density. Glynn (1993b) found, as I did, that algae in both control and UVR protected corals declined when elevated. It is more difficult to account for the difference between the panels on the fringing reef, where corals under the UVR transmitting panel had the highest algal density. Significant PAR may have also been blocked by the UVR blocking panel. I have relied on the manufacturer's specifications. This question may be resolved by testing light transmission through the panels.

Loss of zooxanthellae is an indicator of stress and can result not only in decreased photosynthesis, but reduced growth and reproduction (Jones 1997). Although I did not measure MAAs or photosynthesis, the significantly higher algal density in corals transplanted to the barrier reef compared to the fringing reefs suggests that they were under less stress, and that the lower algal density on the fringing reef is not a response to the increase in available light at 1m.

Hard corals live within a narrow temperature range, and even slight increases (0.5-1.5°C) over a period of weeks can lead to death (Glynn and D'Croz 1990). Mass bleachings of Acropora and Pocillopora on Moorea in 1994 were attributed to an increase of 1° C (Hoegh-Guldberg 1995). Gleason (1993a) does not a mention a difference in temperature in his elevation experiment, but it appears that the subtle change in temperature affected the density in my study. This could be tested by measuring density in *P. lutea* on Moorea at different times of the year or perhaps the density of the same species at different latitudes. It would be interesting to see if corals moved 1m to 5m increase in algal density. Recent work has shown that higher temperatures damage the symbionts ability to photosynthesize, and that light is an important, but secondary factor (Jones et al 1998).

The UV transmitting panel used as a control demonstrates the difference in sedimentation on the reefs. At all locations, the panels were covered in a uniform layer of sediment after 48 hours, whenever I failed to wipe them clean. The amount of sediment was roughly equal, but the character was very different: a light, calcareous sand on the barrier reef and heavier terrigenous sand on the fringing reef. Hard corals are able to knock off fairly large grains of sand with their tentacles (Riegl 1995). Sedimentation on reefs leads to a decline in coral abundance and diversity, because of the metabolic cost of clearing sediment (McClanahan and Obura 1997). More needs to be known about the effects of different types of sedimentation on different species of corals, and what effect this has on biodiversity on fringing and barrier reefs.

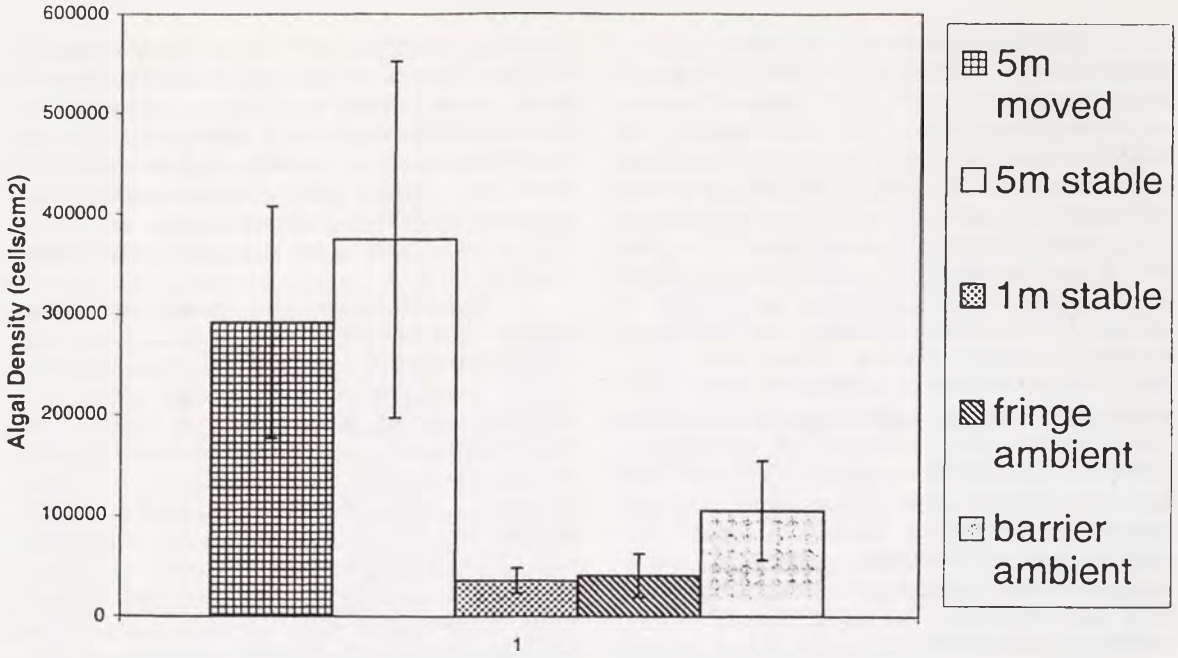
## Conclusions

Algal density in *Porites lutea* increases with depth. Algal density changes when moved to shallow water for reasons other than increased UVR. *Porites* is able to live on and dominate the fringing reef on Moorea despite decreased algal density. Terrigenous sedimentation may be responsible for lower zooxanthellae density in shallow lagoon corals. Because bleaching experiments on different genera of coral have produced very different results, researchers must consider the sensitivity of hermatypic corals to stressors on a case by case basis and be aware of the history of the study site.

## Acknowledgments

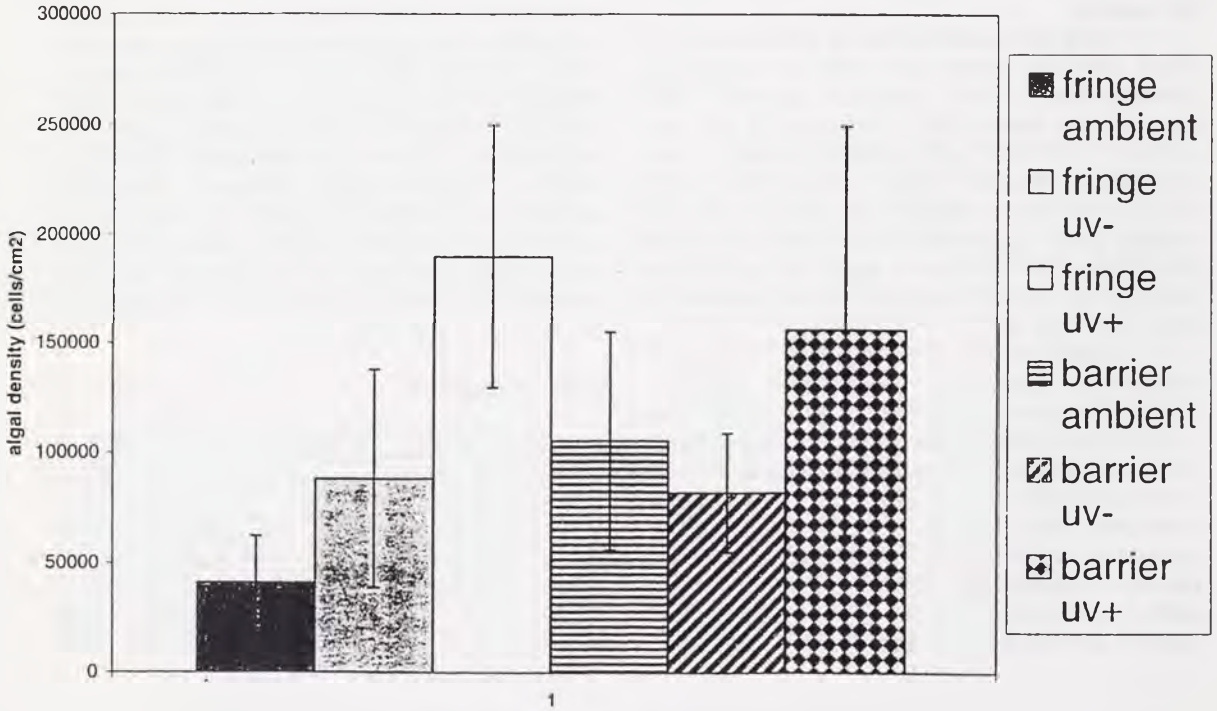
I thank Prof. Deborah Penry for her valuable suggestions and comments on the manuscript. For all their advice and help with the experiment, I would also like to thank the teaching assistants Virginia Matzek , Amy Lesen, and Tegan Churcher; the professors: Jere Lipps, Vince Resh, David Lindberg , David Stoddart, and Cherie Northon; the staff of the Gump Research Station: John and Debbie, Jacques, Tony and Irma; the SCUBA divers Joe and Audrey; my friends Doug and Stan for logistical help in Berkeley; and all my classmates for a wonderful time on Moorea.

Figure 3 : Algal Density in *Porites lutea* at 5m and 1m




"Stable" corals are controls that were freshly collected; "5m moved" are corals that were moved to another spot at 5m without panels for 5 weeks; "fringe" and "barrier ambient" corals were elevated to 1m on the reefs without panels for 5 weeks.

Figure 4: Algal Density of *Porites* Elevated to 1m on Fringing and Barrier Reefs




Coral Treatments: ambient (no panels), UV- (protected) and UV+ (transmitted) panels on fringing and barrier reefs

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# The Effects of Overwater Hotel Bungalows on Coral Health and Diversity on the Island of Moorea, French Polynesia

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ABSTRACT. The increasing popularity of coastal tourist developments in the tropics has impacted the fragile coral reef ecosystems that support this industry. A recent trend in hotel accommodations is the overwater bungalow, a structure covering approximately 4 x 6 m built on pilings several meters offshore. The purpose of this study was to quantitatively evaluate the effects of overwater bungalows on the fringing reef environment on Moorea (17° 30'S, 149° 50'W), French Polynesia, by examining live coral cover and diversity, dead coral cover, algae cover and diversity, and the species inhabiting the artificial bungalow piling habitat at both bungalows and controls at three study sites. Bungalows and controls at each site were found to differ significantly from one another with respect to live coral cover (site one, P=0.003, site two, P=0.002, site three, P=0.001). Dead coral and algae cover were both found to differ significantly between bungalows and controls at site one (P= 0.012 & P=0.003) and site two (P=0.005 & P=0.005), but not at site three(P=0.860 & P=0.132). The mean number of coral species present at each of the three location's control sites was higher than the mean under the bungalows. Several possible factors may be affecting overall coral health including, the bungalows, initial construction of the bungalows, mechanical damage to coral, coral collection, and pollution. Low percent live coral and high percent dead coral and algae cover present under bungalows compared to control sites suggest two possible causes; either it is an effect of the bungalow itself, or it is a response to the initial construction of the overwater bungalow. Globally, the effects of overwater bungalows on coral reefs are currently minuscule, but if this development trend continues to grow it could lead to a widespread decline in coral health and diversity in the tropics.

## Introduction

Coral reefs, one of the most productive biological environments on Earth, occupy about 15% of the shallow littoral areas in the world and represent an important economic resource for most of the countries where they are found (Porcher 1995). In French Polynesia, development of tourism along coral reefs is essential to the economy, providing the primary source of income for the region. In 1997, 330 million US dollars were spent by tourists in French Polynesia, accounting for over 33% of the market share value for the entire South Pacific (TCSP 1998). The tourism industry is expanding rapidly in French Polynesia and tourists have increased in number from 82, 822 in 1975 to 180,440 in 1997 (TCSP 1998).

The increasing popularity of coastal tourist developments in the tropics, particularly areas with beaches and fringing reefs, has impacted the fragile coral reef ecosystems that support this industry. In French Polynesia, 6,000 $km^2$ of reef area are at risk, with overexploitation of marine resources and coastal development posing the greatest threats (Bryant et al. 1998). Reefs around Moorea are suffering from sedimentation resulting from agriculture on steep slopes and from tourist developments, particularly in the north-west; reefs from Pointe Tiahura through to the Club Mediterranee development are said to be badly damaged (Wells 1988). A number of environmental impact studies have been carried out on Moorea including Anon. (1977), Porcher and Bouilloud (1984), and Porcher and Gabrie (1987) and a current study is under way to investigate the impact of human activities on the reef. The damaging effects of sewage related nutrient enrichment due to coastal development on coral reefs has been well documented in Kanoehe Bay, Hawaii. Large mats of the green algae *Dictyosphaeria cavernosa* formed, covering and killing corals in Kaneohe Bay, while large portions of the community changed from a coral-dominated autotrophic community to an algae-dominated suspension feeding community due of eutrophication (Richmond 1993). Fringing reefs are often the preferred location for large-scale tourist developments and as a result these areas are often disturbed.

The number of islands in French Polynesia with resorts is increasing each year, although Tahiti and Moorea still account for more than 80% of the total hotel capacity (Hutchings et al. 1994). An increasingly popular trend in hotel accommodations, on Moorea and elsewhere, is the overwater bungalow. Resorts have constructed these to cater to wealthy foreign clientele.

Overwater bungalows are wood and concrete structures covering approximately 4 x 6 m, built on pilings several meters offshore and accessible by boardwalk from the beach. The first of their kind on Moorea were constructed in 1965 at the Hotel Bali Hai (Druet 1998). Two other resorts on the island have since built a combined total of 24 units, with a third hotel in the planning stages of development. At least 60 other partial overwater bungalows, that is bungalows that are built on the beach or a motu and extend out over the fringing reef, can be found on the shores of Moorea. Overwater bungalows have the potential to damage the coral reefs that attract tourists and support this lucrative industry by shading out and killing coral and favoring a community dominated by algae.

The purpose of this study was to quantitatively evaluate the effects of overwater bungalows on the fringing reef environment on Moorea by examining live coral cover and diversity, dead coral cover, algae cover and diversity, and the species inhabiting the artificial bungalow piling habitat.

## Materials and Methods

*Study Sites*

Moorea (17° 30'S, 149° 50'W), a high volcanic island approximately 1.2 million years in age, is located in the central south Pacific Ocean within the Society Archipelago of French Polynesia. Its 61 km of coastline are encircled by a barrier reef with a lagoon 500-1500 m in width (Galzin and Pointier 1985). The climate is tropical and warm with average annual temperatures ranging from 24° to 31°C. Moorea is only 25 km northwest of Tahiti, providing tourists an attraction just a short flight or ferry ride from the central port of French Polynesia, Papeete. This study focused on the overwater hotel bungalows of three resorts on Moorea (Figure 1). Study sites were chosen for their presence of overwater bungalows of varying age on the fringing reef environment.

*Site One*

Site one, Hotel Bali Hai, is located on the northern side of Moorea, just east of Cook's Bay (Figure 1). Built in 1965, the hotel contains nine 4.47 x 6.25 m overwater bungalows. The structures were constructed on the crest of the fringing reef, approximately 35 m offshore. Each is accessible by boardwalk from the beach. The building materials used in construction were wood for the boardwalks and bungalows and cement for the pilings and their bases. Coral was excavated from the reef in order to secure pilings and their bases into the substrate. No maintenance involving construction has been done since the initial development. Coral was also removed to provide a swimming area and a channel was dredged for boats, providing sand to enhance the beach. No coral was imported for aesthetic enhancement.

*Site Two*

Site two, Moorea Beachcomber Parkroyal, is located on the northern side of Moorea, west of Opunohu Bay and just southeast of Motu Tiahura (Figure 1). It was built in 1976 and contains four 3.32 x 5.10 m overwater bungalows and 46 partial overwater bungalows (Bion 1998). The structures were also constructed on the crest of the fringing reef, approximately 13 m offshore, and are accessible by boardwalk from a nearby artificial motu. The building materials and construction type were similar to those at Hotel Bali Hai. Artificial channels, beaches, and motus were designed to enhance the previous marsh environment of the site landward of the fringing reef. No alterations to the fringing reef environment were made besides the original construction.

*Site Three*

Site three, Hotel Sofitel Ia Ora, is located on the eastern side of the island, just south of Lake Temae, on the southern end of the public beach (Figure 1). Built in 1996, it is the youngest of the three sites and contains twenty 3.20 x 4.60 m overwater bungalows (Martial 1998). The structures were constructed on the sandy bottom patch reef, approximately 30 m offshore and are accessible by boardwalk from the beach. Building materials and construction type were similar to those at Hotel Bali Hai and the Beachcomber Parkroyal. Corals were imported from the nearby barrier reef by transporting them underwater to sites directly under overwater bungalow windows and popular sitting areas on the boardwalk. No beach enhancement occurred at this site.

*Sampling Method Under Bungalows*

Initially meetings were scheduled in September 1998 with the general managers from each hotel to gain permission to snorkel under and around their bungalows and to question them

about the history of design, construction, and maintenance procedures. Field work was conducted during October and November 1998. Preliminary studies found water temperature and velocity to be similar among sites. A preliminary survey of biota under bungalows found species to be very similar in composition among sites (Appendix 1).

Each bungalow and each control were treated as separate units of measurement. Four bungalows and four controls were randomly selected and measured at each of the three sites. For each bungalow the following parameters were measured by snorkeling in water 25 cm to several meters deep: the area under the four main corner pilings, an estimate of percent live coral cover, identification of live coral species and percent cover of each, an estimate of percent dead coral cover, an estimate of percent algae cover, identification of algae type and percent cover of each, and an estimate of percent substrate and substrate type (Appendix 2). The same parameters were measured at nearby control sites, which were in the same environment, based on substrate and habitat type, and at least 20 m from the nearest bungalow to insure that shading would not be a factor. Percent coral, algae, and substrate coverage were estimated by dividing the entire area into four quadrats, estimating percent coverage in each, and adding the four numbers and dividing by four to get a percent coverage for the entire area. All corals were identified to the species level using Vernon (1986).

*Sampling Method for Pilings*

Four corner pilings were sampled under two randomly selected bungalows at each of the three sites (Appendix 3). In order to accommodate varying water depths at each site, a 75 cm sampling depth was chosen from the high tide water level down the piling. All organisms present on this 75 cm extent of piling were identified, counted, and recorded. Percent cover was used to quantify algae and number of individuals was used when appropriate. Coral growths were measured by recording length, width, and height to get a relative volume for each. Measurements were rounded to the nearest 0.5 cm due to wave action. Live coral was identified to the species level using Vernon (1986).

## Results

*Live Coral Cover*

Bungalows and controls at each site were found to differ significantly from one another with respect to mean percent live coral cover (Site one, P=0.003, Site two, P=0.002, Site three, P=0.001) (Figure 2). Bungalows had a mean of 3.8% live coral cover, while controls had a mean of 81.4%. Further comparison showed live coral cover under bungalows differed significantly only between Hotel Bali Hai and the Beachcomber Parkroyal (P=0.045). Hotel Bali Hai, the oldest of the three sites, had the highest mean percent live coral cover under bungalows (6%). The Sofitel, the youngest site, had the next highest mean percent live coral cover under bungalows (4.4%). The Beachcomber Parkroyal, intermediate in age, had the smallest mean percent live coral cover under bungalows (0.73%) and the highest percent live coral cover at a control (92%).

*Dead Coral Cover*

Mean percent dead coral cover was found to differ significantly between bungalows and controls at Hotel Bali Hai (P= 0.012) and the Beachcomber Parkroyal (P=0.005), but not at the Sofitel Ia Ora (P=0.860) (Figure 3). Bungalows had a mean of 59.3% dead coral cover, while controls had a mean of 8.4%. Further comparison showed dead coral cover under bungalows differed significantly between Hotel Bali Hai and the Sofitel (P=0.007) and between the Beachcomber Parkroyal and the Sofitel (P=0.012). Mean dead coral cover under bungalows, however, did not differ significantly between Hotel Bali Hai and the Beachcomber Parkroyal (P=0.239). The Beachcomber had the highest mean percent dead coral cover under bungalows at 93%. Hotel Bali Hai had the next highest mean percent dead coral cover under bungalows (77.4%), followed by the Sofitel with the lowest mean (6.5%). Hotel Bali Hai had the highest mean percent dead coral cover at a control (14.8%).

*Algae Cover*

Mean percent algae cover was found to differ significantly between bungalows and controls at Hotel Bali Hai (P=0.003) and the Beachcomber Parkroyal (P=0.005), but not at the Sofitel Ia Ora (P=0.132) (Figure 4). Bungalows had a mean of 59% algae cover, while controls had a mean of

7.6%. Further comparison showed algae cover under bungalows differed significantly between Hotel Bali Hai and the Sofitel (P=0.0001) and between the Beachcomber Parkroyal and the Sofitel (P=0.001), but not between Hotel Bali Hai and the Beachcomber (P=0.832). Algae was typically found covering dead coral at the Hotel Bali Hai and at the Beachcomber, but no algae was present under bungalows at the Sofitel. Mean percent algae cover under bungalows for the three sites followed an age progression from oldest to youngest. Hotel Bali Hai had the highest mean percent algae cover under bungalows at 94%. The Beachcomber had the next highest mean percent algae cover under bungalows (93%), followed by the Sofitel with the lowest mean (0%). Hotel Bali Hai had the highest mean percent algae cover at a control (14.8%).

*Coral Diversity*

The mean number of coral species present at each of the three location's control sites was higher than the mean under the bungalows (Figure 5). The mean number of coral species present at the control sites (7.5) at Hotel Bali Hai were 2.1 times as diverse as the bungalows (3.5). The mean number of coral species present at the control sites (4.5) at the Sofitel were 3.6 times as diverse as the bungalows (1.25). The mean number of coral species present at the control sites (5.5) at the Beachcomber were 1.1 times as diverse as the bungalows (5.0). The oldest site, Hotel Bali Hai, had the highest mean number of coral species present at control sites (7.5), while the youngest site, the Sofitel, had the lowest mean (1.25). Bungalows did not follow the same pattern.

*Pilings*

Gastropods, fish, echinoderms, other marine organisms, and algae were found on pilings sampled (Appendix 3). Species other than algae were found to be very similar in composition among sites. Only algae types were found to be significantly different among sites of varying age. Fleshy algae cover on pilings was found to differ significantly between Hotel Bali Hai and the Beachcomber (P=0.0002) and the Sofitel and Beachcomber (P=0.037), but not between Hotel Bali Hai and the Sofitel (P=0.316). The highest mean percent fleshy algae cover was found at the Beachcomber (90.5%) and the lowest was found at Hotel Bali Hai (13.1%). Encrusting calcareous algae cover on pilings was found to differ significantly among the three sites. The highest mean encrusting calcareous algae cover was found at Hotel Bali Hai (75.1%), followed by the Beachcomber (4%), and the Sofitel (0%). Algae type at the Sofitel was more fleshy green algae, whereas Hotel Bali Hai was characterized by encrusting calcareous red algae. The Beachcomber had a combination of both fleshy and calcareous algae. Coral growths, measured by relative volume, got progressively larger with age. The only live coral species present on pilings was *Pocillopora damicornis*.

## Discussion

The low percent live coral and high percent dead coral and algae cover present under bungalows indicate a major difference in overall coral health between the bungalows and controls at each site (Figures 2, 3, 4). Several possible factors may be affecting overall coral health including, the bungalows, initial construction of the bungalows, mechanical damage to coral, coral collection, and pollution.

*Bungalows*

Low percent live coral under bungalows may be a result of a combination of factors contributed by the overwater bungalows. Shading out of corals may greatly impact their survival. Although no light measurements were taken during this study, clearly there is less light in the shadow of a bungalow. Reef-building corals - specifically the algae (zooxanthellae) within their coral polyps, which generate energy through photosynthesis - require sunlit waters to survive (Bryant et al. 1998). The basic aspects of light that will have an effect on the coral symbionts are light quantity (the amount of energy delivered) and light quality (spectral composition) (Tomascik et al. 1990). Changes in wave action and currents in the water due to the presence of bungalow pilings may also be a factor in coral health, although it is probably minor in comparison to the shading effects.

*Initial Construction*

The original construction of the overwater bungalows may have had a lasting impact on the health of corals. Some coral was directly removed, while more was most likely damaged or killed in the process of burying pilings in the substrate to secure the overwater bungalows. Coral reef organisms are usually considered stenotypic, exhibiting a relatively narrow range

of tolerances to environmental conditions, hence small changes in environmental quality can affect critical biological processes (Richmond 1993). Sediment released during construction may also create unfavorable conditions for coral growth. Corals are very sensitive to sediment, which can kill them directly by smothering, reduce their growth rates and ability to settle (Hawkins and Roberts 1994). As most reef-building corals obtain the majority of their nutritional requirements via translocation of metabolites from their photosynthetic partners, any reduction in the available quality and/or quantity of light will affect coral nutrition, growth, reproduction and depth distribution (Richmond 1993). Coastal infilling and beach enhancement also produce turbid waters, reducing the light available for photosynthesis. Channel dredging may have removed even more coral from near or under bungalows that border nautical channels.

*Mechanical Damage*

Fin and bootie damage to coral by swimmers and inexperienced snorkelers was observed in the field. Broken coral existed under bungalows and at control sites. Tourists were observed both stepping on and kicking coral heads. Direct damage is caused by tourists kicking, trampling or holding onto corals which, once damaged, may be more susceptible to disease and algal competitors (Hawkins and Roberts 1994). Boat anchors can also damage the reef by breaking off large pieces of coral. Evidence of this was observed near control sites.

*Coral Collection*

Coral collection by tourists was also observed in the field, suggesting another possible source of coral mortality. The demand for coral and shell curios increases as tourist numbers grow.

*Pollution*

Trash deposited by tourists was probably not serious, since minimal debris was observed under bungalows and at control sites. Sewage effluent is piped from the bungalows back to the hotel then to a central fallout beyond both the bungalows and controls. Boat pollution is probably diluted in such large volumes of water that it is not an important factor. Pollution may exist from land based-sources.

Since the impacts under the bungalows and at the control sites are potentially the same in regard to mechanical damage, collection, and pollution, then there is not a substantial impact on coral health by these factors. With no baseline data available for the three study sites prior to construction, it is difficult to assess the many potential factors and develop cause and effect relationships.

Conclusions

Low percent live coral and high percent dead coral and algae cover present under bungalows suggest two possible causes; either it is an effect of the bungalow itself, or it is a response to the initial construction of the overwater bungalow. Low light over time coupled with the lasting effects of the initial construction create an environment that favors the growth of encrusting calcareous red algae to coral. The ability of corals to build reefs using the energy of the sun, is the key to the existence of all modern coral reefs, and perhaps all reefs in all geological time (Vernon 1995).

Globally, the effects of overwater bungalows on coral reefs are currently minuscule, but if this development trend continues to grow it could lead to a widespread decline in coral health and diversity in the tropics. With careful planning and development, tourism should bring prosperity to the region, not threaten reefs. The advantages of increased accessibility and enhancement of the marine-based tourist experience may generally outweigh their adverse effects, provided careful design, siting and operational criteria are applied (Kelleher and Dutton 1985).

Currently much of the economy of French Polynesia is largely dependent upon reef resources, such as tourism, fisheries and pearl culture, therefore the maintenance of "healthy reefs" is vital, and yet little enforcement of even existing legislation appears to be occurring; this despite the reefs of French Polynesia being better known than many other reefs in the South Pacific (Hutchings et al. 1994). As tourism is a major part of the economy of French Polynesia there may be occasions when not all the long-term considerations are taken fully into account, basically when economic benefits outweigh environmental considerations (Hutchings et al. 1994).

Moorea and other tropical destinations can learn from successful management strategies that strive to balance public use with ecosystem abuse and are based on both biological and recreational use data. Ecotourism, as a strategy and incentive for preserving natural resources, pinpoints the

continual monetary value of a live organism as opposed to the one time economic value of a dead one (Churcher 1994). Hotel managers and environmental agencies need to evaluate closely the impacts of recreational activities on the coral reef environment, since it is this very resource that needs to be protected in order to draw the tourist dollars that support these regions.

Acknowledgments

I would like to thank Tegan Churcher, Amy Lesen, and Virginia Matzek for their invaluable guidance and patience. Special thanks to Jere Lipps, Vince Resh, David Stoddart, David Lindberg, and the entire IB 158 class for making my experience unforgettable.

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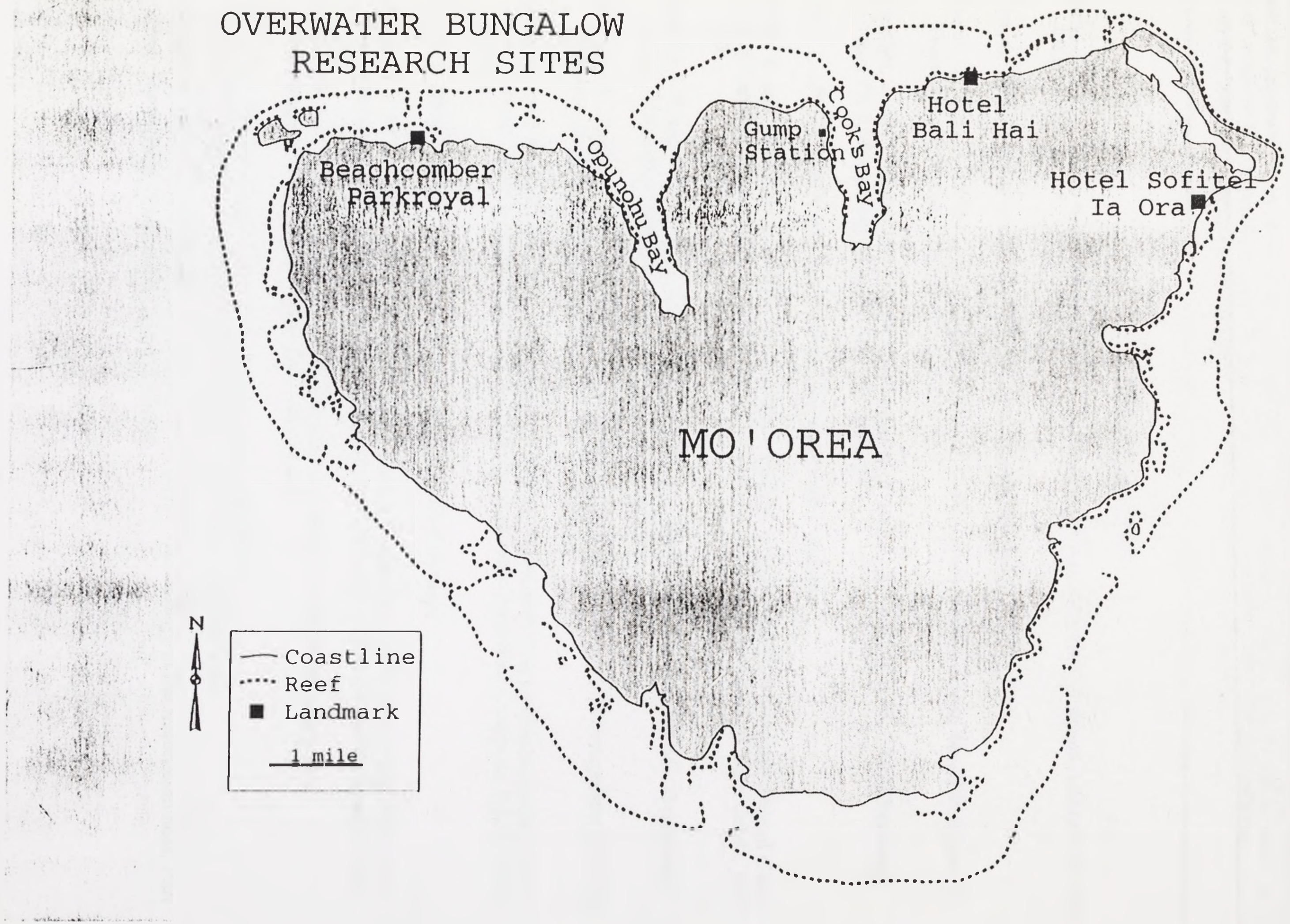


Figure 1. Map of Moorea showing overwater bungalow research sites

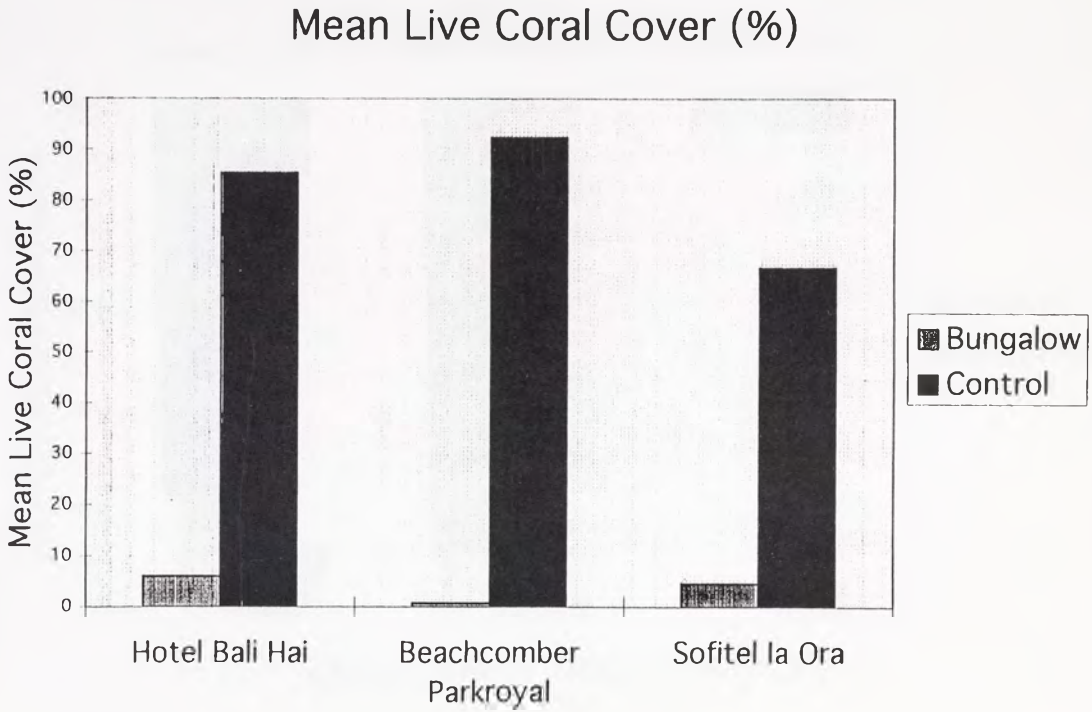


Figure 2. Mean percent live coral cover for each of the three study sites. Notice the difference between bungalows and controls. Bungalows had a mean of 3.8% live coral, while controls had a mean of 81.4%.

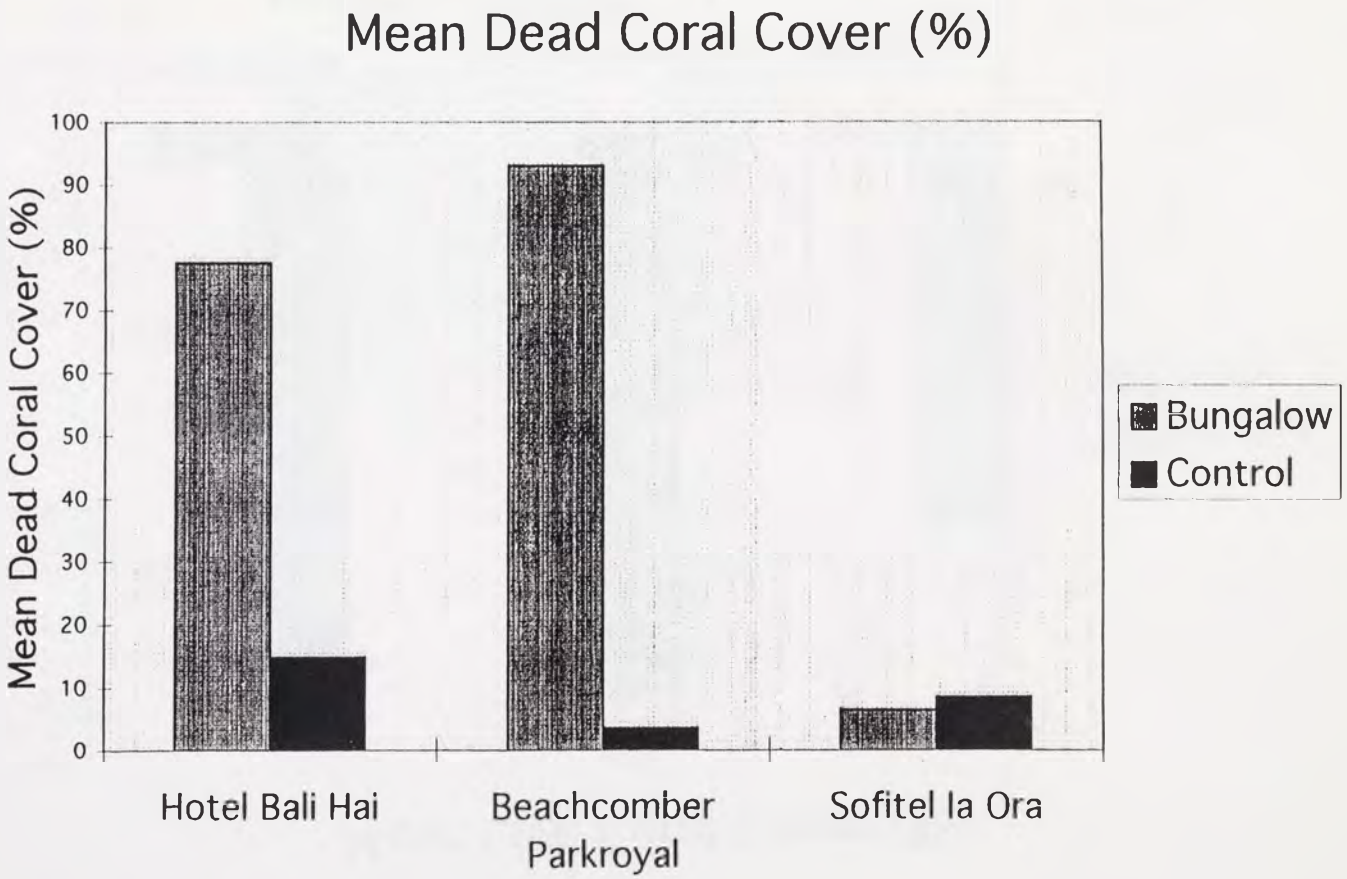


Figure 3. Mean percent dead coral cover for each of the three study sites. Notice the difference between bungalows and controls. Bungalows had a mean of 59.3% dead coral, while controls had a mean of 8.4%.

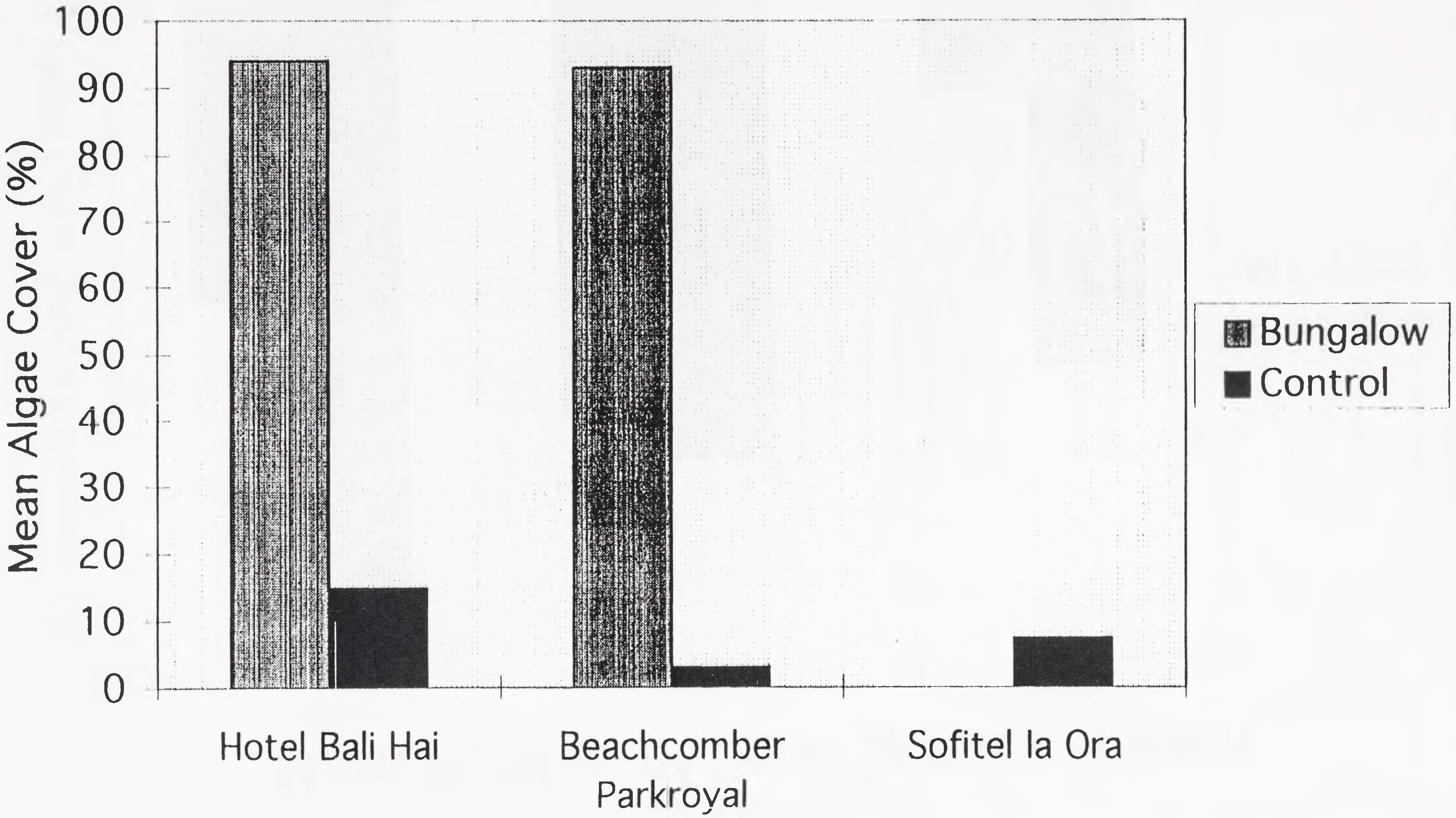


Figure 4. Mean percent algae cover for each of the three study sites. Notice the difference between bungalows and controls. Bungalows had a mean of 59% algae cover, while controls had a mean of 7.6%.

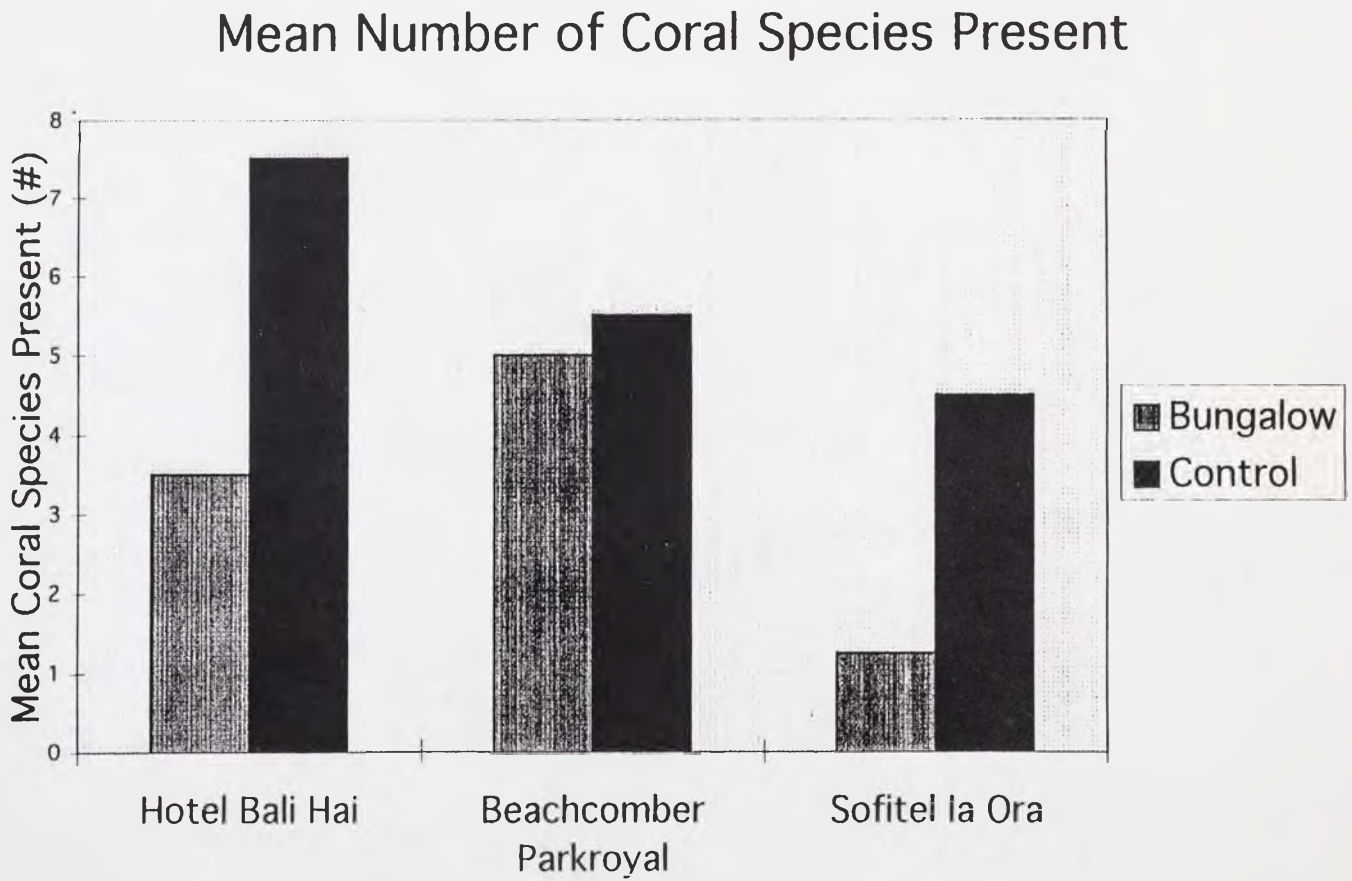


Figure 5. Mean number of coral species present for each of the three sites. The mean number of coral species at the control sites at Hotel Bali Hai were 2.1 times as diverse as the bungalows, 3.6 times at the Sofitel, and 1.1 times at the Beachcomber.

Appendix 1

| Site Name | Bungalow # | Area (m) | Species name | Number of Individuals |
|---|---|---|---|---|
| Hotel Bali Hai | B46 | 4.47 x 6.25 | *Echinothrix calamaris* | 3 |
| | | | *Valonia ventricosa* | 47 |
| | | | *Palythoa sp.* | 12 |
| | | | *Stephanoscyphus sp.* | 1 |
| | | | Yellow encrusting #1 | 3 |
| | | | Purple encrusting #1 | 4 |
| | | | Stonefish #1 | 1 |
| | | | Hermit crab #1 | 1 |
| | | | *Bohadschia argus* | 1 |
| | | | *Echinometra mathaei* | 4 |
| Sofitel Ia Ora | B102 | 3.20 x 4.60 | *Diadema savignyi* | 54 |
| | | | *Mespilia globulus* | 2 |
| | | | Fish #1 | 1 |
| Beachcomber Parkroyal | B510 | 3.32 x 5.10 | *Trochus niloticus* | 2 |
| | | | *Holothuria atra* | 5 |
| | | | *Padina gymnospora* | 3 |
| | | | *Echinometra mathaei* | 6 |
| | | | *Valonia ventricosa* | 14 |
| | | | Nudibranch #1 | 2 |
| | | | *Diadema savignyi* | 2 |
| | | | Blue encrusting #1 | 4 |
| | | | Yellow encrusting #1 | 3 |
| | | | *Stephanoscyphus sp.* | 10 |
| | | | Green clam#1 | 3 |
| | | | *Dictyota sp.* | 5 |

# Appendix 2

| Site Name | Bungalow # | Area (m) | % Live Coral | Coral Species | % Cover | % Dead Coral | % Algae Cover | Algae Type | % Cover | % Substrate |
|---|---|---|---|---|---|---|---|---|---|---|
| Hotel Bali Hai | B46 | 4.47 x 6.25 | 15% | *Pavona cactus* | 90% | 85% | 85% | *Halimeda micronesica* | 100% | 0% |
| | | | | *Fungia sp.* | 10% | | | | | |
| | B45 | 4.47 x 6.25 | 5% | *Porites rus* | 95% | 75% | 95% | Encrusting calcareous red algae (mauve) | 60% | 20% coral rubble |
| | | | | *Fungia sp.* | 1% | | | Encrusting calcareous red algae (burgandy) | 40% | |
| | | | | *Favia stelligera* | 2% | | | | | |
| | | | | *Porites annae* | 2% | | | | | |
| | B43 | 4.47 x 6.25 | 5% | *Porites rus* | 85% | 65% | 95% | Encrusting calcareous red algae (mauve) | 55% | 30% coral rubble |
| | | | | *Favia stelligera* | 10% | | | Encrusting calcareous red algae (burgandy) | 45% | |
| | | | | *Fungia sp.* | 1% | | | | | |
| | | | | *Montipora foveolata* | 4% | | | | | |
| | B41 | 4.47 x 6.25 | 2% | *Fungia sp.* | 60% | 83% | 98% | Encrusting calcareous red algae (mauve) | 35% | 15% coral rubble |
| | | | | *Porites rus* | 30% | | | Encrusting calcareous red algae (burgandy) | 65% | |
| | | | | *Montipora efflorescens* | 2% | | | | | |
| | | | | *Porites annae* | 8% | | | | | |
| | C1 | 4.47 x 6.25 | 85% | *Porites rus* | 80% | 15% | 15% | Fleshy red algae (thick) | 90% | 0% |
| | | | | *Fungia sp.* | 2% | | | *Turbinaria sp.* | 10% | |
| | | | | *Pocillopora damicornis* | 11% | | | | | |
| | | | | *Pocillopora eydouxi* | 1% | | | | | |
| | | | | *Acropora cerealis* | 5% | | | | | |
| | | | | *Pavona cactus* | 1% | | | | | |
| | C2 | 4.47 x 6.25 | 95% | *Porites rus* | 45% | 5% | 5% | Fleshy red algae (thick) | 98% | 0% |
| | | | | *Pocillopora damicornis* | 5% | | | *Turbinaria sp.* | 2% | |
| | | | | *Porites labata* | 3% | | | | | |
| | | | | *Montipora efflorescens* | 30% | | | | | |
| | | | | *Pavona cactus* | 12% | | | | | |
| | | | | *Pocillopora eydouxi* | 2% | | | | | |
| | | | | *Fungia sp.* | 2% | | | | | |
| | | | | *Porites solida* | 1% | | | | | |
| | C3 | 4.47 x 6.25 | 65% | *Pavona cactus* | 10% | 35% | 35% | *Turbinaria sp.* | 100% | 0% |
| | | | | *Porites rus* | 25% | | | | | |
| | | | | *Favites abdita* | 5% | | | | | |
| | | | | *Pocillopora damicornis* | 35% | | | | | |
| | | | | *Pocillopora eydouxi* | 3% | | | | | |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | *Fungia sp.* | 8% | | | | | |
| | | | | *Porites labata* | 5% | | | | | |
| | | | | *Porites solida* | 1% | | | | | |
| | | | | *Montipora efflorescens* | 3% | | | | | |
| | | | | *Acropora cerealis* | 5% | | | | | |
| | C4 | 4.47 x 6.25 | 90% | *Porites rus* | 80% | 10% | 10% *Turbinaria sp.* | 100% | 0% | |
| | | | | *Fungia sp.* | 2% | | | | | |
| | | | | *Pocillopora damicornis* | 11% | | | | | |
| | | | | *Pocillopora eydouxi* | 1% | | | | | |
| | | | | *Acropora cerealis* | 5% | | | | | |
| | | | | *Pavona cactus* | 1% | | | | | |
| Sofitel la Ora | B102 | 3.20 x 4.60 | 10% | *Porites rus* | 10% | 20% | 0% N/A | 0% | 70% sand | |
| | | | | *Porites labata* | 90% | | | | | |
| | B111 | 3.20 x 4.60 | 5% | *Porites labata* | 85% | 20% | 0% N/A | 0% | 75% sand | |
| | | | | *Acropora grandis* | 15% | | | | | |
| | B106 | 3.20 x 4.60 | 10% | *Porites labata* | 100% | 1% | 0% N/A | 0% | 89% sand | |
| | B109 | 3.20 x 4.60 | 0% | *N/A* | 0% | 0% | 0% N/A | 0% | 100% coral rubble | |
| | C1 | 3.20 x 4.60 | 70% | *Pocillopora damicornis* | 5% | 5% | 5% Fleshy red algae (thick) | 100% | 25% sand | |
| | | | | *Acropora cerealis* | 5% | | | | | |
| | | | | *Pavona cactus* | 15% | | | | | |
| | | | | *Montipora efflorescens* | 10% | | | | | |
| | | | | *Porites labata* | 50% | | | | | |
| | | | | *Acropora grandis* | 10% | | | | | |
| | | | | *Porites solida* | 1% | | | | | |
| | | | | *Fungia sp.* | 4% | | | | | |
| | C2 | 3.20 x 4.60 | 80% | *Acropora grandis* | 90% | 5% | 5% Fleshy red algae (thick) | 100% | 15% sand | |
| | | | | *Pocillopora damicornis* | 10% | | | | | |
| | C3 | 3.20 x 4.60 | 65% | *Porites labata* | 70% | 1% | 0% N/A | 0% | 34% sand | |
| | | | | *Pavona cactus* | 20% | | | | | |
| | | | | *Acropora cerealis* | 3% | | | | | |
| | | | | *Pocillopora damicornis* | 7% | | | | | |
| | C4 | 3.20 x 4.60 | 50% | *Pocillopora damicornis* | 80% | 35% | 35% Fleshy red algae (thick) | 100% | 15% sand | |
| | | | | *Fungia sp.* | 5% | | | | | |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | *Porites solida* | 1% | | | | | | | |
| | | | *Pavona cactus* | 14% | | | | | | | |
| Beachcomber Parkroyal B510 | 3.32 x 5.10 | 2% | *Pocillopora damicornis* | 1% | 78% | 78% | *Halimeda micronesica* | 1% | 20% sand | | |
| | | | *Montipora foveolata* | 1% | | | Fleshy red algae (thin) | 85% | | | |
| | | | *Porites labata* | 15% | | | *Dictyota sp.* | 4% | | | |
| | | | *Montipora monasteriata* | 70% | | | Encrusting calcareous red algae (mauve) | 10% | | | |
| | | | *Montipora spumosa* | 1% | | | | | | | |
| | | | *Favites abdita* | 2% | | | | | | | |
| | | | *Porites irregularia* | 10% | | | | | | | |
| | B511 | 3.32 x 5.10 | 1% *Porites rus* | 20% | 94% | 94% | *Halimeda micronesica* | 5% | 5% sand | | |
| | | | *Pavona cactus* | 15% | | | *Dictyota sp.* | 10% | | | |
| | | | *Favites abdita* | 15% | | | Encrusting calcareous red algae (mauve) | 30% | | | |
| | | | *Montipora monasteriata* | 20% | | | Fleshy red algae (thin) | 55% | | | |
| | | | *Montipora spumosa* | 15% | | | | | | | |
| | | | *Montipora foveolata* | 15% | | | | | | | |
| | B512 | 3.32 x 5.10 | 0% *N/A* | | 100% | 100% | Dark brown encrusting (soft) | 30% | | 0% | |
| | | | | | | | Encrusting calcareous red algae (mauve) | 15% | | | |
| | | | | | | | Fleshy red algae (thin) | 55% | | | |
| | B514 | 3.32 x 5.10 | 1% *Porites rus* | 15% | 89% | 89% | *Halimeda micronesica* | 2% | 10% sand | | |
| | | | *Porites solida* | 1% | | | *Turbinaria sp.* | 5% | | | |
| | | | *Pavona cactus* | 10% | | | *Dictyota sp.* | 3% | | | |
| | | | *Pocillopora damicornis* | 1% | | | Fleshy red algae (thin) | 90% | | | |
| | | | *Porites labata* | 70% | | | | | | | |
| | | | *Montipora spumosa* | 2% | | | | | | | |
| | | | *Porites irregularia* | 1% | | | | | | | |
| | C1 | 3.32 x 5.10 | 85% *Acropora grandis* | 80% | 10% | 10% | Fleshy red algae (thick) | 100% | 5% sand | | |
| | | | *Pavona cactus* | 10% | | | | | | | |
| | | | *Favites abdita* | 1% | | | | | | | |
| | | | *Porites rus* | 2% | | | | | | | |
| | | | *Pocillopora damicornis* | 1% | | | | | | | |
| | | | *Montipora efflorescens* | 1% | | | | | | | |
| | | | *Porites labata* | 1% | | | | | | | |
| | | | *Pocillopora eydouxi* | 1% | | | | | | | |

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|---|---|---|---|---|---|---|---|---|---|---|
| | | | *Acropora cerealis* | 1% | | | | | | |
| | | | *Favia stelligera* | 1% | | | | | | |
| | | | *Fungia sp.* | 1% | | | | | | |
| C2 | 3.32 x 5.10 | 100% | *Porites rus* | 100% | 0% | 0% | N/A | 0% | | 0% |
| C3 | 3.32 x 5.10 | 95% | *Porites rus* | 92% | 2% | 2% | Fleshy red algae (thick) | 95% | 3% sand | |
| | | | *Fungia sp.* | 2% | | | *Halimeda micronesica* | 5% | | |
| | | | *Pavona cactus* | 4% | | | | | | |
| | | | *Porites solida* | 1% | | | | | | |
| | | | *Porites labata* | 1% | | | | | | |
| C4 | 3.32 x 5.10 | 77% | *Pavona cactus* | 18% | 8% | 5% | Fleshy red algae (thick) | 65% | 15% sand | |
| | | | *Porites rus* | 75% | | | *Dictyota sp.* | 35% | | |
| | | | *Acropora grandis* | 4% | | | | | | |
| | | | *Acropora cerealis* | 1% | | | | | | |
| | | | *Porites labata* | 2% | | | | | | |

# Appendix 3

| Site Name | Bungalow # | Piling Circ. (cm) | Piling Location | Piling Species | # Cover / # | Coral Growths (l x w x h) | Live/Dead, species |
|---|---|---|---|---|---|---|---|
| Hotel Bali Hai | P46 | 69.4 | Front Left | *Littorina coccinea* | 23 ind. | 7.5 x 6 x 5 | Dead |
| | | | | Goby #1 | 1 ind. | 19.5 x 19 x 11 | Dead |
| | | | | *Echinometra mathaei* | 1 ind. | 7 small knobs (4 x 3.5 x 6) | Dead |
| | | | | Encrusting calcareous red algae (burgandy) | 45% | | |
| | | | | Encrusting calcareous red algae (mauve) | 30% | | |
| | | | | Fleshy green algae (thin) | 8% | | |
| | | | | Filamentous green algae | 5% | | |
| | | | | Encrusting (limey yellow) | 10% | | |
| | | | | *Zellera tawallina* | 1 ind. | | |
| | | | Front Right | *Littorina coccinea* | 32 ind. | None | N/A |
| | | | | Limpet #1 | 1 ind. | | |
| | | | | Encrusting calcareous red algae (burgandy) | 90% | | |
| | | | | Encrusting (limey yellow) | 1% | | |
| | | | | Encrusting calcareous red algae (mauve) | 1% | | |
| | | | | Filamentous green algae | 5% | | |
| | | | | Fleshy green algae (thin) | 2% | | |
| | | | Rear Right | *Littorina coccinea* | 7 ind. | None | N/A |
| | | | | Filamentous green algae | 80% | | |
| | | | | Encrusting calcareous red algae (burgandy) | 5% | | |
| | | | | Encrusting calcareous red algae (mauve) | 5% | | |
| | | | | Encrusting (limey yellow) | 10% | | |
| | | | Rear Left | *Littorina coccinea* | 3 ind. | 5.5 x 13 x 2 | Live, *Pocillopora damicornis* |
| | | | | Crab #1 | 1 ind. | | |
| | | | | Limpet #2 | 1 ind. | | |
| | | | | Filamentous green algae | 30% | | |
| | | | | Encrusting (limey yellow) | 50% | | |
| | | | | Encrusting calcareous red algae (mauve) | 10% | | |
| | | | | Encrusting calcareous red algae (burgandy) | 9% | | |
| Hotel Bali Hai | P44 | 69.4 | Front Left | Encrusting calcareous red algae (burgandy) | 60% | 15 x 20.5 x 11 | Dead |
| | | | | *Littorina coccinea* | 11 ind. | 12 smaller knobs (4 x 3.5 x 6) | Dead |
| | | | | Limpet #2 | 1 ind. | 6.5 x 8 x 4 | Dead |
| | | | | Filamentous green algae | 20% | | |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | | | | Encrusting (limey yellow) | | 4% | |
| | | | | Fleshy green algae (thin) | | 15% | |
| | | | | Ascidian #1 | 1 ind. | | |
| | | | | Ascidian #2 | 1 ind. | | |
| | | | Front Right | Encrusting calcareous red algae (burgandy) | | 75% 3 small knobs (4 x 3.5 x 6) | Dead |
| | | | | *Littorina coccinea* | 4 ind. | | |
| | | | | Limpet #2 | 1 ind. | | |
| | | | | *Siphonium maximus* | 5 ind. | | |
| | | | | Encrusting calcareous red algae (mauve) | | 24% | |
| | | | Rear Left | Encrusting calcareous red algae (burgandy) | | 99% 2 small knobs (4 x 3.5 x 6) | Dead |
| | | | | *Littorina coccinea* | 6 ind. | | |
| | | | | Ascidian #1 | 1 ind. | | |
| | | | Rear Right | Encrusting calcareous red algae (burgandy) | | 90% None | N/A |
| | | | | Encrusting calcareous red algae (mauve) | | 9% | |
| | | | | Limpet #2 | 1 ind. | | |
| | | | | *Siphonium maximus* | 3 ind. | | |
| | | | | *Littorina coccinea* | 4 ind. | | |
| Sofitel la Ora | P102 | 92.4 | Front Left | *Mespilia globulus* | 2 ind. | 10 (5 x 7 x 4) | 1 live *Pocillopora damicornis* , 9 dead |
| | | | | Fleshy green algae (thin) | | 59% | |
| | | | | *Siphonium maximus* | 27 ind. | | |
| | | | | Dark brown encrusting (soft) | | 30% | |
| | | | | Filamentous green algae | | 10% | |
| | | | Front Right | *Siphonium maximus* | 5 ind. | 5 (6 x 7 x 4.5) | 5 live *Pocillopora damicornis* |
| | | | Rear Left | *Siphonium maximus* | 9 ind. | 3 small knobs (4 x 3.5 x 6) | Dead |
| | | | | Dark brown encrusting (soft) | | 1% | |
| | | | | *Littorina coccinea* | 33 ind. | | |
| | | | Rear Right | Fleshy green algae (thick) | | 80% 7 (5 x 7 x 4) | 7 live *Pocillopora damicornis* |
| | | | | Fleshy red algae (burgandy) | | 10% | |
| | | | | Fleshy green algae (thin) | | 3% | |
| | | | | Encrusting (limey yellow) | | 5% | |
| | | | | *Padina gymnospora* | | 1% | |
| Sofitel la Ora | P111 | 92.4 | Front Right | Fleshy green algae (thick) | | 60% 3 (6.5 x 8 x 3) | 2 live *Pocillopora damicornis* , 1 dead |
| | | | | *Littorina coccinea* | 15 ind. | | |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | | | Filamentous green algae | | 10% | | |
| | | | Dark brown encrusting (soft) | | 29% | | |
| | | Rear Left | Fleshy green algae (thick) | | 65% | 2 small knobs (4 x 3.5 x 6) | 1 live *Pocillopora damicornis* , 1 dead |
| | | | *Siphonium maximus* | 2 ind. | | | |
| | | | Fleshy red algae (burgandy) | | 15% | | |
| | | | Dark brown encrusting (soft) | | 19% | | |
| | | Rear Right | *Siphonium maximus* | 6 ind. | | None | N/A |
| | | | *Littorina coccinea* | 21 ind. | | | |
| | | | Fleshy green algae (thick) | | 10% | | |
| | | Front Left | Filamentous green algae | | 10% | 6 x 7 x 3 | live *Pocillopora damicornis* |
| | | | *Siphonium maximus* | 7 ind. | | | |
| | | | Dark brown encrusting (soft) | | 5% | | |
| Beachcomber Parkroyal P510 | 105.7 | Front Right | *Siphonium maximus* | 1 ind. | | None | N/A |
| | | | Filamentous green algae | | 99% | | |
| | | Front Left | Filamentous green algae | | 100% | None | N/A |
| | | Rear Right | Filamentous green algae | | 100% | None | N/A |
| | | Rear Left | Filamentous green algae | | 100% | None | N/A |
| Beachcomber Parkroyal P511 | 105.7 | Front Right | *Echinometra mathaei* | 1 ind. | | 6 x 7.5 x 3 | Dead |
| | | | *Siphonium maximus* | 18 ind. | | 5 x 5 x 4.5 | Dead |
| | | | Encrusting calcareous red algae (mauve) | | 30% | 7 small knobs | Dead |
| | | | Encrusting (limey yellow) | | 10% | 7.5 x 9 x 5 | Dead |
| | | | Filamentous green algae | | 19% | | |
| | | | Fleshy green algae (thin) | | 40% | | |
| | | Rear Right | *Holothuria atra* | 1 ind. | | 8 x 11.5 x 7.5 | Dead |
| | | | *Trochus niloticus* | 1 ind. | | 12 x 14 x 9.5 | Dead |
| | | | *Siphonium maximus* | 4 ind. | | 19 x 10 x 13 | Dead |
| | | | *Echinometra mathaei* | 1 ind. | | 3 small knobs | Dead |
| | | | Fleshy green algae (thin) | | 50% | 7 x 4.5 x 5.5 | Dead |
| | | | Filamentous green algae | | 5% | | |
| | | | Dark brown encrusting (soft) | | 25% | | |
| | | | Encrusting calcareous red algae (mauve) | | 15% | | |
| | | | Encrusting (limey yellow) | | 5% | | |
| | | Rear Left | *Siphonium maximus* | 5 ind. | | None | N/A |

| | | | | | |
|---|---|---|---|---|---|
| | Filamentous green algae | | 20% | | |
| | Encrusting calcareous red algae (mauve) | | 10% | | |
| | Dark brown encrusting (soft) | | 7% | | |
| | Encrusting (limey yellow) | | 2% | | |
| | Fleshy green algae (thin) | | 60% | | |
| Front Left | *Siphonium maximus* | 9 ind. | | 7.5 x 7.5 x 5 | Dead |
| | *Echinometra mathaei* | 1 ind. | | 13 x 21 x 9.5 | Dead |
| | Encrusting (limey yellow) | | 5% | 9 x 19 x 10 | Dead |
| | Encrusting calcareous red algae (mauve) | | 9% | | |
| | Dark brown encrusting (soft) | | 10% | | |
| | Fleshy green algae (thin) | | 75% | | |
| | Sea spider #1 | 1 ind. | | | |

# Early Life History Aspects Of Amphidromous Neritid Snails in Moorea, French Polynesia

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ABSTRACT. The freshwater members of the Neritidae (Gastropoda, Neritopsina) on Moorea, French Polynesia exhibit an amphidromous lifestyle, meaning that their larval development takes place in the marine environment. I studied the freshwater and saltwater tolerance of newly hatched neritid veligers in order to determine how they were able to maintain freshwater physiology during their transit from stream to ocean. To this end I considered three hypotheses: (1) Veligers hatch with a freshwater physiology and switch to a saltwater physiology after a set amount of time. (2) Veligers hatch with a freshwater physiology and switch to a saltwater physiology after being exposed to saltwater. (3) Veligers hatch with a high euryhaline tolerance. Veligers in saltwater lived for up to 15 days, while veligers in freshwater all died within 140 hours. Veligers kept in freshwater had slightly better survivorship for the first 96 hours then veligers transferred immediately into saltwater, then went into decline. I concluded that neritid veligers hatch with a high euryhaline tolerance which is lost at around 84 hours, but there is some initial variation in individual tolerance to saltwater. A better understanding of larval freshwater tolerance as an evolutionary innovation may lead to increased knowledge about the distributional limits of different neritid species, as well as the evolution of freshwater tolerance. An additional aquarium study showed that neritid juveniles were positively rheotactic, reacting to current flow as little as 0.43 L/min. When responding to a current, the individuals tended to aggregate and move in lines, which may be a behavioral feature designed to aid in the hydrodynamics of migrating snails.

## Introduction

Almost all of the native, stream-dwelling fauna found on Pacific islands is descended from taxa which colonized freshwater from the ocean relatively recently, due to the formidable barrier to dispersal which the Pacific Ocean presents to continental freshwater fauna (Ford and Kinzie 1982). Consequently, a large proportion of the fauna of tropical Pacific island streams can be characterized as having an amphidromous lifestyle (Resh and DeSzalay 1995). The fish and macroinvertebrates of these freshwater streams recall their marine ancestors, having free-swimming larvae that undergo development in the ocean before migrating back into freshwater, where they live as obligate freshwater organisms.

Neritid snails (Gastropoda, Neritopsina) are one of the most prevalent groups of macroinvertebrates in these insular tropical streams, and have probably been the most studied (e.g. Haynes, 1988; Liu and Resh 1997; Boyer 1998). However, although much work has been done concerning the ecology and distribution of adult neritid snails, not much is known about the ecology of other phases in their life history, such as the veliger larva or the newly metamorphosed juvenile.

Holthuis (1995) lists only eight studies on twelve freshwater species in which the hatching stage of the larvae is even recorded. Nishiwaki and Koike (1985) found that veligers of the freshwater snail *Clithon retropictus* lived for more than 10 days in saltwater, 7-10 days in brackish water, but only two days in freshwater. Adegoke *et al.* (1969) found that larvae of the brackish water snail *Neritina glabrata*, when immersed "for considerable periods in distilled water", were incapable of active swimming when reintroduced to saltwater. Ford (1987) found numerous larvae of freshwater *Neritina granosa* in brackish water at stream mouths and described them as planktotrophic. Boyer (1998) found neritid veligers of three different species (not necessarily freshwater species) in plankton tows of Opunohu Bay. She found that they survived equally well in freshwater and saltwater for several weeks. She also found that larvae which were removed from egg capsules died within a day in saltwater but lived for more than 2 days in freshwater. Nothing

is known about how long neritid veligers spend in the plankton or what causes them to settle and metamorphose.

Very little is known about neritid juveniles immediately following metamorphosis. Holthuis (1995) points out that species whose larvae must undergo development in the ocean must also have the ability to perform upstream migration. Since this is impossible for a planktonic veliger, it must fall to the juvenile to get itself from the estuary up into the flowing freshwater stream. However, there is conflicting evidence regarding the migratory habits of Neritids. Nishiwaki *et al.* (1991) found that adults of *Clithon retropictus* showed no positive rheotaxis, but were just as likely to move downstream as upstream. Yelenik (1996) noted that adults of *Clithon spinosa* do not orient themselves to flow when kept in flow-through aquaria. However, Liu and Resh (1997) observed adults of *Clithon spinosa* travelling in a straight line along the sides of an aquarium at night. Schneider and Frost (1986) observed long lines, tens of meters long, of *Neritina latissima* migrating upstream. About 60% of the migrating snails were less than 4 mm long. Several of their observations suggested that the snails were orienting themselves into the current (positive rheotaxis). Resh *et al.* (1990) showed that *Neritina canalis* (on Moorea) increased significantly in size from downstream sites to upstream sites. Haynes (1988) found *Neritina pulligera* at a site 33 km from the ocean, implying an upstream migration of quite some distance.

From these sparse data and observations, one might infer the following life history for the freshwater neritid snails on Moorea. The snails seem to follow the insular freshwater pattern of amphidromy. Adults lay egg capsules on hard substrates, out of which hatch a few hundred veliger larvae that are swept by the stream water down into the ocean. During the time that they are in the stream, the veligers must have some physiological tolerance to freshwater, but it is unknown how this tolerance works. The veligers spend an unknown amount of time in the plankton before metamorphosing and migrating back into freshwater streams, possibly by orienting themselves into the stream's current.

The overall purpose of the current study was to supplement the sparse knowledge about freshwater neritid life histories with data from the species that occur on Moorea. The first objective of the study was to answer the question: What is the nature of the osmotic tolerance to freshwater exhibited by newly hatched neritid snails? In order to accomplish this I considered three hypotheses: (1) Veligers hatch from their egg capsules with a freshwater physiology and switch to a saltwater physiology after a set amount of time. (2) Veligers hatch from their egg capsules with a freshwater physiology and switch to a saltwater physiology after being exposed to saltwater. (3) Veligers hatch from their egg capsules with a high euryhaline tolerance. The second objective of the current study was to make observations on the migratory behavior of neritid juveniles. I hypothesized that juvenile neritid snails would show positive rheotaxis when exposed to a current.

## Methods

This study was conducted on the island of Moorea, French Polynesia, (17°30'S, 149°50'W) during October and November 1998 (austral spring). I collected neritid juveniles and rocks that had neritid egg capsules on them from a site 400m upstream from Opunohu Bay in a fourth-order tributary of the Opunohu watershed (site MPIV in Resh et al. 1990) (see Figure 1). This site is located at the first road bridge on the Opunohu-Belvedere road. I chose this site for its ease of access and its great abundance of neritid snails and their eggs. There were four species of neritid snails present at this site: *Neritina canalis* Lamark, *Neritina turrita* Gmelin, *Clithon spinosa* Budgin, and *Septaria porcellana* Linnaeus. Rocks as well as juveniles were collected from the riffles at this site.

### I. Salinity Tolerance Experiments

The neritid snails used in this study lay their egg capsules in patches of 2 to >500. Since I could not differentiate between the eggs of each of the different species, I used a single egg patch for this study. Although the species identification of this patch is unknown, all veligers in this study were of the same species. At least fifty percent of the eggs in the chosen patch had already hatched, which ensured that the veligers that I used were at hatching stage. During experimentation, the rock on which the egg patch had been laid was kept in a flow-through freshwater aquarium.

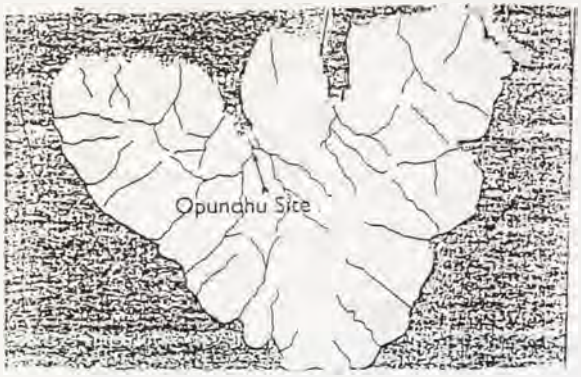


Figure 1. Map of the streams of Moorea, with the location of the collecting site.

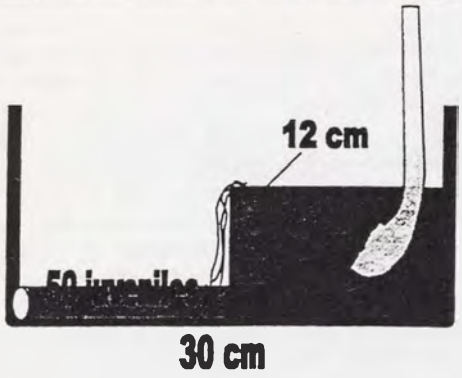


**Figure 2.** Experimental setup for migration experiments. The first compartment is on the right, with a hose feeding flow into it, the second compartment is on the left.

Veligers were not given anything to eat during the experiments (they were kept in filtered water). Starvation was probably not a factor which affected survivorship, due to the fact that I observed oil droplets within the veligers bodies which could provide energy for at least a few days.

*Freshwater vs. Saltwater Experiments*

I artificially opened the egg capsules with a scalpel under a binocular dissecting microscope and transferred the larvae into a small petri dish (5 cm diameter) of 15 ml freshwater for sorting. After a half-hour sorting period, I placed 20 veligers into a similar petri dish of 15 ml filtered seawater and 20 veligers into 15 ml filtered freshwater (water was filtered through No. 1 coffee filters). I then monitored survivorship at uniform intervals throughout the day until all veligers in one dish were dead. I determined veligers to be dead when I could not detect any movement of the velum. Every 24 hours I removed 5 ml of water from both dishes and replaced it with 5 ml of freshly oxygenated, filtered water.

*Freshwater to Saltwater Transfer Experiment*

I performed this experiment to find the optimum range of time for veligers to be in freshwater before being transferred into saltwater. In this experiment I started as above, but with five freshwater petri dishes and one saltwater petri dish of 20 veligers each. I transferred the veligers from one freshwater petri dish into saltwater after the following periods of time: 4 hours, 24 hours, 48 hours and 72 hours. I monitored survivorship every four hours, and changed the water every 24 hours. I accidentally ended this experiment at 96 hours by transferring saltwater into the freshwater dish.

*Saltwater to Freshwater Transfer Experiment*

This experiment was performed to determine whether the veligers change to an exclusively marine physiology upon contact with seawater. I hatched an egg capsule into filtered seawater, and started with three saltwater petri dishes. I transferred the veligers from one petri dish into freshwater after 6 hours, and 24 hours. I monitored survivorship every six hours, and changed the water every 24 hours. Additionally, following the two saltwater vs. freshwater experiments, I transferred half of the surviving saltwater veligers back into freshwater, and monitored their survival hourly.

II. Migration Experiments

In order to measure the rheotactic response of neritid snail juveniles I constructed a miniature "riffle" effect in a divided flow-through aquarium (see Figure 2) by filling the first compartment with freshwater until it spilled over the dividing wall and into the second compartment. The water level in the second compartment was kept lower than 3 centimeters by a drainage hole in the side of the compartment, which was at that level. At the beginning of each experiment, I placed 50

neritid juveniles (length < 4mm) of the same (unknown) species into the second compartment of the aquarium, at the bottom of the "riffle". I then flowed freshwater through the aquarium at the following rates: 3 L/min, 1.09 L/min, 0.43 L/min and 0 L/min. I observed the juveniles' behavior, and made periodic counts of how many had climbed into the first compartment.

## Results

### I.Salinity Tolerance Experiments

*General Observations*

Newly hatched veligers tended to remain on the bottom of the petri dish for a few minutes before swimming around. This inactive period was much longer when veligers were hatched into saltwater. Once swimming, the veligers tended to stay near the surface of the water, often moving in circles. Occasionally a veliger would stop swimming and drop to the bottom for a few minutes before actively swimming again. Live veligers always swim with their velum pointed upward, unless they are close to death, in which case they lie on the bottom with weakly beating cilia. An exception to this was when veligers that were hatched in seawater were transferred to freshwater (see below). Veligers which die in saltwater tend to simply stop moving and gradually decay, whereas veligers which die in freshwater generally show an explosion of their velum and soft body parts, possibly as a result of osmotic pressure.

Neritid veligers seem to be strongly phototaxic. If a petri dish were left near a light source for a few minutes before being counted, most of the veligers would be in the quarter of the dish closest to the light.

*Freshwater vs. Saltwater Experiments 1 & 2*

This experiment was performed twice, using egg capsules from the same rock. In Experiment 1, veligers which had been kept in freshwater showed a steep decline in their population after 84 hours (3.5 days) (Figure 3). All veligers in this experiment were dead after 140 hours. Veligers that had been kept in saltwater showed a small initial mortality of 4 individuals, as well as another small decline starting at about 84 hours. Veligers were able to survive for 15 days in a saltwater petri dish with no water changes. In Experiment 2, two separate petri dishes of veligers kept in freshwater went into decline after 53 hours (2.2 days) (Figure 4). All veligers but 1 were dead after 84 hours. Veligers kept in saltwater showed an initial drop of 5 individuals and another slight decline after 75 hours.

*Freshwater to Saltwater Transfer Experiment*

The veligers that were immediately transferred into saltwater showed the same initial population decline as the saltwater petri dishes in the previous two experiments (Figure 5). The second largest initial decline was in veligers which had been transferred to saltwater after 4 hours. The large decline in the population of the freshwater dish between 92 and 96 hours was caused by human error (see methods).

*Saltwater to Freshwater Transfer Experiment*

There was no difference in survival curves when veligers were transferred from saltwater into freshwater (Figure 6). However, although veligers from both petri dishes which were transferred into freshwater remained alive, they tended not to swim, but remained stuck in the surface tension, weakly beating their cilia. All veligers that were transferred into freshwater after more than 90 hours in saltwater died within one hour. Veligers that were hatched directly into saltwater (Figure 6) showed no difference in their survival curve from veligers which were hatched into freshwater and immediately transferred into saltwater (Figure 7).

### II. Migration Experiments

When there was zero flow, neritid snail juveniles had a scattered distribution over the floor of compartment two in the experimental aquarium. After zero flow was maintained for two hours, the juveniles would move around the sides of the tank, in both clockwise and counterclockwise directions, in lines of two or three individuals. However, as soon as flow was turned on at any level, the snails showed instantaneous movement both toward and away from the flow. Those that reacted towards the flow tended to all crawl towards one corner of the compartment and then

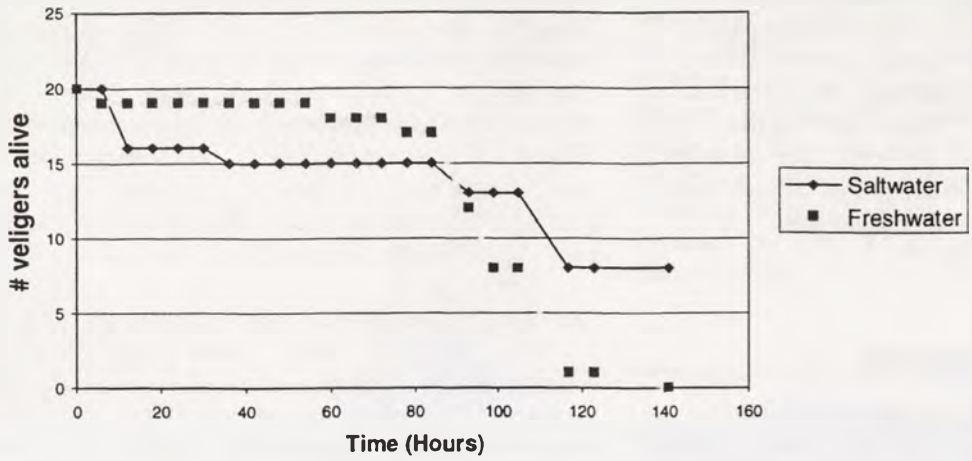


**Figure 3.** Freshwater vs. saltwater experiment 1. Veliger survivorship in freshwater vs. saltwater.

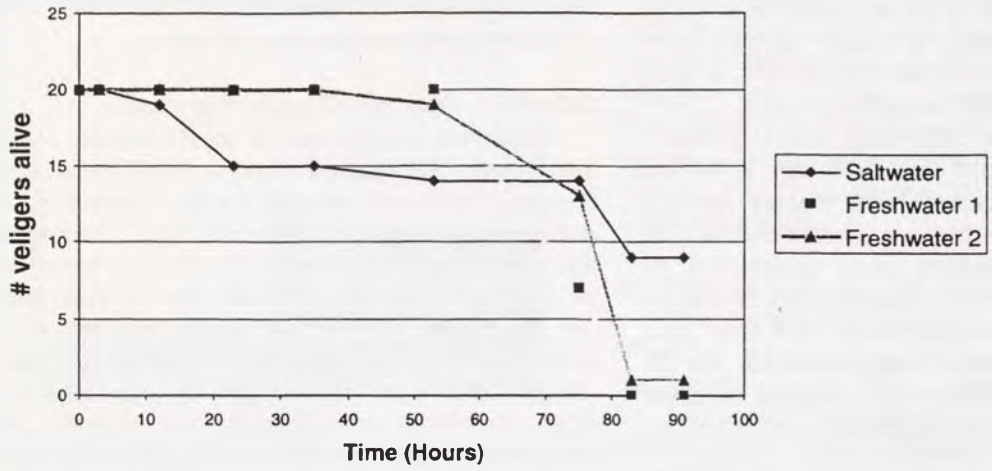


**Figure 4.** Freshwater vs. saltwater experiment 2. Veliger survivorship in saltwater vs. freshwater.

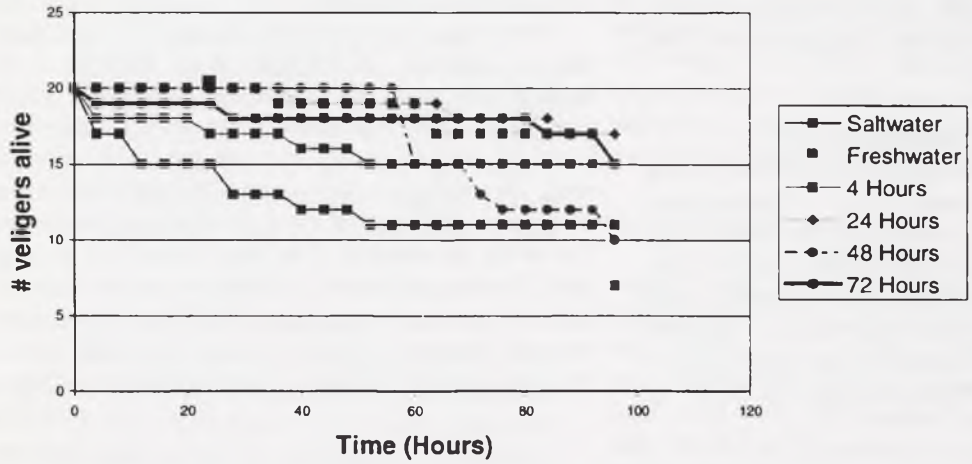


**Figure 5.** Freshwater to saltwater transfer experiment. Veliger survivorship when hatched in freshwater and switched to saltwater after varying amounts of time.

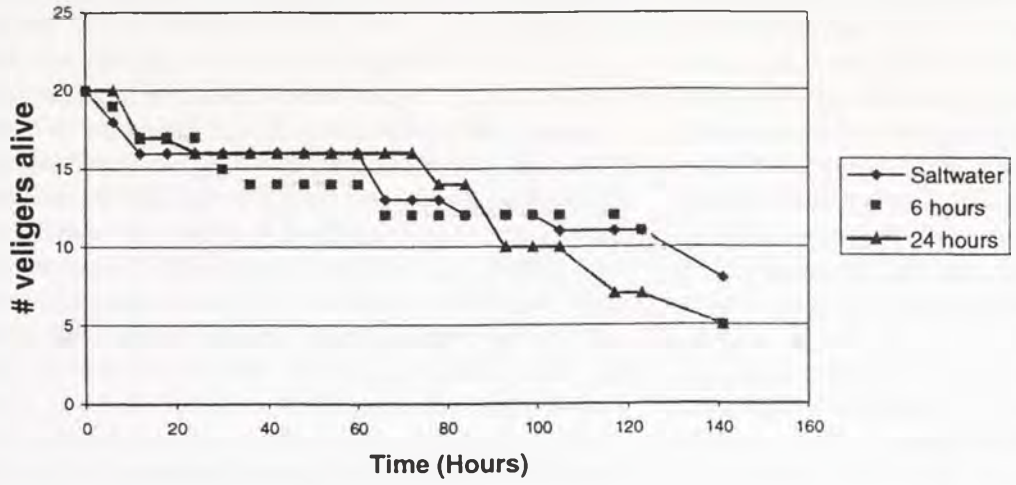


**Figure 6.** Saltwater to freshwater transfer experiment. Veliger survivorship when hatched in saltwater and transferred to freshwater after varying amounts of time.

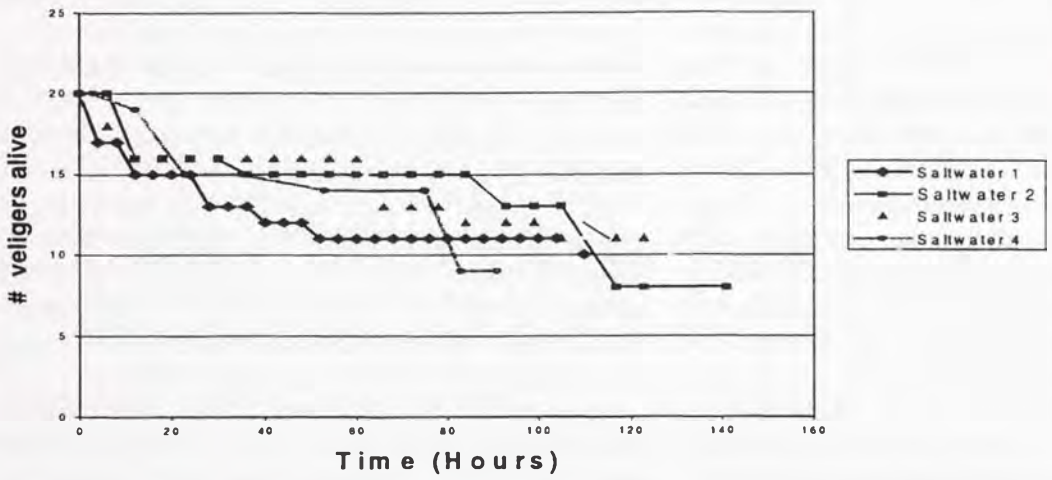


**Figure 7.** A comparison of veliger survivorship when transferred immediately into saltwater. Note the similarity at 20 hours.

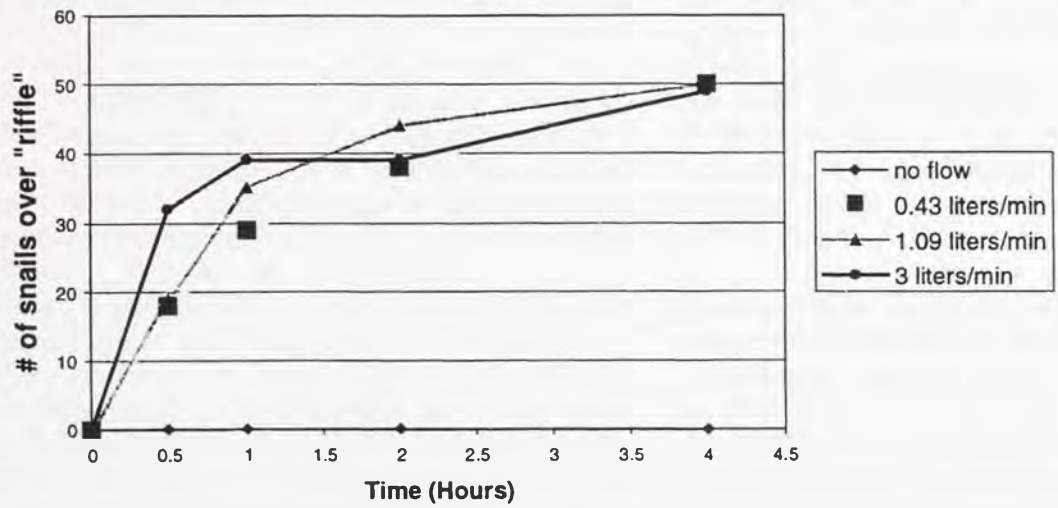


**Figure 8.** Migration experiments. The juvenile snails reacted more quickly to higher flow, but all made it over the riffle within 4 hours.

proceed in a line up the artificial riffle and into compartment one. Upon reaching compartment one, the snails continued moving in a line and aggregated as close as they could to the hose providing the flow, and if the hose was touching the wall of the aquarium, they climbed up the hose. The snails which moved away from the flow crawled in a line towards the drainage hole in compartment two. Upon reaching this hole, they turned around and moved over the riffle in the same manner as the ones which had proceeded them. Snails showed a slightly faster response to higher levels of flow, but in each case almost all of them had climbed the "riffle" within four hours (figure 8).

## Discussion

Before discussing the results of my study, I must address a problem of primary importance to this analysis. The patch of eggs which I used for my experiments could have been laid by any one of the four species of neritid snails which occurred at my site. These four species include three different genera: *Clithon*, *Neritina* and *Septaria*. According to Holthuis' (1995) most parsimonious phylogenetic trees, each of these genera invaded the freshwater environment separately. Consequently, each genus must have evolved a different mechanism of initial tolerance to freshwater, and possibly a different mechanism for upstream migration as well. If the mechanisms are similar, then this is probably the result of convergence. I have preserved voucher shells of the juveniles (also of unknown genus and species) used in the migration experiments in the University of California's Museum of Paleontology, pending identification. Since my results apply only to a single genus which remains unknown, the bulk of this study must be regarded as a pilot study which can be repeated and expanded upon in the future.

### I.Salinity Tolerance Experiments

*Freshwater vs. Saltwater Experiments 1 & 2*

The data from these experiments show fairly conclusively that neritid veligers lose their tolerance to freshwater after a certain amount of time. There is a discrepancy of about 56 hours between the two experiments. This discrepancy can best be explained by the fact that the egg capsule used in experiment 2 had been kept in the flow-through aquarium for six days longer than the egg capsule in experiment 1 (remember that all experiments were conducted from the same egg patch). Although the flow-through aquarium was an attempt to recreate conditions in the field, it tended to build up silt on the bottom, which may have prevented the eggs from being oxygenated as well as they would have been in a riffle. I am inclined to believe that the data from experiment 1 are more accurate with regard to time, while the results from experiment 2 are valuable in reproducing the result that veligers will die after a certain amount of time in freshwater.

*Freshwater to Saltwater Transfer Experiment*

This experiment was important in showing how veligers which were immediately placed in saltwater always showed an initial population decline. Petri dishes of veligers which were placed in saltwater after longer periods of time in freshwater showed a much higher level of survival. This would seem to imply that a fraction of the population of newly hatched veligers (about 25% based on the current experiments) are not capable of immediately living in saltwater when they are first hatched. Figure 7 shows the survival curves for all petri dishes, from all experiments, which were immediately placed into saltwater. All four survival curves show an initial mortality of 4 or 5 veligers in the first 20 hours, followed by a much reduced loss of no more than 8 veligers in the next 120 hours. Survival was much higher in veligers which were allowed to stay in freshwater for a longer time before being transferred (Figure 5).

*Saltwater to Freshwater Transfer Experiment*

The results from this experiment refute both hypotheses 1 and 2. By showing that veligers can survive after being hatched directly into saltwater, they refute the first hypothesis that veligers maintain freshwater physiology for a certain amount of time. In addition, by showing that veligers continue to live after being transferred from saltwater into freshwater, they refute the second hypothesis that veligers lose their freshwater tolerance after being exposed to saltwater. The results uphold my third hypothesis by showing that the veligers can live equally well in saltwater and freshwater, for at least the first 96 hours.

This almost instantaneous euryhaline tolerance is rare among the larvae of non-neritid molluscs, and among invertebrates in general. Holthuis (1995) found that only 10 percent of freshwater invertebrates and only 4 non-neritid freshwater molluscs had free-swimming (thus, possibly euryhaline) larvae. I would postulate that this tolerance consists of an osmotic equilibrium of the blood and tissues to seawater, as is the case with most saltwater molluscs (Robertson 1964; Berger and Kharazova 1997), with freshwater tolerance being maintained by a temporary mechanism of osmotic regulation. This mechanism may consist of changes in RNA and protein synthesis on a cellular level (Berger and Kharazova 1997), or it may be due a larval kidney which could produce urine which is hypoosmotic to the blood (Robertson 1964). Ion uptake to replace those lost by diffusion probably is important as well. In either case, I believe that a developmental loss of this mechanism at around 84 hours after hatching may mark the end of freshwater tolerance for the veligers.

The lack of saltwater tolerance in about 25% of the population of newly-hatched veligers is probably compensated by a longer period of freshwater tolerance. This may be a form of evolutionary "bet-hedging", which would preserve 25% of the population in the event of a drought which supplied insufficient water to wash the veligers into the ocean (Lindberg, personal comm.)

II. Migration Experiments

Neritid juveniles showed extremely strong rheotaxis in this experiment. Under any amount of current flow over the artificial "riffle", the snails would immediately climb it and head towards the hose that was providing the current. They would always do this gregariously, aggregating in a corner of the aquarium (presumably where the flow was lowest) and climbing in lines of up to ten snails long. The snails that initially moved away from the flow were probably reacting to an artificial eddy caused by the shape of the lower compartment. Nevertheless, they always reversed their direction and climbed the riffle within 4 hours. It could be argued that under conditions of zero flow, there was no water covering the riffle and therefore the snails would be unable to climb it. However, under conditions of zero flow, the juveniles showed no specific directionality in their movements either.

The tendency of the snails to travel over the riffle in lines continues to be a mystery. It could be that this aggregation was coincidental. Since the current was turned on at a discrete time, if the juveniles all reacted at once and all climbed the riffle where it was easiest to climb, then the aggregation could merely be one of chance. However, in two of the experiments, the large group of snails which headed toward the drainage hole did this in a line. Also, under conditions of zero flow, although the snails showed no specific directionality in their movements, they still tended to aggregate into small lines of two or three. All these data tend to make me believe that aggregation and mass migration is a behavioral feature of neritid juveniles. Statzner *et al.* (1988) suggested that this behavior might be useful in streamlining the animals, making it easier for the ones behind the leader to move against the flow. It may be that the juveniles lose this migratory behavior after a certain amount of time, or that it only occurs in certain species. The fact that mass migration has never been observed in the wild on Moorea may be because the migrations are somewhat rare and seasonal, or else because the cobbly substrate in most of the streams of Moorea hides or even impedes such migrations.

Conclusions

Analysis of the results has led me to several conclusions regarding the initial freshwater tolerance of neritid snails of the genus that I worked with. First of all, veligers of this genus are born with a high euryhaline tolerance. This tolerance probably consists of an underlying saltwater physiology overlaid with a temporary mechanism of freshwater tolerance which is lost developmentally starting at about 84 hours. Additionally, there was consistent 25% mortality in veligers that were transferred immediately into saltwater, which may be a safety measure against drought years of low flow in the streams.

Experiments in the lab showed conclusively that neritid juveniles possess a strong positive rheotaxis, just as predicted. Furthermore, the juveniles show a tendency to aggregate and follow one another in lines, even when not migrating against flow. While this aggregation may be coincidental, it seems highly likely that

this is a behavioral modification that aids the hydrodynamics of the migrating snails.

There are several important ecological and evolutionary implications which stem from these conclusions. If different genera of Neritids have different mechanisms of initial tolerance to freshwater then this could help to explain the distribution of species. Resh *et al.* (1990) noted the contradictory fact that although *Neritina turrita* was the most motile species in the laboratory, it was restricted in streams to less than 5m in elevation. This distributional limit could be the result of a shorter timespan of larval freshwater tolerance, which forces the snails to lay their eggs near the ocean.

Finally, although free-swimming planktonic larvae are an ancestral trait in the neritid snails (Holthuis 1995), the initial tolerance of their larvae to freshwater is probably an evolutionary innovation. A future study determining the nature of this tolerance as well as the length of time that it lasts for different genera may be important in understanding the phylogenetic relationships of the Neritids, and the evolution of freshwater tolerance in general.

**Acknowledgements**

I would like to thank Dr. Lipps for all his hard work in organizing this class and looking for the scientist in each of us. I would also like to say *merci beaucoups* to Dr. Lindberg, Dr. Hickman and Dr. Resh for their expert advice and remarkable enthusiasm for my project. Of course, *maruuru roa* to Amy Lesen, Virginia Matzek and Tegan Churcher for their hard work in making the class run smoothly in every aspect: from food to equipment to chauffeur-services. Their advice was helpful, their encouragement was indispensable, and their friendship unforgettable. Finally I would like to thank each and every one of my classmates for their extraordinary friendship and companionship on our adventures together in the South Pacific

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# Physico-chemical factors affecting community structure in intertidal rocky pools on a coral conglomerate platform

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ABSTRACT. Habitat islands are useful to study in biogeography because they are physically extreme–small, isolated, and temporary. Rates of colonization are low and rates of extinction, even for native well-adapted species, tend to be high. Intertidal rocky pools are an excellent example of a habitat island because they limit the dispersal of organisms. This study examined the community structure in pools on the northern edge of Tiahura, a coral island off the northwest coast of Moorea, French Polynesia. For this conglomerate platform rocky pool system, variation in species richness, diversity, and density were correlated with the physical characteristics of the pools: size, distance from reef flat, salinity, temperature, pH, and dissolved oxygen content. Sampling was conducted on macroscopic organisms (>2mm). Specific species counts were assigned to fish, algae, or macrobenthos guilds. A multiple linear regression analysis of this data was then conducted using JMPin™ statistical software. It was found that changes in mean pool depth decreased with distance from the reef flat. This implies decreased tidal inundation. As expected, the most isolated pools showed a reduction in biota diversity. The measured physical characteristics correlated with the community structure of the pools, showing significant non-random results. In the future, this study could be supplemented with a substrate analysis between pools. Further field operations would also yield insight into the resiliency of the ephemeral populations of the pools.

## Introduction

The existence of repeated, non-random patterns in species distributions implies the operation of general causal processes. An understanding of these patterns can provide an explanation for the present day distribution of species.

Small, isolated islands almost invariably support fewer species than local sites of comparable size and habitat on nearby mainlands (Williamson 1981). This generalization applies not only to true islands of land surrounded by water, but also to small, isolated patches of habitat that are separated from other, larger patches by environments that constitute barriers to dispersal (Myers and Giller 1988). These kinds of harsh environments are physically extreme; they are small, isolated, and short-lived. Not only are rates of colonization low, but also rates of extinction, even for native, well-adapted species, tend to be high (Terborgh 1973).

Intertidal pools possess this "island" quality. The physical, chemical, and biological features of the intertidal zone form a complex system connected with the semi-diurnal rise and fall of the tide. The tidal-dependent factors restrict the distribution of animals and plants. Organisms have less time to feed and respire, and particular zones are subjected to temperature extremes and desiccation (Micallef and Bannister 1967). Tidal-independent factors are also important. Exposure to wave action increases the effective submersion period. Topography, water content of the sand, and biological factors (e.g. presence of algae and browsing activities of herbivores) also affect the features of the intertidal zone (Newell 1970).

Rock pools form an obvious habitat within the intertidal zone, and the specialized nature of their fauna and flora has long been recognized. There are two principal patterns generally accepted of intertidal pools. As higher shore levels are approached 1) there is a larger fluctuation in a pool's physico-chemical features and 2) there is a reduction in the diversity of the biota, with a corresponding population increase for remaining species (Newell 1970).

Such pools occur on tropical oceanic coral reef islands ("motu" in the Tahitian language). Motu formation begins with a catastrophic storm sweeping up coral in large fragments, from the outer reef slope into piles on the reef flat. This new foundation erodes with lower energy events (tidal and wave action) over long stretches of time. These processes also introduce sand deposits, and with the cementation of mobile features and the colonization by plants, a more stable (yet still ephemeral) islet is formed (Bayliss-Smith 1988).

Along with beachrock and cay sandstone, a common cemented feature of motus is conglomerate platforms. The vast majority of literature supports that conglomerate platforms are the result of cementation of sediment deposited by cyclones (Darwin 1889; Newell 1956;

Shepard 1967; Stoddart 1975; Scoffin 1978; Montaggioni 1984; Guilcher 1988). Cementation occurs in carbonate sediments by the dissolution of calcium carbonate in either seawater or fresh water and the subsequent precipitation of aragonite or calcite crystals in pore spaces (Bricker 1971; Scoffin 1987). The surface of the conglomerate platform is generally horizontal. On a micro-scale however, the surface of the platform is rough textured from karstic erosion. Large coral boulders have commonly been detached and transported by wave action onto the platform. Over time, they cement to the surface of the platform and eventually are incorporated into it (Richmond 1992). On its seaward edge, the platform is usually abrupt but can merge gently with the reef flat. Sand deposits collect on the lagoon-side, supported by the platform's presence.

Insular habitats are created within the conglomerate platform. The surface of the conglomerate has been smoothed by weathering and darkened by cyanobacteria. Channels that cut back into the platform heavily dissect the exposed perimeter (Murphy 1992). This dissolution also creates pools in the interior of the platform. These pools are presumably formed from karst erosion and contain seawater that rises and falls with the tide.

The physical processes between Newell's model of the rocky pool system are highly analogous to the conglomerate platform pool system. They diverge primarily in their fill/drain sequence. An "island's" connection with the tide is typically in a vertical gradient. The conglomerate platform however, is horizontal in nature; pools more horizontally distant from the exposed outer edge of the conglomerate generally experience less wave action. Some pools are continually flushed by this wave action above the conglomerate. Others only receive wave action at higher tides and some pools are always out of reach of daily tides (Figure 1). As sea levels rise and fall, all pools fill and drain through pores in the platform. Macroscopic organisms cannot migrate into the pools through this latter mechanism.

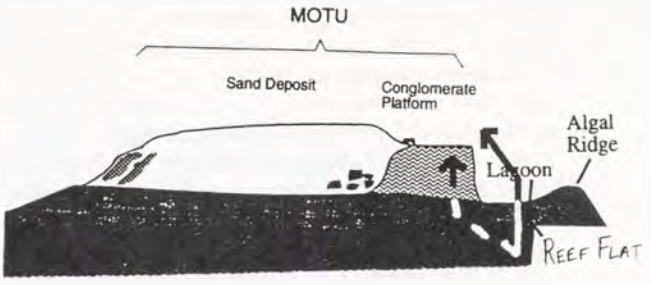


**Figure 1.** horizontal profile of conglomerate platform system, showing the two mechanisms of tidal inundation

The MacArthur -Wilson equilibrium theory of island biogeography has set the stage for experiemental biogeography. It is a quantitative basis for explaining species richness patterns observed on islands. In the Theory, these species distributions are only affected by the physical characteristics of island area and degree of isolation (MacArthur and Wilson 1967). Other climate factors on an island, biological interactions between species, or disturbance effects are not taken into account. A more unified study will describe the interactions of a number of largely independent variables, such as island area, isolation, habitat diversity, and position (Cox and Moore 1993).

This study is concerned with the physico-chemical parameters affecting the community structure of conglomerate pools. How do the variation in species richness, concentration, and diversity of plants and animals correlate with the physical characteristics of the pool system: tidal level, depth, surface area, temperature, salinity, pH, and dissolved oxygen content? What are the relationships of such parameters to one another and to the rock pool biota, and do they vary in space along the conglomerate platform?

## Materials and Methods

*Site Description*

Approximately 400 meters off the Northwest coast of Moorea (Figure 2), French Polynesia lies Motu Tiahura (17$^0$ 29` S, 149$^0$ 54` W). The conglomerate platform under study is approximately 500m in length and forms the seaward edge of this coral island.

All data was collected in October and November of 1998. It is expected that the temperature on Moorea remains in the ten degree range of 22-32°C, and the relative humidity lies above 60% (Murphy 1992). Moorea's tidal amplitude was recorded as 68cm in 1981 (Coulon), but no long-term records have been kept. The tidal cycle has a regular diurnal rhythm--low at 6:00AM and 6:00PM and high at noon and midnight, approximately. The cycle fluctuates slightly.

Twenty-six pools were examined (Figure 3). They display considerable variability in size, degree of isolation from their surface seawater source (the lagoon, reef flat, or each other), tidal flux, and inhabitants. Pools that fill only at extremely high tides or after heavy rain were not included in this study.

*Physical parameters and analytical procedures*

The physico-chemical parameters measured in the pools were size, distance from reef flat / lagoon, salinity, temperature, pH, and dissolved oxygen content.

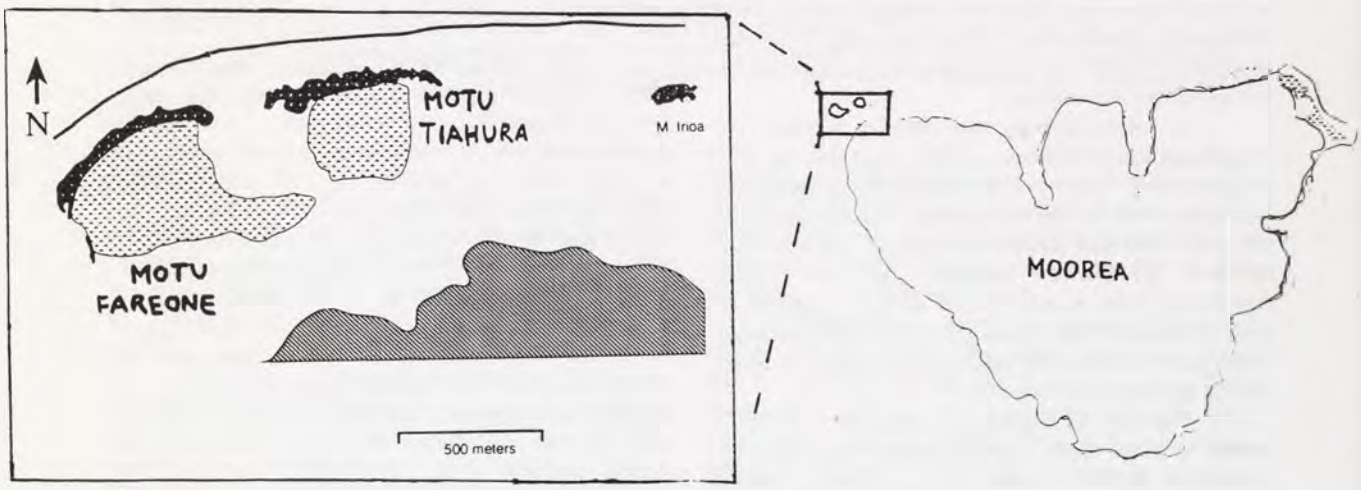


**Figure 2.** map of Moorea (right), with enlarged view of northwest corner (left)

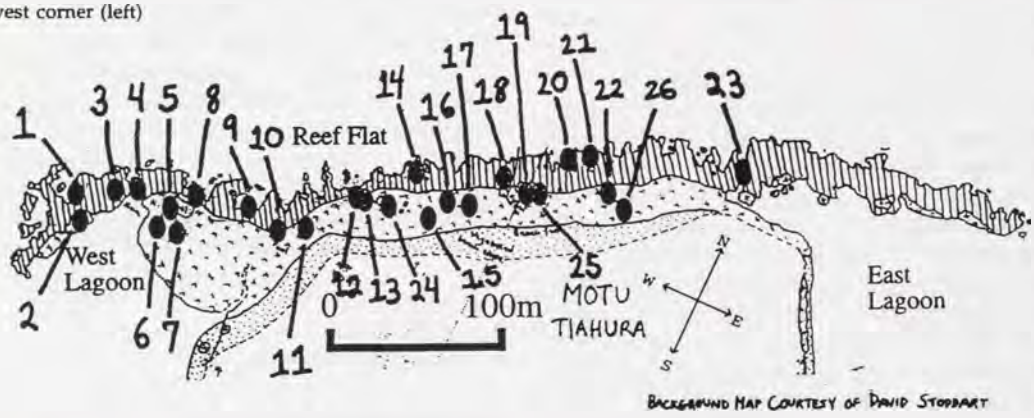


**Figure 3.** top view of Tiahura conglomerate platform, showing locations of 26 pools and larger water sources (west lagoon, reef flat, east lagoon)

*Pool size.* Pool dimensions were collected for a size analysis. Depth was measured at

benchmarks from the deepest part of the pool. The pools were idealized as ellipses and a major and minor axis was measured. Data was collected at low, intermediate and high tides. Together, the dimensions give a simplified means of relating the surface areas and volumes of the conglomerate pools.

*Distance from reef flat / lagoon.* Along with their relative sizes, pools' relative positions were measured. This included distances to the reef flat (or lagoon) and to a nearest neighbor. A GPS was used to obtain accurate coordinates for a waypoint on the northwest corner of the platform. From this waypoint, a compass and 30-meter transect tape were used to accurately map the layout of the rocky pools.

*Water chemistry.* Water chemistry was surveyed using temperature, salinity, pH, and dissolved oxygen measurements. The majority of data were collected in the six hours surrounding the high tide (8:30AM-2:30PM, with high tide at 12noon). Some data however was collected at night and before the first low tide (6:00AM). Those parameters that fluctuated more dramatically were measured more frequently. Measurements at three other localities (reef flat, west lagoon, east lagoon) were taken to compare differences between the water in the pools to water in larger surrounding habitats.

The oxygen sensor and pH electrode were calibrated daily on a Corning© meter. Dissolved oxygen measurements were recorded as a percent of total air saturation and converted to mg/L. Temperature was measured simultaneously with the probe under use (pH, or dissolved oxygen). A Leica© hand-held temperature compensated refractometer was used in the field for salinity measurements (units of parts per thousand).

*Biota sampling methods*

Biota was sampled to measure the biotic diversity, richness, and densities of the pools. Surveying was conducted on a macroscopic scale; the minimum size for a collected specimen was set at 2mm.

Three sampling methods were used. For small and high count species, as well as relatively sessile species (e.g. algae, mollusks, arthropods), a proportional quadrat method was used at high tide to extrapolate total counts or percent coverage of species on the substratum. The number of $0.25m^2$ quadrats that could fit in a pool was established. Sampling was conducted on a subset of these quadrats (selected with a random numbers table). Data was then extrapolated to the known surface area to estimate the pool's benthic population. This method gave similar results to sampling the benthos in its entirety, without quadrats (Appendix A).

Species too large for the quadrat method (or species with very low density, e.g. fish, urchins, cucumbers, upside-down jellyfish, shrimp) were counted directly. Certain arthropods that could easily migrate between pools (e.g. insects, large crustaceans) were excluded from sampling. To keep fish from being scared into hiding, the surveyor allowed fish to acclimate to his presence for 5 minutes before counting.

Stable populations of mosquito larvae existed in a few pools. To measure their concentrations a "scoop" method was used. A site in the pool was randomly selected. The water would be stirred to even out the mosquito distribution. Water samples (with larvae) were collected. Multiple samples were then taken to the laboratory, totaled, and averaged to yield a counts/volume concentration.

*Statistical analysis*

JMPin™ statistical software was used for a multivariate analysis on the pool system. Biota was divided into 3 guilds: algae, fish, and macrobenthos. The guild richness, concentration, and diversity (using Simpson's index) were formulated for the 3 guilds. Multiple physico-chemical parameters were then correlated with these 9 community structure indicators to form fit models on JMPin™.

**Results**

*Physico-chemical measurements*

Dimensional analysis suggests a dependency of pool surface area and volume on the rise and fall of the tide. While most of the pools retained water through the low tide, many experienced drastic reductions in their surface areas and volume (Appendix B).

A horizontal gradient of pool distribution exists, with nearest distances ranging from 0-31m (Appendix C). Other physical data (water depth, temperature, salinity, pH, and dissolved oxygen content) was measured in the pools multiple times over many days. There were notable differences between the chemical composition of the conglomerate pools and their

larger, feeder sources of sea water and sea life (e.g. reef flat, west lagoon, east lagoon) (Table 1).

*Biotic sampling*

Similarly to their physical characteristics, pool communities were diversified along the platform.

| pools | <depth> | SD | min | max | <salinity> | SD | min | max | <temp.> | SD | min | max | <pH> | SD | min | max | <D.O.> | SD |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 38.0 | 11.6 | 11.5 | 55 | 36.5 | 0.806 | 35 | 38 | 28.17 | 1.1 | 25.9 | 29.8 | 8.166 | 0.241 | 7.69 | 8.56 | 6.5 | 1.0 |
| 2 | 44.4 | 10.2 | 34 | 52.3 | 37 | 0.632 | 36 | 38 | 29.69 | 2.0 | 26.2 | 33.2 | 8.139 | 0.231 | 7.82 | 8.54 | 3.7 | 1.6 |
| 3 | 6.9 | 6.4 | 0 | 18.2 | 34.5 | 4.062 | 29 | 39.5 | 32.25 | 3.5 | 26 | 37 | 8.014 | 0.26 | 7.69 | 8.29 | 1.9 | 0.7 |
| 4 | 3.7 | 5.3 | 0 | 13.5 | 36.5 | 1.291 | 35 | 38 | 29.33 | 2.2 | 27 | 32.6 | 7.765 | 0.02 | 7.75 | 7.78 | | |
| 5 | 36.1 | 6.6 | 24.6 | 44 | 37.55 | 2.252 | 34 | 40 | 31.05 | 2.7 | 26.2 | 35.6 | 8.363 | 0.312 | 7.96 | 8.9 | 4.2 | 2.0 |
| 6 | 19.8 | 6.4 | 7.9 | 27.5 | 38.68 | 3.068 | 34 | 44.5 | 31.85 | 3.6 | 25.4 | 37.6 | 8.197 | 0.236 | 7.87 | 8.54 | 4.1 | 1.9 |
| 7 | 19.5 | 6.2 | 7.5 | 27.3 | 37.55 | 2.505 | 34 | 40 | 31.71 | 3.7 | 25.9 | 37.5 | 8.332 | 0.299 | 7.94 | 8.71 | 5.1 | 2.0 |
| 8 | 14.0 | 7.6 | 0 | 30.5 | 33.89 | 5.862 | 21 | 40 | 31.99 | 3.6 | 25.2 | 38.6 | 8.218 | 0.166 | 7.97 | 8.44 | 3.7 | 2.2 |
| 9 | 27.9 | 12.8 | 7.6 | 55 | 36.54 | 1.613 | 32 | 38 | 30.58 | 2.2 | 26.2 | 34.1 | 8.316 | 0.318 | 7.92 | 8.93 | 4.4 | 1.6 |
| 10 | 58.4 | 8.1 | 46.5 | 72 | 34.69 | 2.983 | 30 | 40 | 31.06 | 2.6 | 26.7 | 35.6 | 8.328 | 0.288 | 7.88 | 8.81 | 3.6 | 1.4 |
| 11 | 31.4 | 5.1 | 20.7 | 38 | 32.23 | 1.739 | 30 | 36 | 30.87 | 2.4 | 26.8 | 35.1 | 8.152 | 0.234 | 7.83 | 8.55 | 3.5 | 1.3 |
| 12 | 22.2 | 6.3 | 9 | 32 | 33.55 | 2.382 | 31 | 39 | 29.43 | 2.0 | 26.2 | 33.3 | 8.109 | 0.168 | 7.86 | 8.41 | 3.0 | 1.7 |
| 13 | 23.9 | 5.8 | 11.5 | 32 | 33.45 | 3.698 | 27 | 41 | 31.69 | 3.1 | 25.8 | 36.9 | 8.333 | 0.283 | 7.94 | 8.74 | 4.3 | 1.7 |
| 24 | 28.6 | 5.8 | 16.8 | 37.3 | 32.36 | 2.248 | 30 | 38 | 32.05 | 3.0 | 26.5 | 37.3 | 8.188 | 0.311 | 7.73 | 8.64 | 5.2 | 1.5 |
| 14 | 35.3 | 11.4 | 19.8 | 54 | 37.36 | 4.985 | 30 | 41 | 31.92 | 3.7 | 25.8 | 39.2 | 8.846 | 0.488 | 8.15 | 9.71 | 5.2 | 1.6 |
| 15 | 24.7 | 11.3 | 10.1 | 27.5 | 31.08 | 2.397 | 28 | 38 | 34.28 | 4.0 | 25.9 | 39.6 | 8.402 | 0.419 | 7.82 | 8.99 | 6.0 | 1.7 |
| 16 | 18.4 | 5.1 | 8.5 | 27.5 | 30.82 | 4.238 | 24 | 39 | 32.98 | 3.5 | 26.1 | 38.6 | 8.675 | 0.457 | 8.2 | 9.39 | 5.0 | 1.4 |
| 17 | 13.4 | 6.1 | 2 | 23 | 34.08 | 7.681 | 22 | 47 | 33.97 | 3.6 | 26.3 | 39.5 | 8.856 | 0.409 | 8.16 | 9.33 | 5.3 | 1.4 |
| 18 | 15.7 | 11.0 | 1 | 44.5 | 26.33 | 9.95 | 11 | 41 | 31.72 | 3.1 | 25.5 | 36.7 | 8.113 | 0.259 | 7.7 | 8.52 | 2.2 | 1.6 |
| 19 | 24.8 | 5.0 | 14 | 33.2 | 31.09 | 3.39 | 26 | 39 | 31.37 | 2.7 | 25.8 | 35.8 | 8.241 | 0.21 | 7.88 | 8.52 | 6.6 | 1.1 |
| 25 | 9.9 | 4.9 | 0 | 19 | 30.29 | 4.499 | 26 | 39 | 32.81 | 3.5 | 25.8 | 37.6 | 8.223 | 0.196 | 7.88 | 8.51 | 7.1 | 1.4 |
| 20 | 37.1 | 8.5 | 19 | 45 | 36.64 | 0.674 | 36 | 38 | 30.53 | 2.4 | 26.3 | 34.5 | 8.27 | 0.33 | 7.39 | 8.65 | 5.1 | 0.9 |
| 21 | 24.5 | 8.9 | 15 | 34 | 36.73 | 0.467 | 36 | 37 | 28.72 | 1.0 | 26.8 | 30.1 | 8.235 | 0.205 | 7.98 | 8.59 | 7.4 | 1.8 |
| 22 | 22.5 | 6.3 | 9.4 | 32 | 33.27 | 2.284 | 29 | 38 | 34.13 | 3.5 | 26.4 | 38.8 | 8.171 | 0.275 | 7.79 | 8.59 | 6.0 | 2.1 |
| 26 | 13.7 | 6.5 | 0 | 21 | 33.78 | 2.489 | 30 | 38 | 31.92 | 3.1 | 26.5 | 37.4 | 7.983 | 0.201 | 7.66 | 8.22 | 4.8 | 2.8 |
| 23 | 26.8 | 8.8 | 13.4 | 35.4 | 36.82 | 1.168 | 35 | 38 | 30.6 | 2.4 | 24.6 | 34.9 | 8.09 | 0.307 | 7.62 | 8.57 | 4.0 | 1.9 |
| west lagoon | | | | | 36.46 | 0.519 | 36 | 37 | 30.07 | 2.2 | 25.8 | 33.6 | 8.179 | 0.219 | 7.88 | 8.55 | 4.9 | 1.1 |
| reef flat | | | | | 36.67 | 0.888 | 35 | 38 | 28.72 | 0.9 | 26.9 | 30.2 | 8.208 | 0.221 | 7.94 | 8.57 | 8.0 | 1.9 |
| east lagoon | | | | | 37 | 0.816 | 35 | 38 | 31.6 | 2.5 | 24.8 | 34.9 | 8.126 | 0.373 | 7.71 | 8.77 | 4.5 | 0.6 |

**Table 1.** Physical parameter summary for the 26 pools and 3 control sites (west, east lagoon, reef flat). Mean, standard deviation, and maximum/minimum recorded values. Units: depth-cm; salinity-parts per thousand; temperature-degrees celcius; dissolved oxygen-mg/mL

Certain organisms were pervasive in the pools (*Chrysiptera glauca, Stegastes nigricans, Nerita sp., Littorina sp.*) while others were more anomalous (*Acanthurus lineatus, Fasciolaris sp., Echinothrix calamanis, turbinaria sp.*) (Appendix D).

Stable populations of fish were found in 16 of the 26 pools, with counts ranging from 3 to 249 fish. Every pool contained macrobenthos representatives (counts of 13-431) but only 4 housed enduring populations of mosquito larvae. Algal distribution took 3 forms: microscopic algal/bacterial film that was apparently used by grazers; distinct macroscopic algae of low density (e.g. *Turbinaria sp., Valonia sp.*); and composite algal mats typically formed of filamentous and matrix-forming blue-green alga, pinnate diatoms, and even foraminifera. Algal mats were characterized by their macroscopic morphology. A reference collection was made for future identification (Appendix E)

*Pool community structure*

Diversity (D), richness (R), and specie density (ρ) in pools was characterized from raw biota sampling data. D, R, and ρ were then obtained for each guild (table 2).

| pools | $R_{fish}$ | $R_{algae}$ | $R_{mac}$ | algae % coverage | fish/$m^3$ | mac/$m^2$ | mosq/100mL | $D_{fish}$ | $D_{algae}$ | $D_{mac}$ |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 11 | 9 | 4 | 36% | 27 | 3.3 | | 3.95 | 2.77 | 2.68 |
| 2 | 9 | 5 | 10 | 8% | 19 | 6.3 | | 5.10 | 3.46 | 6.68 |
| 3 | 0 | 1 | 3 | 1% | 0 | 18.0 | | | 1.00 | 2.42 |
| 4 | 0 | 1 | 3 | 1% | 0 | 32.0 | | | 1.00 | 1.40 |
| 5 | 15 | 4 | 4 | 19% | 12 | 1.5 | | 5.47 | 1.72 | 2.55 |
| 6 | 0 | 1 | 2 | 1% | 0 | 18.6 | | | 1.00 | 1.48 |
| 7 | 0 | 1 | 2 | 1% | 0 | 21.4 | 0.826 | | 1.00 | 1.79 |
| 8 | 0 | 1 | 2 | 1% | 0 | 12.5 | | | 1.00 | 1.92 |
| 9 | 1 | 1 | 2 | 1% | 38 | 15.7 | | 1.00 | 1.00 | 1.38 |
| 10 | 10 | 2 | 6 | 26% | 9 | 5.3 | | 5.57 | 1.08 | 3.27 |
| 11 | 4 | 2 | 7 | 15% | 5 | 9.1 | | 3.61 | 1.15 | 1.73 |
| 12 | 1 | 1 | 4 | 1% | 25 | 76.0 | | 1.00 | 1.00 | 2.71 |
| 13 | 4 | 2 | 3 | 31% | 3 | 9.6 | | 2.29 | 1.07 | 1.22 |
| 24 | 5 | 2 | 2 | 43% | 6 | 3.2 | | 4.17 | 1.05 | 1.36 |
| 14 | 2 | 2 | 2 | 67% | 2 | 45.0 | | 1.80 | 1.03 | 1.80 |
| 15 | 0 | 3 | 2 | 24% | 0 | 8.5 | 7.41 | | 1.10 | 1.48 |
| 16 | 4 | 2 | 2 | 56% | 3 | 9.7 | | 3.33 | 1.04 | 1.78 |
| 17 | 0 | 2 | 2 | 23% | 0 | 8.0 | 1.48 | | 1.09 | 1.51 |
| 18 | 0 | 1 | 3 | 1% | 0 | 108.6 | | | 1.00 | 1.85 |
| 19 | 4 | 2 | 5 | 11% | 35 | 78.0 | | 4.66 | 1.22 | 2.43 |
| 25 | 0 | 1 | 2 | 1% | 0 | 13.0 | | | 1.00 | 1.55 |
| 20 | 7 | 1 | 6 | 1% | 48 | 13.5 | | 4.72 | 1.00 | 2.75 |
| 21 | 11 | 7 | 4 | 13% | 24 | 5.2 | | 2.14 | 3.06 | 2.16 |
| 22 | 0 | 2 | 2 | 31% | 0 | 26.9 | 4.24 | | 1.07 | 1.42 |
| 26 | 0 | 1 | 2 | 1% | 0 | 75.0 | | | 1.00 | 1.20 |
| 23 | 5 | 2 | 7 | 58% | 19 | 24.0 | | 2.56 | 1.04 | 2.56 |

**Table 2.** summary of community indicators--richness (R), density, diversity (D) for fish, algae, macrobenthos (mac.), and mosquito larvae (mosq.)

Using multiple linear regression, fit models were applied to the 9 indicators. This analysis revealed the factors that positively and negatively correlated with biota R, D, and ρ.

*Richness*. The biota richness varied over a wide range. $R_{fish}$ ranged from 0-15, $R_{algae}$ from 1-9, and $R_{macrobenthos}$ from 2-10. The richest pools in algae and fish were relatively large (Figure 4). Pools closest to the water housed the highest algae richness (Figure 5). $R_{fish}$ correlated with $R_{algae}$. $R_{macrobenthos}$ positively correlated with depth and negatively correlated with mean temperature and distance from reef flat / lagoon.

*Concentration*. Along with guild richness, the densities in which species were distributed was compared with physical parameters. Fish concentrations, ranging from 0-50/$m^3$ tapered off with increased distance from the reef flat, mean temperature (Figure 6), and variance in temperature. Algae percent coverage of substrate (0-67%) increased with variance in pH. Macrobenthos concentrations (1.5-109/$m^2$) showed a fairly random distribution.

A fourth guild was assigned to mosquito larvae to conduct a density study. Mosquito larvae have an advantage over fish, algae, and macrobenthos organisms to colonize the pools. Mosquitos can fly to any of the pools on the conglomerate to disperse their eggs. Two major obstructions to larvae survival, though, are predation and dessication. Mosquito larvae were never found in pools with fish. And while short-lived (<5 day) populations of larvae were found on occasion, no stable mosquito larvae community existed in pools that reached zero depth. In the four pools housing larvae, density values ranged from 0.83/100mL to 7.41/100mL. A negative correlation existed with mean salinity level (Figure 7).

*Diversity*. Simpson's diversity indices were obtained and analyzed from the fish, algae, and macrobenthos distributions in pools. $D_{algae}$ values, ranging from 1-3.46, decreased with distance from reef flat / lagoon and mean temperature. On the other hand, $R_{fish}$ and $D_{macrobenthos}$ positively correlated with $D_{algae}$. Larger Simpson's indices (1-5.57 range) were found for fish living in deeper habitats (Figure 8). Like algae diversity, $D_{macrobenthos}$ values negatively correlate with distance from ocean (Figure 9).

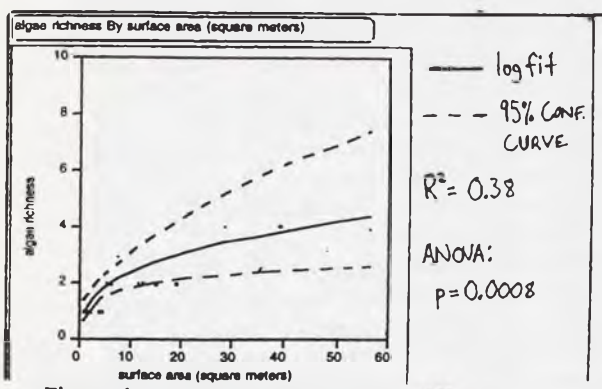


**Figure 4.** log of algae richness vs. surface area

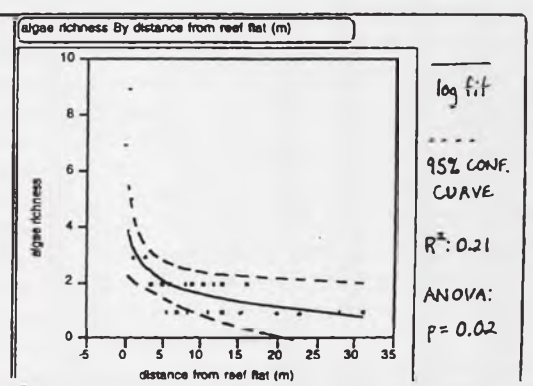


**Figure 5.** log of algae richness vs. distance from reef flat

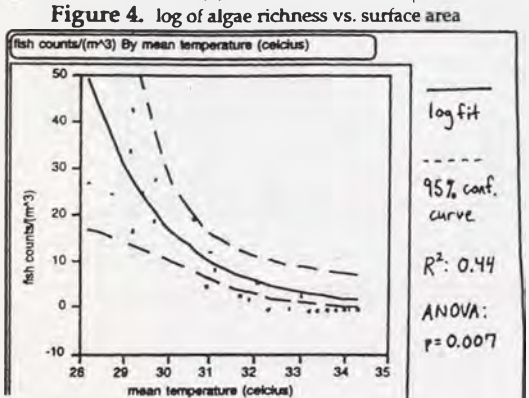


**Figure 6.** log of fish density vs. mean temperature

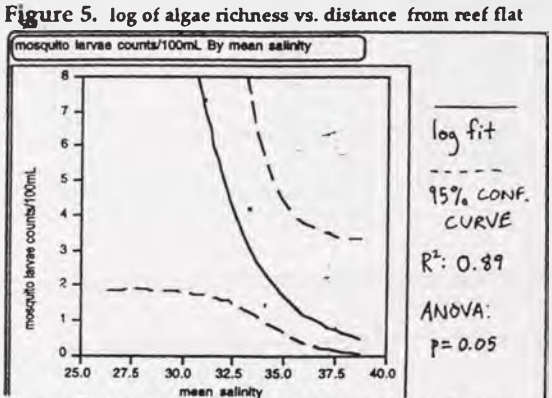


**Figure 7.** log of mosquito larvae density vs. mean salinity

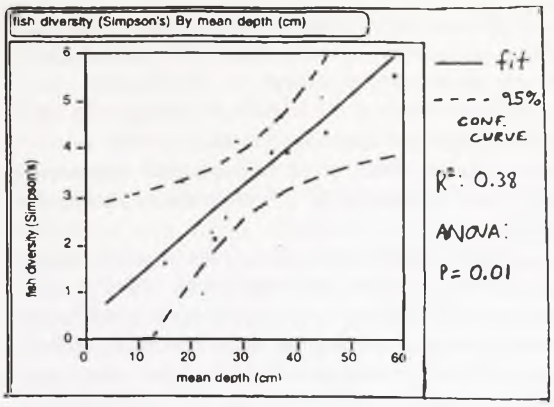


**Figure 8.** fish diversity vs. mean depth

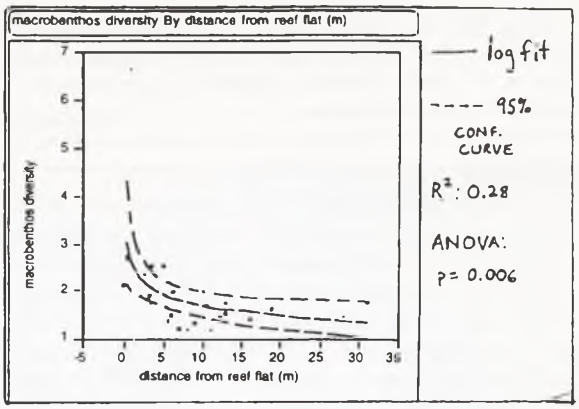


**Figure 9.** log of macrobenthos diversity vs. distance

*Organism tolerance levels.* A record of the extreme conditions that the sampled species were able to tolerate was compiled (Appendix F)

## Discussion

*Pool size/biota relationships*

As dimension analysis revealed, the topography of the conglomerate platform is such that the species-area relationship must be analyzed on a relatively short time scale. Although cylindrically shaped pools have a constant surface area, other pools in the system show drastic fluctuations in their dimensions in a day's tidal cycle. Data on area and species number can be regarded as secondary variates. The number of species reflects the population dynamics of the individual species, encompassing the four primary processes of birth, death, immigration and emigration (Kostitzin, 1939; Williamson, 1972). Although MacArthur and Wilson have been described as using an area *per se* hypothesis (McGuinness, 1984), they used area in lieu of better information: "Neither area nor elevation exerts a direct effect on numbers of species; rather, both are related to other factors, such as habitat diversity, which in turn controls species diversity" (MacArthur and Wilson 1967). In general, the number of species increases with increasing area, but only $R_{algae}$ and $R_{fish}$ supported this. Macrobenthos richness was more dependent on depth, implying that other variables are affecting habitat heterogeneity.

*Depth impacts*

Most suspension feeders are only able to feed when immersed by the tide or splashed by the waves, and a variety of browsing organisms are active mainly when recently exposed (Newell 1970). In the conglomerate system, $R_{algae}$, $D_{fish}$ (Figure 8), $R_{macrobenthos}$ and $D_{macrobenthos}$ all correlated with mean depth.

There are other implications of the depth of a given pool. Temperature was recorded for the surface water of pools. However, deeper pools have cooler water near their bottoms. This aspect of deep pools gives them an advantage other than being large; cooler microhabitats within pools give organisms the opportunity to migrate to more favorable conditions. The variance in depth of pools, a major indication of tidal inundation, decreases with distance from shore (Figure 10). This pattern further complicates the distance effect model on community structure. Also, anomalous situations occur in pools observed to reach zero depths. Fish and mosquito larvae never formed stable populations in these transient pools. While mean depth revealed apparently continuous gradients in community structure, zero depth levels completely excluded fish and mosquito larvae.

*Distance effects*

The effect of distance, when appreciable, was to depress the species-area effect. Islands distant from continents have fewer species than near ones, and the distance effect for a particular taxon is related to dispersal ability (Williamson, 1981). Richness (algae [figure 5], macrobenthos), diversity (fish, macrobenthos [figure 9]) and concentration (fish) all negatively correlated with distance from the reef flat. Physical factors were also tied with distance, offering a possible explanation for the biotic

effects. While depth varied less with distance from the reef flat (Figure 10), temperature (Figure 11) and salinity (Figure 12) positively correlated with distance.

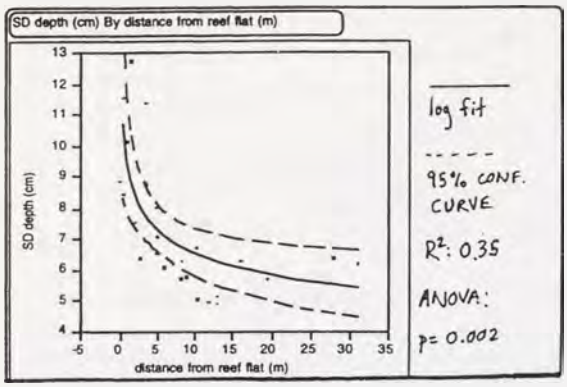


**Figure 10.** log of depth variance vs. distance from reef flat

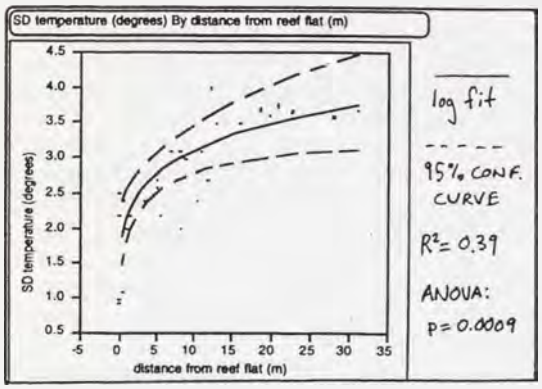


**Figure 11.** log of temperature variance vs. distance

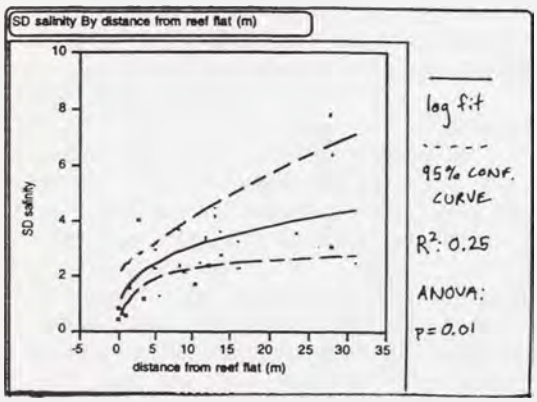


**Figure 12.** log of salinity variance vs. distance from reef flat

In a traditional tidal pool system, distance would also be connected with elevation. The conglomerate platform is horizontal in nature, thus reducing the impact of distance as an isolation mechanism. Personal observation showed that a relatively small vertical increase in tide could significantly change its horizontal breadth.

Some stable pools were observed to dry out (or nearly so) at extremely low tides. At extremely high tides (very rarely witnessed in 9 weeks of field operations), many pools became connected to the ocean and to each other, forming large composite pools (Appendix G). Extremely high tide observations give insight into introduction mechanisms and support the similar findings in biota of certain neighboring pools. What was never witnessed in this study was the effect of a large storm, which would undoubtedly inundate and connect a majority (if not all) of the conglomerate pools. This "superpool" would then fragment anew into isolated pools, with the return of milder ocean conditions.

*Temperature effects*

Another factor that may play a part in controlling the distance from shore at which a particular species is able to survive is the temperature extremes to which particular pools are subjected. The temperature of the seaward edge of the conglomerate platform approximates the sea temperature, whereas pools with less mixing approach the air temperature or may even exceed this on bare rock surfaces exposed to the sun (Newell 1970). The conglomerate pool system agreed with this temperature trend, with organism distribution being influenced. Algae diversity, fish concentration (Figure 6), and macrobenthos richness all decreased with mean temperature. The variance in temperature is another stress intertidal species must endure. Algae R, fish density, and macrobenthos D negatively correlated with variance in temperature.

A factor facilitating the tolerance of high environmental temperatures during the emersion period by intertidal and semi-terrestrial organisms may be the ability to withstand appreciable water loss. Transpiration allows organisms to remain at lower temperatures than their surroundings. In this respect the stresses of temperature and desiccation are interdependent, and resistance to one factor

increases the risk of damage by the other (Edney 1961, 1962).

*Salinity effects*

The salinity variations of rockpools is primarily determined by three factors: the amount of rainfall, the evaporation, and the frequency and extent of tidal inundation (Clark 1968). The degree to which such factors influence the salinity depends upon the level of the rockpool on the shore, the depth and surface area of the pool, and the immediate topography of the shore around the rockpool (for example, whether the pool is shaded from direct sunlight or from the evaporative action of the wind). Of all these factors, the major one controlling not only the extent but also the duration of salinity changes in rockpools is the access of seawater (Clark 1968). The conglomerate system matched this finding. What limited the access to sea water for conglomerate pools, though, was distance from shore (Figure 10). Pools located farther from shore experienced less variance in depth (i.e. tidal flux) and greater variance in salinity, accordingly. Mosquito larvae concentrations, in particular, appear connected with this pattern (Figure 7).

*pH extremes*

The maximal pH values occurred at approximately midday. Inundation by tide at this time would have a more pronounced effect on the rock pool than inundation at times when the pH approximates to that of the sea. The maximum variation in the pH depends primarily upon the balance between algae and animals (Newell 1970). While algae richness was lower in pools with high mean pH values, algae concentrations were larger. This effect is reasonable; with fewer species to compete for space, those species that do survive should be in higher densities (Newell 1970).

*Dissolved oxygen*

Dissolved oxygen content was difficult to measure accurately. Equipment problems only compounded the water agitating effects of wave and wind disturbances. Data is still valuable on a relative level, though. Data collected at night yielded dissolved oxygen levels much lower than in the day. It is feasible that the algae in the pools are responsible for this effect. Photosynthesis during the day keeps dissolved oxygen levels high. When the sun goes down, these levels then drop (Stephenson 1934).

Conclusion

This study suggests that the degree of tidal inundation is a key determinant of community structure. The more mixing that occurs in a pool, the more closely that habitat will match the reef flat. This is evident by increased diversity levels. On the other hand, isolation implies reduced diversity. A major influence on pool isolation is its distance from the reef flat. This clearly portrays the island-like quality of these pools. Physically, the distant pools are harder to colonize. Migration is restricted, and those organisms that are introduced into the distant pools find a harsher habitat to live in.

A substrate comparison between pools would supplement the physico-chemical analysis done in this study. The variability of a pool's physical structure has multiple implications. Habitat heterogeneity directly facilitates coexistence because species are able to tolerate different physical conditions, take refuge from their enemies, and reduce competition by exploiting different resources (Myers 1988). The size of channels between sand grains affects the rate of tidal inundation (Bruce 1928), which in turn will affect the physico-chemical nature of the pool. Sediment type has found to be a major factor in the overall composition of the benthic community (Bakri 1997). Applying Island Biogeography Theory to temporary pools would suggest that species richness and the total number of individuals should increase with pool size (March 1995). In addition, the larger pools should support more functional feeding groups than smaller pools. March's (1995) results, though, were "probably a reflection of greater microhabitat availability in the larger pools." A substrate analysis could test these effects on the conglomerate platform.

Future research would also yield insight into the resiliency of the pool populations over a longer time scale. The facet of the Theory on Island Biogeography that predicts that the number of species will remain at an equilibrium despite both immigration and extinction refers to a situation in which the environment remains relatively constant (Cox and Moore 1993). The conglomerate system however, is not static. In this study, a nine-week subset of the year did not shed light on seasonal changes or major

disturbances in the conglomerate pools. For instance, Lardner (1993) found that pool fish populations can show considerable variation in the numbers of component species over the long term (> 1 year), but species composition remains relatively constant. Dethier (1984) views disturbance in intertidal pools as "the stochastic factor overlying other, more predictable, community-structuring factors such as tidal height, pool size, wave exposure, and levels of herbivory, predation, and competition." No tidepool assemblange is "stable" over many generations. Rather, they seem to exist in a dynamic state where disturbances are an integral structuring factor (Dethier 1984). The species composition of a pool does not simply vary from pool to pool but also from time to time.

**Acknowledgments**

I would like to thank my friend Peter Vallejo for his field assistance on the motu. Debbie Woodward and David Lindberg were great aides in algae and gastropod identification, respectively. I am grateful for the previous work on the motu done by David Stoddart and Frank Murphy, which gave me great insight into the conglomerate platform. Bruce McGibbon and Victor Holmes constructively criticized various drafts of this paper. Finally, special thanks go to the graduate student instructors and professors of the Moorea class that made this project possible; it was logistically difficult at times but well worth the extra effort.

## APPENDICES

**Appendix A: Comparing accuracy of quadrat vs. complete sampling**

Quadrat method- **42.2%** coverage of substrate by algae (obtained from 6 quadrats)
**16** hermit crabs (from S.A. extrapolation)

Complete sampling- **49.08%** coverage by algae
**18** counted hermit crabs

Comparison- algae % coverage: **14%** discrepancy;
macrobenthos counts: **11%** discrepancy

data collected from "pool 24" on 10/24/98

**Appendix B: Pool dimension changes with tide**

*data sets were measured at low tide; mid tide; high tide

| pools | length (m) | width (m) | depth (cm) |
|---|---|---|---|
| 1 | 3.98; 4.2; 4.55 | 2.5; 2.5; 2.65 | 11.5; 36-43; 50-60 |
| 2 | 3.7; 4; 4.65 | 2.54; 4.7; 5.15 | 21.4; 47; 52.3 |
| 3 | 0; 0.8; 1.9 | 0; .7; 1.35 | 0; 4.5; 12.5 |
| 4 | 0; 0; 1.25 | 0; 0; .75 | 0; 0; 8 |
| 5W | 11.5; 11.8; 13.65 | 11.5; 11.8; 13.65 | 24.6; 26.2; 41 |
| 5E | 13 ; 17.4; 19.45 | 3.6; 3.75; 5.35 | 20.1; 22.9; 36 |
| 6 | 2.8; 3.2; 9.15 | 2.3; 2.5; 3.45 | 7.9; 11.7; 25.2 |
| 7 | 2.3 ; 2.7; 6.65 | 1.4; 1.8; 2.65 | 7.5; 11.6; 25 |
| 8 | 0; 1.65; 4.15 | 0; 1.05; 3.15 | 0; 8; 30.5 |
| 9 | 0.6; 1.35; 3.65 | 0.6; 1.05; 3.65 | 7.6; 25.7; 55 |
| 10 | 5.9; 6.3; 8.15 | 5.2; 5.7; 6.65 | 46.5; 53; 72 |
| 11 | 9; 9.2; 9.75 | 3.9; 4.3; 4.9 | 20.7; 26.7; 38 |
| 12 | 2.3; 2.5; 2.75 | 1.5; 1.95 | 9; 21; 32 |
| 13W | 4; 4.3; 4.65 | 3; 3.2; 3.75 | 11.5; 21.5; 32 |
| 13E | 0; 4.7; 6.15 | 0; 1.7; 2.65 | 0; 7; 18.5 |
| 24 | 6.3; 6.65; 8.15 | 2.7; 3; 3.85 | 16.8; 25.5; 37.3 |
| 14 | 5.1; 5.1; 9.15 | 1.72; 1.75; 2.65 | 19.8; 20.9; 54 |
| 15 | 5.1;6; 8.15 | 1.65; 2.25; 3.15 | 10.1; 17.2; 27.5 |
| 16 | 7; 7.6; 8.15 | 7; 7.5; 7.65 | 8.5; 12.5; 27.5 |
| 17 | 8.6; 8.6; 17 | 3.55; 3.85; 15 | 2; 3.7; 23 |
| 18 | 0.45; 1.15; 4.65 | 0.32; 1.05; 2.15 | 1; 10.4; 44.5 |
| 19 | 4; 4.3; 8.45 | 1.8; 3.6; 4.45 | 14; 22.5; 33.2 |
| 25 | 0 ; 3; 4.9 | 0; 1.4; 2.9 | 0; 7; 19 |
| 20 | 2.2; 3.3; 3.55 | 1.3; 2.9; 3.15 | 19; 32.5; 45 |
| 21 | 7; 7.4; 8.65 | 1.7; 1.7; 1.7 | 12-18; 15-21; 28-40 |
| 22 | 3.5; 5; 6.35 | 1.4; 2; 2.85 | 9.4; 19.8; 32 |
| 26 | 0; 2.3; 4.05 | 0; 1.25; 2.15 | 0; 11; 21 |
| 23 | 4.75; 4.8; 4.8 | 3; 3; 3 | 13.4; 22; 35.4 |

*pools 5, 13 were divided into two ellipses

Appendix C: pool distances to reef flat

| | reef flat | lagoon | neighbor 1 | neighbor 2 |
|---|---|---|---|---|
| 1 | 0.5 | | | |
| 2 | 6.2 | 1 | | |
| 3 | 2.6 | 6.9 | | |
| 4 | 5.5 | 3.6 | | |
| 5 | 5 | | 2.8 | 3.7 |
| 6 | 28 | | 2.8 | 4.5 |
| 7 | 31 | | 3.7 | 4.5 |
| 8 | 2 | | 3.5 | |
| 9 | 1.5 | | 11.2 | |
| 10 | 5 | | 11.2 | 16 |
| 11 | 10.5 | | 16 | |
| 12 | 8.3 | | 3 | |
| 13 | 8.2 | | 3 | |
| 24 | 8.9 | | | |
| 14 | 3.5 | | | |
| 15 | 12.2 | | | |
| 16 | 13 | | | |
| 17 | 6 | | 8 | |
| 18 | 7 | | 8 | |
| 19 | 11.8 | | 1.8 | |
| 25 | 13 | | 1.8 | |
| 20 | 0.5 | | 8 | |
| 21 | 0 | | 8 | |
| 22 | 16 | | 3 | |
| 26 | 11 | | 3 | |
| 23 | 3.5 | 0.5 | | |

*distances (in meters) from a pool to the reef flat, lagoon, or its nearest neighbor

## Appendix D: species counts in pools (fish, algae, macrobenthos guilds)

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 24 | 14 | 15 | 16 | 17 | 18 | 19 | 25 | 20 | 21 | 22 | 26 | 23 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Stegastes nigricans* | 5 | 2 | | | 50 | | | | | 8 | 8 | | | | | | 1 | | | 8 | | | 1 | | | |
| *Chrysiptera glauca* | | 8 | | | 12 | | | | | 10 | 7 | | 1 | 3 | | | 4 | | | 8 | | | | | | |
| *Acanthurus triostegus* | 20 | 1 | | | 5 | | | | | | | | | | 1 | | | | | | | 2 | 8 | | | |
| *Abudefduf sordidus* | 5 | 5 | | | 65 | | | | | 17 | 4 | | 1 | 1 | | | | | | 5 | | 5 | 1 | | | 1 |
| *Dascyllus aruanus* | | | | | | | | | | | | | | | | | | | | | | | 3 | | | |
| *Halichoeres ornatissimus* | | | | | | | | | | | | | | | | | | | | | | | 1 | | | |
| *Thalassoma hardwickei* | | | | | | | | | | | | | | | | | | | | | | 1 | 1 | | | |
| *Acanthurus lineatus* | | | | | | | | | | | | | | | | | | | | | | | 1 | | | |
| *Acanthurus nigrofuscus* | 1 | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Halichoeres marginatus* | 1 | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Chaetodeu lunula* | | | | | 1 | | | | | | | | | | | | | | | | | | | | | |
| *Myripristis berndti* | | | | | 1 | | | | | | | | | | | | | | | | | | | | | |
| *Rhinecanthus aculeatus* | | | | | | | | | | 2 | | | | | | | | | | | | | | | | |
| *Canthigaster bennetti* | | | | | | | | | | 1 | | | | | | | | | | | | | | | | |
| Fish A | 3 | | | | | | | | | | | | | | | | | | | | | 10 | | | | |
| Fish B | | | | | | | | | | | | | | | | | | | | | | | 2 | | | |
| Fish C | 1 | | | | | | | | | | | | | | | | | | | | | | | | | |
| Fish D | 1 | | | | | | | | | | | | | | | | | | | | | | | | | |
| Fish E | | | | | | | | | | 3 | | | | | | | | | | | | | | | | |
| Fish F | | 5 | | | 25 | | | | | 2 | | 7 | | | | | 2 | | | 10 | | 15 | | | | 1 |
| Fish G | 5 | 15 | | | 10 | | | | 12 | 4 | | | 5 | 2 | 2 | | 3 | | | 12 | | 25 | | | | 2 |
| Fish H | 1 | | | | | | | | | | | | | | | | | | | | | | | | | |
| Fish I | | | | | | | | | | | | | | | | | | | | | | | 1 | | | |
| Fish J | | 1 | | | | | | | | | | | | | | | | | | | | | 1 | | | |
| Fish K | | 12 | | | 3 | | | | | | | | | | | | | | | | | 5 | 40 | | | 12 |
| Fish L | | | | | | | | | | | | | | | | | | | | | | 8 | | | | |
| Fish M | | | | | 60 | | | | | 15 | | | | 3 | | | | | | | | | | | | 15 |
| Fish N | | | | | 10 | | | | | | | | | | | | | | | | | | | | | |
| Fish O | | | | | 2 | | | | | | | | | | | | | | | | | | | | | |
| Fish P | | | | | 1 | | | | | 1 | 2 | | 1 | 1 | | | | | | | | | | | | |
| Fish Q | | | | | 2 | | | | | | | | | | | | | | | | | | | | | |
| Fish R | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Mosquito Larvae | | | | | | | 0.8 | | | | | | | | | 7.4 | | 1.5 | | | | | | 4.2 | | |

*fish populations in the 26 pools; mosquito larvae are represented by counts/100mL (concentration)

| | Turbinaria sp. | | Valonia ventricosa | Algae A | Algae B | Algae C | Algae D | Algae E | Algae H | Algae I | Algae K | Algae Q | Algae R | Algae T | Algae U | Algae V | grazed algal film | Coral A | Coral B |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 0.25m2 | | 0.02 | 0.04 | 10cm2 | | | | 0.2 | 1m2 | | | | | | | 0.0017 | | 0.07 |
| 2 | | | 0.04 | 0.04 | 0.25m2 | 5cm2 | | | | | | | | | | | | | |
| 3 | | | | | | | | | | | | | | | | x | | | |
| 4 | | | | | | | | | | | | | | | | x | | | |
| 5 | | | | 0.01 | | | | 0.14 | | | 0.03 | | | | | | | | |
| 6 | | | | | | | | | | | | | | | | x | | | |
| 7 | | | | | | | | | | | | | | | | | | | |
| 8 | | | | | | | | | | | | | | | | x | | | |
| 9 | | | | | | | | | | | | | | | | x | | | |
| 10 | | | | | | | | | | | | 0.26 | | | | | | | |
| 11 | | | | | | | 0.14 | | | | | | | | | | | | |
| 12 | | | | | | | | | | | | | | | | x | | | |
| 13 | | | | | | | | 0.3 | | | | | | | | | | | |
| 24 | | | | | | | | 0.42 | | | | | | | | | | | |
| 14 | | | | | | | | 0.66 | | | | | | | | | | | |
| 15 | | | | | | | | 0.21 | | | | | 0.02 | | | | | | |
| 16 | | | | | | | | 0.55 | | | | | | | | | | | |
| 17 | | | | | | | | 0.22 | | | | | | | | | | | |
| 18 | | | | | | | | | | | | | | | | x | | | |
| 19 | | | | | | | | 0.09 | | | | | | | | | | | |
| 25 | | | | | | | | | | | | | | | | x | | | |
| 20 | | | | | | | | | | | | | | | | x | | | |
| 21 | 3 stalks | 10 | | | | | | | | | | | | 3m2 | 2m2 | | 0.05m2 | 0.2m2 | |
| 22 | | | | | | | | 0.3 | | | | | | | | | | | |
| 26 | | | | | | | | | | | | | | | | x | | | |
| 23 | | | | | | | | 0.57 | | | | | | | | | | | |

***algae percent coverage of substrate (as decimal), direct counts, and exact area in the 26 pools**

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 24 | 14 | 15 | 16 | 17 | 18 | 19 | 25 | 20 | 21 | 22 | 26 | 23 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Echinometra mathaei* | | 1 | | | | | | | | | 3 | | | | | | | | | | | | | | | |
| *Echinothrix calamanis* | | | | | | | | | | 1 | | | | | | | | | | | | | | | | |
| *Ophsocoma sp.* | 1 | 1 | | | 1 | | | | | | 1 | | | | | | | | | | | | | | | |
| *Holothuria leucopilata* | 1 | 2 | | | | | | | | 1 | 1 | | | | | | | | | | | | | | | |
| *Holothuria difficilis* | | | | | | | | | | | | | | | | | | | | | | | 1 | | | |
| *Echidna nebulosa* | 1 | 1 | | | 2 | | | | | | 1 | | | | | | | | | | | | | | | |
| *Nerita plicata* | 5 | 10 | 8 | 20 | 15 | | | 15 | 15 | 20 | | | | | | | | | 25 | 10 | | 3 | 25 | | | 25 |
| *Drupa mora* | | 5 | | | | | | | | | | | | | | | | | | | | 5 | 1 | | | |
| *Littorina obesa* | | | | | 25 | | | | | 5 | | 10 | | | | | | | | | | 30 | | | | |
| *Neria neglecta* | | | | | | 16 | 30 | 10 | | | 20 | 10 | 189 | | 75 | 51 | 60 | 94 | 50 | 62 | 10 | | | 138 | 68 | |
| *Fasciolaris sp.* | | 2 | | | | | | | | 11 | | | | | | | | | | 74 | | | | | | 5 |
| *Fasciolaris sp.* | | | | | | | | | | | | | | | | | | | | | | | | | | 5 |
| **Mac. A** | | 4 | | | | | | | | | | | | | | | | | | | | | | | | 10 |
| **Mac. B** | | 5 | 5 | 3 | | | | | | | 100 | 25 | 5 | | | | | | 1 | | | 5 | | | | |
| **Mac. C** | | | | | | | | | | | | | | | | | | | | 18 | | | | | | 5 |
| **Mac. D** | | | | | | | | | | | | | | | | | | | | | | 1 | | | | |
| **Mac. E** | | 2 | | | | | | | | | | | | | | | | | | | | | | | | |
| **Mac. F** | 6 | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Mac. G** | | 5 | 2 | 1 | 46 | 63 | 61 | | 3 | 28 | 10 | 50 | 16 | 16 | 150 | 13 | 125 | 26 | | 239 | 3 | 10 | 25 | 30 | 7 | 9 |

***macrobenthos populations in the 26 pools along the conglomerate platform**

Appendix E: Algae reference guide

Algae I: "spongy algal mat" containing filamentous blue-green algae, red filamentous algae, green uniseriate algae, pinnate diatoms
Algae C: *Caulerpa serrulata*
Algae P: "spongy algal mat" containing filamentous blue-green algae, mucalagonous matrix of blue-green algae, pinnate diatoms, double-celled green algae
Algae O: "spongy algal mat" with similar microscopic composition to Algae P
Algae Q: "brown-orange, spongy, stringy algae" containing filamentous blue-green algae, Foraminifera, double-celled green algae, pinnate diatoms
Algae E: "brown-orange ‡ lime-green spongy algae" containing filamentous green algae (one-cell thick, length = 13Xwidth, reticulated chloroplasts, branching filaments), unicellular golden brown algae
Algae T: "stringy, green, tubular green algae"; *Enteromorpha sp.*
Algae H: "orange, red, brown algal mat" containing filamentous blue-green algae, blue-green algal matrix, pinnate diatoms, double-celled green algae
Algae V: "spongy algal mat" containing filamentous blue-green algae, filamentous brown algae (one cell thick, intercalary growth, length = 4Xwidth)
Algae U: "burgandy, burly" red algae

*specimens of algae are in a reference collection at the UC Berkeley Herbarium (Valley Life Sciences Building, basement)

Appendix F: Organism tolerance levels

| species/pools | salinity | temperature | pH |
|---|---|---|---|
| **ALGAE** | | | |
| *Turbinaria sp.* | 35/38 | 25.9/30.1 | 7.7/8.6 |
| *Valonia ventricosa* | 36/37 | 26.8/30.1 | 8/8.6 |
| **FISH** | | | |
| *Stegastes nigricans* | 24/40 | 25.8/38.6 | 7.7/9.4 |
| *Chrysiptera glauca* | 24/41 | 25.8/38.6 | 7.7/9.4 |
| *Acanthurus triostegus* | 34/40 | 25.9/35.6 | 7.4/8.9 |
| *Abudefduf sordidus* | 27/41 | 24.6/37.3 | 7.4/8.9 |
| *Dascyllus aruanus* | 36/37 | 26.8/30.1 | 8/8.6 |
| *Halichoeres ornatissimus* | 36/37 | 26.8/30.1 | 8/8.6 |
| *Thalassoma hardwickei* | 36/38 | 26.3/34.5 | 7.4/8.7 |
| *Acanthurus lineatus* | 36/37 | 26.8/30.1 | 8/8.6 |
| *Acanthurus nigrofuscus* | 35/38 | 25.9/29.8 | 7.7/8.6 |
| *Halichoeres marginatus* | 35/38 | 25.9/29.8 | 7.7/8.6 |
| *Chaetodeu lunula* | 34/40 | 26.2/35.6 | 8/8.9 |
| *Myripristis berndti* | 34/40 | 26.2/35.6 | 8/8.9 |
| *Rhinecanthus aculeatus* | 30/40 | 26.7/35.6 | 7.9/8.8 |
| *Canthigaster bennetti* | 30/40 | 26.7/35.6 | 7.9/8.8 |
| **MACROBENTHOS** | | | |
| *Echinometra mathaei* | 30/38 | 26.2/35.1 | 7.8/8.6 |
| *Echinothrix calamanis* | 30/40 | 26.7/35.6 | 7.9/8.8 |
| *Ophsocoma sp.* | 30/38 | 25.9/35.6 | 7.7/8.9 |
| *Holothuria leucopilata* | 30/40 | 25.9/35.6 | 7.7/8.8 |
| *Holothuria difficilis* | 36/37 | 26.8/30.1 | 8/8.6 |
| *Echidna nebulosa* | 30/40 | 25.9/35.6 | 7.7/8.9 |
| *Nerita plicata* | 11.0/41 | 24.6/38.6 | 7.4/8.9 |
| *Drupa mora* | 36/38 | 26.2/34.5 | 7.4/8.7 |
| *Littorina obesa* | 30/40 | 26.2/35.6 | 7.4/8.9 |
| *Nerita neglecta* | 11.0/47 | 25.6/39.6 | 7.7/9.7 |
| *Fasciolaris sp.* | 26/40 | 24.6/35.8 | 7.6/8.8 |
| *Fasciolaris sp.* | 35/38 | 24.6/34.9 | 7.6/8.6 |
| hermit crabs | 22/47 | 24.6/39.6 | 7.4/9.7 |
| upside-down jellyfish | 35/38 | 24.6/34.9 | 7.6/8.6 |
| mosquito larvae | 22/47 | 25.9/39.6 | 7.8/9.3 |

***species environmental tolerance data, as measured during field operations**

**salinity units: parts per thousand**
**temperature units: degrees celcius**

**Appendix G: Witnessed pool interconnections**

pool-->reef flat: 1, 3, 5, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 19, 20, 21, 23, 24, 25
pool-->west lagoon: 2
pool-->east lagoon: 23
pool-->pool: 5-->6,7,8; 10-->11; 13-->24; 16-->17,18; 19-->25; 22-->26

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# Octopus Color Phenotypes: A Comparison Between *O. bocki* and *O. cyanea*

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ABSTRACT. Color phenotypes of *Octopus bocki* and *O. cyanea* were compared using visual observation and multivariate statistical analysis. Thirteen individuals were collected from the fringing reef crest of Cook's Bay, Moorea, French Polynesia. Tests were run with variable foreground color, background color, and light intensity, herein referred to as format. Four questions were addressed: 1) Will octopuses become cryptic to a given format? 2) Will octopuses of any species react similarly to environmental variations? 3) Will juveniles and adults of *O. bocki* demonstrate the same phenotypic range? 4) Will juvenile *O. cyanea* of different sizes (Small: comparable to juvenile *O. bocki*, and Large: comparable to adult *O. bocki*) demonstrate the same phenotypic range? Observed phenotypes are detailed in the complete data set including color and placement (e.g., mantle, arms, web, eyes), texture, and pattern. Both *O. bocki* and *O. cyanea* demonstrated complex phenotypic ranges including the ability to iridesce. However, ranges differed between the species. Neither species became cryptic during tests. Direct sunlight increased changes in appearance in both species. *O. cyanea* exhibited more variable texturing than *O. bocki*. *O. bocki* demonstrated variations in eye color, *O. cyanea* did not. Both species used only one phenotype while engaged in head first swimming. *O. bocki* juveniles and adults expressed the same phenotypic range. Similarly, both small and large juvenile *O. cyanea* demonstrated the same phenotypes. Iridescence may be a warning mechanism in this colorblind animal. Unique phenotypic ranges suggest niche partitioning between the species.

## Introduction

It is widely known that octopuses have the ability to change colors. However, few studies have concentrated on the differences in color phenotypic range between species. Holmes (Holmes, 1940 in Packard, 1995) documented that all octopuses of a single species can exhibit the same variety of patterns. In contrast, individuals of other polymorphic species, for example reptiles, fish, and butterflies cannot demonstrate the entire repertoire of patterns.

Octopuses can change not only color but also pattern, and texture. They change instantaneously, and can alter any or all of the elements listed above at any given moment. This independent alteration enables them to display a complex array of phenotypes.

These phenotypes are expressed using both active and passive tactics. Active expression is accomplished through expansion of chromatophore cells in radial muscle tissue. These cells are controlled by the suboesophageal ganglia and the optic lobes (Serini and Young, 1932; Dubas et al., 1986; in Ferguson et al., 1994). Passive expression occurs through a reflecting system, which may have evolved when early coleoid cephalopods lost their protective shell. The cells in this system are iridophores and leucophores, which lie in dermal layers below the chromatophores (Messenger 1974).

The combination of these systems allows the octopus that sees no color (Hanlon et al. 1994) to blend to a colored background. Active control of the chromatophores is limited to *intensity* rather than *color* matching. While the passive system adds color to the octopuses phenotype in the form of reflected incident light (Messenger, 1974).

My research on the fringing reef in Moorea, French Polynesia, contrasted the color variance of two species of octopus, *O. bocki* and *O. cyanea*. I compared the species in terms of color reaction in response to variable contrast and color.

*cyanea*. I compared the species in terms of color reaction in response to variable contrast and color. I then analyzed the data using multivariate statistics for species comparison. I also examined variance within each species by comparing adults and juveniles.

Typical phenotypes of *O. bocki* and *O. cyanea* are examined here by answering four questions. First, will octopuses become cryptic to a given format (Format is herein defined as the combination of experimental fore- and background)? Second, will octopuses collected in the same manner, from the same site react to environmental variations, such as substrate color, background color, contrast, and light intensity, with similar phenotypes? Third, will juveniles and adults of *O. bocki* demonstrate the same phenotypes? Fourth, will juveniles of different size classes of *O. cyanea* demonstrate the same phenotypes? In addition to these questions, lists of color phenotypes for both *O. cyanea* and *O. bocki* are documented.

## Materials and methods

*i. Study site*

Research was conducted at Gump Biological Research Station, Moorea French Polynesia. Moorea is part of the Society Archipelago at 17°30'S latitude and 149°50'W longitude, 25 km Northwest of Tahiti. All specimens were collected from the fringing reef of Cook's Bay directly in front of the research station, Pk11. This site was chosen for its close proximity to lab facilities and for the abundance of coral rubble.

*ii. Collection and Habitation*

Sampling and experimentation were conducted in October and November 1998. The animals were obtained by free diving for coral rubble in water 1-4m deep. All rubble was at least 10cm in diameter. The pieces were placed in a large container held at the surface. After filling the container it was brought to land for rubble sorting. The container was left to drain and to allow the animals the chance to emerge and settle to the bottom. After 10 minutes the rubble pieces were removed into a second container and animals were collected. At the same time, crabs were gathered as food for octopuses.

Animals were fed every day, or as often as they would eat. Crabs were selected according to size; octopuses were never given a crab with a carapace width larger than the length of their mantle. Crabs were left in the tanks for 24 hours, then removed if they were not eaten.

Individuals were kept for up to one month, each in its own aquarium. The tanks were outfitted with standpipes half the height of the tank to allow constant seawater flow while minimizing the chance for escape. If there were no tanks available, new individuals were kept in small jars, capacity of at least 8oz., and covered with netting. Seawater was changed daily.

*ii. Experimental Procedure*

Experiments were conducted during the day. Octopuses were placed in a jar with one net as test foreground. The jar was placed in a box, the test background. Two boxes were used, one lined with white paper and one lined with black. Each octopus was tested on four foreground nets in each box. The netting (holes ~1mm squared) was fashioned into cylinders which fit into the jar; they differed only in color: 1)green 2)grey 3)black 4)white and 5) control (no net). The top of the box was open to allow light and observation.

When tested against the 2 backgrounds both contrast (e.g. white net and black background) and non-contrast (e.g. white net and white background)and color (e.g. green net and black background) were tested.

An octopus was tested on one background with one net for 6 minutes total. First, the octopus was for observed 3 minutes in the shade, then for 2 minutes in the sun, and finally 1 minute more in the shade. The sunlight increased effect of contrast. After each 6-minute session the octopus was removed to a waiting tank. The tank was covered with a large box, and the octopus rested for 8 minutes.

This sequence was run on an individual 5 times in one day. The background (box) remained the same throughout, and the foreground (net color) was varied. The nets were always run in the same sequence: green, grey, black, white, and control. After the experiment the octopuses were fed. An individual was never tested 2 days in a row.

## Results

*i. General trends*

Octopuses exhibited many phenotypes. Most individuals exhibited the ability to change color, texture, and pattern. All animals demonstrated the ability to change the coloration of one section of their body without altering another. For example *O. bocki* might show one arm spotted white and clear and the other 7 arms entirely brown.

Another phenotype exhibited by *O. bocki* was clear arms with brown mantle and web. In addition an individual might add iridescent green spots to their whole body, just to their web, or just to their mantle, or to both. These examples are minimal descriptions of the abilities and ranges of phenotypes of both species. (A full data report is found in *Appendix A.*)

Shading was also used to express of patterns. Octopuses displayed various colors using the elements of contrast and intensity in their patternization. However, in order to simplify data for statistical analysis, variation in contrast and intensity are not included in data charts. In addition, although animals were observed and color change was documented for several minutes, data listed in the charts represents only the first phenotypic expression in each light environment.

*ii. Crypsis*

Although the test colors were within the range of their repertoires, the animals did not generally turn cryptic to match background. Discriminant function analyses showed no correlation between background, foreground, and light.

**Figure 1: Spearman correlation matrix: background, foreground and lighting for all species**

| | BACKGROUND | FOREGROUND | LIGHTING |
|---|---|---|---|
| BACKGROUND | 1.000 | | |
| FOREGROUND | 0.000 | 1.000 | |
| LIGHTING | 0.000 | 0.000 | 1.000 |
| MANTLE | 0.053 | -0.038 | -0.099 |
| ARMS | 0.023 | -0.063 | -0.058 |
| WEB | 0.013 | -0.036 | -0.076 |
| EYES | -0.032 | 0.154 | -0.009 |
| TEXTURE | -0.087 | 0.031 | -0.012 |
| IRIDESCENCE | 0.188 | -0.035 | -0.020 |
| PATTERN | -0.103 | -0.048 | -0.036 |
| SPOTTING | 0.059 | -0.069 | -0.135 |

*iii. Variance between species*

Discriminant function analyses were also used to compare phenotypic expression between *O. bocki* and *O. cyanea.* Those variables that provided the greatest discrimination between species were texture and iridescence.

**Figure 2: Canaonical discriminant functions**

| | |
|---|---|
| MANTLE | 0.207 |
| ARMS | -0.039 |
| WEB | 0.007 |
| EYES | 0.990 |
| TEXTURE | 2.231 |
| IRIDESCENCE | -0.326 |
| PATTERN | -0.083 |
| SPOTTING | -0.186 |

*O. bocki* individuals generally remained smooth, but they did exhibit rough texture on some occasions. In contrast, *O. cyanea* individuals used texture frequently. In addition *O. cyanea* expressed a shaggy texture never observed in *O. bocki*.

*O. bocki* used iridescence with a higher frequency than *O. cyanea*. In addition, although not separated in these analyses, *O. bocki* demonstrated a purple hued iridescence not observed in *O. cyanea*.

In both species, coloration correlated positively with all body parts except eyes. Correlations between body parts were higher in *O. cyanea* than *O. bocki*. Eyes were negatively correlated in *O. bocki* and no correlation existed for *O. cyanea* because *O. cyanea* only demonstrated one eye phenotype. Spearman correlation matrixes show the correlation of phenotypic expression according to body part.

**Figure 2: Spearman correlation matrixes of body parts**

**a) All species**

| | MANTLE | ARMS | WEB | EYES |
|---|---|---|---|---|
| MANTLE | 1.000 | | | |
| ARMS | 0.626 | 1.000 | | |
| WEB | 0.637 | 0.871 | 1.000 | |
| EYES | -0.025 | -0.195 | -0.219 | 1.000 |

**b) *O. bocki***

| | MANTLE | ARMS | WEB | EYES |
|---|---|---|---|---|
| MANTLE | 1.000 | | | |
| ARMS | 0.560 | 1.000 | | |
| WEB | 0.568 | 0.840 | 1.000 | |
| EYES | -0.215 | -0.253 | -0.288 | 1.000 |

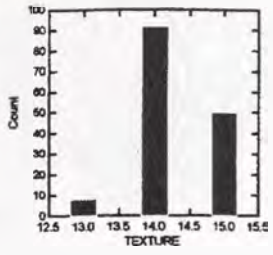
**c) *O. cyanea***

| | MANTLE | ARMS | WEB | EYES |
|---|---|---|---|---|
| MANTLE | 1.000 | | | |
| ARMS | 0.990 | 1.000 | | |
| WEB | 0.987 | 0.997 | 1.000 | |
| EYES | | | | |

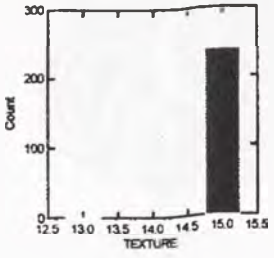
Repertoires varied between species. *O. cyanea* could exhibit a higher degree of texture than *O. bocki*. *O. cyanea* could raise small patches of skin and color their entire body with white and black dots to appear exactly like a sandflat. The most extreme texturing observed in *O. bocki* was rough, slightly ridged, skin. In contrast, *O. bocki* could change eye color. Three colors were exhibited: brown, turquoise and blue. *O. cyanea* never demonstrated eye color change.

**Figure 3: Texturing in *O. cyanea* vs. *O. bocki***

Texture key: 13 = rough 14 = shaggy 15 = smooth



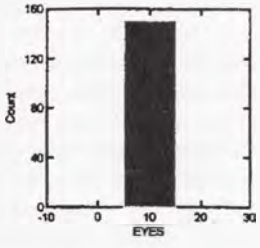

*O. cyanea*



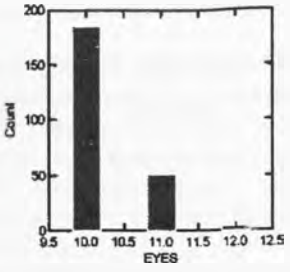

*O. bocki*

**Figure 4: Eye color *O. cyanea vs. O. bocki***

**Color key: 10 = brown 11 = turquoise 12 = blue**




*O. cyanea*




*O. bocki*

However, this variable was not statistically significant because brown was the predominant color expressed by both species.

One variable not statistically analyzed, which seemed to affect phenotype was position. For example, while engaging in headfirst swimming both species adopted smooth texture and no pattern. *O. bocki* always swam with a deep brown morphology while *O. cyanea* exhibited a mustard yellow color.

When placed in the sun, animals of both species exhibited more color changes in faster sequence and with higher intensity than they showed in the shade. While under direct sunlight, animals would often crawl around the jar and change colors as they moved.

Individuals of one species used the same general spotting designs. For instance, *O. cyanea* individuals consistently exhibited 4, brown, open rings down the length of their mantle.

**Figure 5: Example of a typical *O. cyanea* phenotype (Specimen j6)**

characteristic mantle pattern of brown rings

**Figure 6: Example of a typical *O. bocki* phenotype (Specimen j4)**

characteristic line of iridescent green dots

An analogous *O. bocki* example is 3 iridescent green dots also in a line the length of their mantle.

*iv. Comparison of juveniles and adults in O. bocki*

Differences in repertoires between juveniles and adults of a single species were not statistically significant. The Spearman correlation matrix shows the absence of correlation between age and every other variable tested.

**Figure 7: Spearman correlation matrix *O. bocki* age**

| | SPECIES | AGE |
|---|---|---|
| SPECIES | . | |
| AGE | . | 1.000 |
| BACKGROUND | . | 0.000 |
| FOREGROUND | . | 0.000 |
| LIGHTING | . | 0.000 |
| MANTLE | . | 0.258 |
| ARMS | . | 0.253 |
| WEB | . | 0.227 |
| EYES | . | -0.307 |
| TEXTURE | . | -0.084 |
| IRIDESCENCE | . | -0.176 |
| PATTERN | . | 0.162 |
| SPOTTING | . | -0.093 |

However, in general observation *O. bocki* juvenile were completely clear with a much higher frequency than adults were. Adults rarely became clear, but would often appear milky white.

*v. Comparison of juvenile O. cyanea size classes*

As in *O. bocki* age, the size class of *O. cyanea* did not determine phenotypic expression. Neither class, small or large, reacted differently to the variables tested.

**Figure 8: Spearman correlation matrix *O. cyanea*, age (as size class)**

| | SPECIES | AGE |
|---|---|---|
| SPECIES | . | |
| AGE | . | 1.000 |
| BACKGROUND | . | 0.000 |
| FOREGROUND | . | 0.000 |
| LIGHTING | . | 0.000 |
| MANTLE | . | 0.025 |
| ARMS | . | 0.035 |
| WEB | . | 0.025 |
| EYES | . | . |
| TEXTURE | . | -0.122 |
| IRIDESCENCE | . | -0.237 |
| PATTERN | . | 0.055 |
| SPOTTING | . | 0.016 |

## Discussion

*i. General trends*

Both species demonstrated iridescence. While only *O. bocki* demonstrated a purple iridescent hue, both *O. bocki* and *O. cyanea* showed the same arrangement of iridescent green spots along the length of their arms. Purple iridescence in *O. bocki* may indicate purple-blue chromatophores such as exists in two pelagic octopuses *Tremoctopus*, and *Argonauta* (Messenger, 1974). Green iridescence also seems to be controlled actively rather than passively because this phenotypic element was exhibited on all foregrounds not just green. Thus, iridescence may serve some function other than simple camouflage. Perhaps this ability serves as an instinctual warning mechanism for these colorblind animals.

*ii. Crypsis*

Animals did not become cryptic to experimental substrates. Although, preliminary observations assured that the octopuses could achieve phenotypes similar to the tests. Crypsis is generally considered the primary defense mechanism for cephalopods (Hanlon et al., 1994). Thus, the results of this experiment may indicate a secondary defense prompted by unnatural lab conditions.

In a study on *Octopus briareus* Hanlon and Wolterding state "once detected by a predator, they either flee, or use some sort of flash behavior to make a predator hesitate in its attack sequence (Hanlon et al., 1989). The described 'flash behavior' is similar to behavior observed here, where the octopuses most likely considered the observer a predator. As well as following the secondary defense explanation, these results support further the explanation of the use of iridescence in the previous section.

*iii. Variance between species*

*O. bocki* and *O. cyanea* demonstrated very different phenotypic ranges. This suggests chromatophore arrangement is significantly different. Unique ranges may imply changes in arrangement occurring through species evolution. One explanation for this repertoire variance is niche partitioning. Both species dwell in similar coral, however, *O. bocki* is nocturnal, while *O. cyanea* is diurnal. This may be different from Voight's findings that "[morphologic] characters contribute to shape variation in a seemingly random manner and do not indicate that ecological role is associated with shape" (Voight, 1993).

*iv. Comparison of juveniles and adults in O. bocki and comparison of juvenile O. cyanea size classes*

There were no significant differences in phenotypic expression between juveniles and adults, or juveniles of different size classes found. These data suggest that phenotypic schemes are not a learned phenomena. Rather, they must be instinctual and used by all individuals of a species from birth on. Alternatively, differences in body

patterns have been documented between hatchlings and adults in squid species *Sepia officinalis*. Perhaps there is a difference at birth that develops at a very early age and was not documented here because all specimens had already completed that stage of development.

## Conclusions

Although a lot of work has been done on cephalopods and their unique phenotypic abilities, there is much more to be done. Further work should include taxonomy especially with regard to the two systems of phenotypic expression. Also investigations with linking ecological niches and phenotypic variation may help determine evolutionary relationships between species. In addition, there is a large gap in the literature with regard to most pygmy species. Many species need to be further described, and studied in order to compare them to full size species.


## Acknowledgements

Thank you so much to Dave Lindberg and Jere Lipps for their support and inspiration in the field and in the classroom. Also, special thanks to Amy Lesen and Virginia Matzec for their boundless stamina and patience.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# Appendix A- Complete data set

Numerical Transformantion Key

| # | color | species | age/ size class | background | foreground | lighting | pattern | spots |
|---|---|---|---|---|---|---|---|---|
| 0 | absence | cyanea | juvenile / small | white | | | absence | absence |
| 1 | presence | bocki | adult / large | black | green | shade | bands | presence |
| 2 | clear | | | | grey | sun | rings | |
| 3 | white | | | | black | reshade | dipped | |
| 4 | cream | | | | white | | | |
| 5 | beige | | | | control | | | |
| 6 | creamy yellow | | | | | | | |
| 7 | yellow | | | | | | | |
| 8 | olive yellow | | | | | | | |
| 9 | light brown | | | | | | | |
| 10 | brown | | | | | | | |
| 11 | turquoise | | | | | | | |
| 12 | blue | | | | | | | |
| 13 | rough | | | | | | | |
| 14 | shaggy | | | | | | | |
| 15 | smooth | | | | | | | |

* denotes added texture, iridescense, or pattern on a specific body part. An explanation is given in the P+B4attern column

O1 (*O.cyanea* )

| | background | foreground | lighting | color mantle | arms | web | eyes | texture | pattern color | iridescence | pattern | spotting |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | white | green | shade | cream* | 4 cream* | 4 cream* | 4 brown | 10 smooth | 15 TOTAL- stoney: black, white, brown | 0 | 0 | 1 |
| 2 | | | sun | beige* | 5 beige* | 5 beige* | 5 brown | 10 smooth | 15 TOTAL- stoney: black, white, brown | 0 | 0 | 1 |
| 3 | | | reshade | cream | 4 cream* | 4 cream | 4 brown | 10 smooth | 15 ARMS- spots: irr.green | 1 | 0 | 1 |
| 4 | | grey | shade | cream* | 4 cream* | 4 cream* | 4 brown | 10 smooth | 15 TOTAL- stoney: black, white, brown | 0 | 0 | 1 |
| 5 | | | sun | yellow* | 7 yellow* | 7 yellow* | 7 brown | 10 smooth | 15 TOTAL- stoney: black, white, brown | 0 | 0 | 1 |
| 6 | | | reshade | yellow* | 7 yellow* | 7 yellow* | 7 brown | 10 smooth | 15 TOTAL- stoney: black, white, brown | 0 | 0 | 1 |
| 7 | | black | shade | cream* | 4 cream* | 4 cream* | 4 brown | 10 shaggy | 14 TOTAL- rings: black w/ white inside | 0 | 0 | 0 |
| 8 | | | sun | beige* | 5 beige* | 5 beige* | 5 brown | 10 shaggy | 14 TOTAL- rings: black w/ white inside | 0 | 2 | 0 |
| 9 | | | reshade | cream* | 4 cream* | 4 cream* | 4 brown | 10 shaggy | 14 TOTAL- rings: black w/ white inside | 0 | 2 | 0 |
| 10 | | white | shade | white* | 3 white* | 3 white* | 3 brown | 10 shaggy | 14 TOTAL- stoney: black, white, brown | 0 | 0 | 1 |
| 11 | | | sun | white | 3 white | 3 white | 3 brown | 10 smooth | 15 TOTAL- spots: white | 0 | 0 | 1 |
| 12 | | | reshade | yellow | 7 yellow | 7 yellow | 7 brown | 10 shaggy | 14 | 0 | 0 | 0 |
| 13 | | control | shade | cream* | 4 cream* | 4 cream* | 4 brown | 10 smooth | 15 TOTAL- stoney: black, white, brown | 0 | 0 | 1 |
| 14 | | | sun | beige* | 5 beige* | 5 beige* | 5 brown | 10 smooth | 15 TOTAL- stoney: black, white, brown | 0 | 0 | 1 |
| 15 | | | reshade | cream | 4 cream | 4 cream | 4 brown | 10 smooth | 15 | 0 | 0 | 0 |
| 16 | black | green | shade | yellow* | 7 yellow** | 7 yellow* | 7 brown | 10 shaggy | 14 TOTAL- stoney: black, white, brown/ ARMS- spots: irr.green | 1 | 0 | 1 |
| 17 | | | sun | cream* | 4 cream | 4 cream | 4 brown | 10 rough | 13 MANTLE- rings: brown | 0 | 2 | 0 |
| 18 | | | reshade | cream* | 4 cream | 4 cream | 4 brown | 10 rough | 13 MANTLE- rings: brown | 0 | 2 | 0 |
| 19 | | grey | shade | yellow | 7 yellow | 7 yellow | 7 brown | 10 shaggy | 14 | 0 | 0 | 0 |
| 20 | | | sun | olive yellow | 8 olive yellow* | 8 olive yellow | 8 brown | 10 shaggy | 14 ARMS- spots: irr.green | 1 | 0 | 0 |
| 21 | | | reshade | yellow* | 7 yellow* | 7 yellow* | 7 brown | 10 shaggy | 14 TOTAL- spots: white | 0 | 0 | 1 |
| 22 | | black | shade | olive yellow* | 8 olive yellow* | 8 olive yellow* | 8 brown | 10 shaggy | 14 TOTAL- spots: white | 0 | 0 | 1 |
| 23 | | | reshade | olive yellow* | 8 olive yellow* | 8 olive yellow* | 8 brown | 10 shaggy | 14 TOTAL- spots: white | 0 | 0 | 1 |
| 24 | | | sun | brown* | 10 brown* | 10 brown* | 10 brown | 10 shaggy | 14 ARMS- spots: irr.green | 1 | 0 | 0 |
| 25 | | white | shade | cream | 4 cream | 4 cream | 4 brown | 10 smooth | 15 | 0 | 0 | 0 |
| 26 | | | sun | brown | 10 brown* | 10 brown | 10 brown | 10 smooth | 15 ARMS- spots: irr.green | 1 | 0 | 1 |
| 27 | | | reshade | yellow | 7 yellow | 7 yellow | 7 brown | 10 smooth | 15 | 0 | 0 | 0 |
| 28 | | control | shade | brown* | 10 brown* | 10 brown* | 10 brown | 10 smooth | 15 TOTAL- stoney: black, white, brown | 0 | 0 | 1 |
| 29 | | | sun | creamy yellow | 6 creamy yellow* | 6 creamy yellow | 6 brown | 10 rough | 13 ARMS- spots: irr.green | 1 | 0 | 1 |
| 30 | | | reshade | brown* | 10 brown* | 10 brown* | 10 brown | 10 smooth | 15 TOTAL- stoney: black, white, brown | 0 | 0 | 1 |

O2 (*O.cyanea* )

| | background | foreground | lighting | color | | | | | texture | | | pattern | iridescence | pattern | spotting |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | mantle | | arms | | web | eyes | | | color | | | |
| 1 | white | green | shade | creamy yellow | 6 | creamy yellow* | 6 | creamy yellow | 6 brown | 10 | smooth | 15 ARMS- spots: brown | 0 | 0 | 1 |
| 2 | | | sun | yellow | 7 | yellow* | 7 | yellow | 7 brown | 10 | shaggy | 14 ARMS- spots: irr.green/ MANTLE- spots: brown | 1 | 0 | 1 |
| 3 | | | reshade | yellow | 7 | yellow* | 7 | yellow | 7 brown | 10 | shaggy | 14 ARMS- spots: irr.green/ MANTLE- spots: brown | 1 | 0 | 1 |
| 4 | | grey | shade | yellow | 7 | yellow* | 7 | yellow | 7 brown | 10 | shaggy | 14 ARMS- rings: brown | 0 | 2 | 0 |
| 5 | | | sun | olive yellow | 8 | olive yellow* | 8 | yellow | 7 brown | 10 | shaggy | 14 ARMS- rings: brown | 0 | 2 | 0 |
| 6 | | | reshade | olive yellow | 8 | olive yellow* | 8 | yellow | 7 brown | 10 | shaggy | 14 ARMS- rings: brown | 0 | 2 | 0 |
| 7 | | black | shade | yellow** | 7 | yellow* | 7 | yellow* | 7 brown | 10 | rough | 13 TOTAL- spots: brown/ MANTLE-lines: brown | 0 | 0 | 1 |
| 8 | | | sun | olive yellow* | 8 | olive yellow* | 8 | olive yellow* | 8 brown | 10 | rough | 13 TOTAL- spots: black | 0 | 0 | 1 |
| 9 | | | reshade | olive yellow* | 8 | olive yellow* | 8 | olive yellow* | 8 brown | 10 | rough | 13 TOTAL- spots: black | 0 | 0 | 1 |
| 10 | | white | shade | yellow* | 7 | yellow* | 7 | yellow* | 7 brown | 10 | shaggy | 14 TOTAL- spots: white | 0 | 0 | 1 |
| 11 | | | sun | olive yellow* | 8 | olive yellow* | 8 | olive yellow* | 8 brown | 10 | shaggy | 14 TOTAL- stoney: black, white, brown | 0 | 0 | 1 |
| 12 | | | reshade | yellow* | 7 | yellow* | 7 | yellow* | 7 brown | 10 | shaggy | 14 TOTAL- stoney: black, white, brown | 0 | 0 | 1 |
| 13 | | control | shade | white | 3 | white | 3 | white | 3 brown | 10 | shaggy | 14 | 0 | 0 | 0 |
| 14 | | | sun | white | 3 | white* | 3 | white | 3 brown | 10 | smooth | 15 ARMS- dipped: brown | 0 | 3 | 0 |
| 15 | | | reshade | cream | 4 | cream | 4 | cream | 4 brown | 10 | shaggy | 14 | 0 | 0 | 0 |
| 16 | black | green | shade | yellow | 7 | yellow | 7 | yellow | 7 brown | 10 | smooth | 15 | 0 | 0 | 0 |
| 17 | | | sun | cream | 4 | cream | 4 | cream | 4 brown | 10 | shaggy | 14 | 0 | 0 | 0 |
| 18 | | | reshade | cream | 4 | cream | 4 | cream | 4 brown | 10 | shaggy | 14 | 0 | 0 | 0 |
| 19 | | grey | shade | cream* | 4 | cream | 4 | cream | 4 brown | 10 | shaggy | 14 MANTLE- rings: brown | 0 | 2 | 0 |
| 20 | | | sun | cream* | 4 | cream | 4 | cream | 4 brown | 10 | shaggy | 14 MANTLE- rings: brown | 0 | 2 | 0 |
| 21 | | | reshade | cream* | 4 | cream | 4 | cream | 4 brown | 10 | shaggy | 14 MANTLE- rings: brown | 0 | 2 | 0 |
| 22 | | black | shade | brown* | 10 | brown* | 10 | brown* | 10 brown | 10 | shaggy | 14 TOTAL- stoney: black, white, brown | 0 | 0 | 0 |
| 23 | | | sun | brown** | 10 | brown** | 10 | brown** | 10 brown | 10 | shaggy | 14 TOTAL- stoney: white, black, brown/ MANTLE- rings: brown/ ARMS- spots:irr green | 1 | 2 | 1 |
| 24 | | | reshade | brown** | 10 | brown** | 10 | brown** | 10 brown | 10 | shaggy | 14 TOTAL- stoney: white, black, brown/ MANTLE- rings: brown/ ARMS- spots:irr green | 1 | 2 | 1 |
| 25 | | white | shade | cream | 4 | cream | 4 | cream | 4 brown | 10 | shaggy | 14 | 0 | 0 | 0 |
| 26 | | | sun | cream | 4 | cream | 4 | cream | 4 brown | 10 | shaggy | 14 | 0 | 0 | 0 |
| 27 | | | reshade | cream | 4 | cream | 4 | cream | 4 brown | 10 | shaggy | 14 | 0 | 0 | 0 |
| 28 | | control | shade | brown* | 10 | brown* | 10 | brown* | 10 brown | 10 | shaggy | 14 TOTAL- spots: white, black | 0 | 0 | 1 |
| 29 | | | sun | cream | 4 | cream* | 4 | cream | 4 brown | 10 | rough | 13 ARMS- spots: irr.green | 1 | 0 | 1 |
| 30 | | | reshade | brown* | 10 | brown* | 10 | brown* | 10 brown | 10 | shaggy | 14 TOTAL- spots: white, black | 0 | 0 | 1 |

O3 (*O.bocki*)

| | background | foreground | lighting | color | | | | texture | | pattern | iridescence | pattern | spotting |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | mantle | arms | web | eyes | | | color | | | |
| 1 | white | green | shade | brown* | 10 brown* | 10 brown* | 10 brown | 10 smooth | 15 | TOTAL- spots: white | 0 | 0 | 1 |
| 2 | | | sun | brown* | 10 brown* | 10 brown* | 10 brown | 10 smooth | 15 | TOTAL- hue: irr.purple | 1 | 0 | 0 |
| 3 | | | reshade | brown | 10 brown* | 10 brown | 10 turquoise | 10 smooth | 15 | ARMS- bands: clear, brown | 0 | 1 | 0 |
| 4 | | grey | shade | brown | 10 brown* | 10 brown | 10 brown | 10 smooth | 15 | ARMS- bands: clear, brown | 0 | 1 | 0 |
| 5 | | | sun | brown | 10 brown* | 10 brown | 10 brown | 10 smooth | 15 | ARMS- bands: clear, brown | 0 | 1 | 0 |
| 6 | | | reshade | brown | 10 brown* | 10 brown | 10 brown | 10 smooth | 15 | ARMS- bands: clear, brown | 0 | 1 | 0 |
| 7 | | black | shade | brown* | 10 brown** | 10 brown* | 10 brown | 10 smooth | 15 | TOTAL- spots: irr.green/ ARMS- bands: clear, brown | 1 | 1 | 1 |
| 8 | | | sun | brown* | 10 brown** | 10 brown* | 10 brown | 10 smooth | 15 | TOTAL- spots: irr.green/ ARMS- bands: clear, brown | 1 | 1 | 1 |
| 9 | | | reshade | brown* | 10 brown** | 10 brown* | 10 brown | 10 smooth | 15 | TOTAL- spots: irr.green/ ARMS- bands: clear, brown | 1 | 1 | 1 |
| 10 | | white | shade | brown | 10 brown | 10 brown | 10 brown | 10 smooth | 15 | | 0 | 0 | 0 |
| 11 | | | sun | brown | 10 brown | 10 brown | 10 brown | 10 smooth | 15 | | 0 | 0 | 0 |
| 12 | | | reshade | brown | 10 brown | 10 brown | 10 brown | 10 smooth | 15 | | 0 | 0 | 0 |
| 13 | | control | shade | light brown | 9 brown* | 10 brown | 10 brown | 10 smooth | 15 | ARMS- bands: clear, brown | 0 | 1 | 0 |
| 14 | | | sun | brown* | 10 brown** | 10 brown | 10 brown | 10 smooth | 15 | TOTAL- hue: irr.purpleARMS- bands: clear, brown | 1 | 1 | 0 |
| 15 | | | reshade | brown | 10 clear | 2 clear | 2 brown | 10 smooth | 15 | | 0 | 0 | 0 |
| 16 | black | green | shade | brown* | 10 brown* | 10 brown* | 10 brown | 10 smooth | 15 | TOTAL- spots: clear | 1 | 0 | 1 |
| 17 | | | sun | brown* | 10 brown | 10 brown | 10 brown | 10 smooth | 15 | MANTLE- hue: irr.purple | 1 | 0 | 0 |
| 18 | | | reshade | brown* | 10 clear | 2 clear | 2 brown | 10 smooth | 15 | MANTLE- hue: irr.purple | 0 | 0 | 0 |
| 19 | | grey | shade | brown | 10 brown* | 10 brown | 10 brown | 10 smooth | 15 | ARMS- bands: clear, brown | 1 | 1 | 0 |
| 20 | | | sun | brown* | 10 brown** | 10 brown* | 10 brown | 10 smooth | 15 | TOTAL- hue: irr.purple/ ARMS- bands: clear, brown | 0 | 1 | 0 |
| 21 | | | reshade | brown | 10 brown* | 10 brown | 10 brown | 10 smooth | 15 | ARMS- bands: clear, brown | 0 | 1 | 0 |
| 22 | | black | shade | brown* | 10 clear | 2 clear | 2 brown | 10 smooth | 15 | MANTLE- spots: irr.green | 1 | 0 | 1 |
| 23 | | | sun | brown** | 10 clear*** | 2 clear** | 2 brown | 10 smooth | 15 | TOTAL- hue: irr.purple/ TOTAL- spots: irr.green/ ARMS- bands: clear, brown | 1 | 1 | 1 |
| 24 | | | reshade | brown | 10 clear* | 2 clear | 2 brown | 10 smooth | 15 | ARMS- spots: irr.green | 1 | 0 | 1 |
| 25 | | white | shade | brown* | 10 brown* | 10 brown* | 10 brown | 10 smooth | 15 | TOTAL- spots: clear | 0 | 0 | 1 |
| 26 | | | sun | brown* | 10 brown** | 10 brown* | 10 brown | 10 smooth | 15 | TOTAL- spots: clear/ ARMS- bands: clear, brown | 0 | 1 | 1 |
| 27 | | | reshade | brown | 10 brown | 10 brown | 10 brown | 10 smooth | 15 | | 0 | 0 | 0 |
| 28 | | control | shade | brown* | 10 brown** | 10 brown* | 10 brown | 10 smooth | 15 | TOTAL- spots: clear/ ARMS- bands: clear, brown | 0 | 1 | 1 |
| 29 | | | sun | brown** | 10 brown | 10 brown** | 10 brown | 10 smooth | 15 | M & A- spots: irr.green/ M & A- hue: irr.purple | 1 | 0 | 1 |
| 30 | | | reshade | clear* | 2 clear* | 2 clear* | 2 brown | 10 smooth | 15 | TOTAL- spots: irr.green | 1 | 0 | 1 |

O4 (*O bocki* )

| | background | foreground | lighting | color | | | | | texture | | pattern | iridescence | pattern | spotting |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | mantle | | arms | | web | | eyes | | color | | | |
| 1 | white | green | shade | brown | 10 | brown* | 10 | brown | 10 | brown | 10 rough | 13 ARMS- bands: brown, clear | 0 | 1 | 0 |
| 2 | | | sun | brown* | 10 | brown* | 10 | brown* | 10 | brown | 10 smooth | 15 MANTLE & WEB-hue: irr.purple/ ARMS- bands: brown, clear | 1 | 1 | 0 |
| 3 | | | reshade | brown | 10 | light brown | 9 | clear | 9 | brown | 10 smooth | 15 | 0 | 0 | 0 |
| 4 | | grey | shade | brown | 10 | brown* | 10 | brown | 10 | brown | 10 smooth | 15 ARMS- bands: brown, clear | 0 | 1 | 0 |
| 5 | | | sun | brown* | 10 | brown | 10 | brown* | 10 | brown | 10 smooth | 15 MANTLE- hue: irr.purple/ WEB- spots: clear | 1 | 0 | 1 |
| 6 | | | reshade | white | 3 | white | 3 | white | 3 | brown* | 10 smooth | 15 EYES- tint: blue | 0 | 0 | 0 |
| 7 | | black | shade | brown | 10 | brown* | 10 | brown | 10 | brown | 10 smooth | 15 ARMS- bands: brown, clear | 0 | 1 | 0 |
| 8 | | | sun | brown* | 10 | brown* | 10 | brown* | 10 | brown | 10 smooth | 15 TOTAL- hue: irr.purple | 1 | 0 | 0 |
| 9 | | | reshade | light brown | 9 | light brown | 9 | light brown | 9 | brown | 10 smooth | 15 | 0 | 0 | 0 |
| 10 | | white | shade | brown | 10 | brown* | 10 | brown | 10 | brown | 10 smooth | 15 ARMS- bands: brown, clear | 0 | 1 | 0 |
| 11 | | | sun | brown* | 10 | brown* | 10 | brown* | 10 | brown | 10 smooth | 15 TOTAL- hue: irr.purple | 1 | 0 | 0 |
| 12 | | | reshade | brown* | 10 | brown* | 10 | brown* | 10 | brown | 10 smooth | 15 TOTAL- hue: irr.purple | 1 | 0 | 0 |
| 13 | | control | shade | brown | 10 | brown* | 10 | brown | 10 | brown | 10 smooth | 15 ARMS- bands: brown, clear | 0 | 1 | 0 |
| 14 | | | sun | brown | 10 | clear | 2 | clear | 2 | brown | 10 smooth | 15 | 0 | 0 | 0 |
| 15 | | | reshade | brown | 10 | light brown | 9 | light brown | 9 | brown | 10 smooth | 15 | 0 | 0 | 0 |
| 16 | black | green | shade | brown** | 10 | brown** | 10 | brown** | 10 | brown | 10 smooth | 15 TOTAL- hue: irr.purple/ T- spots: irr.green | 1 | 0 | 1 |
| 17 | | | sun | brown** | 10 | brown** | 10 | brown** | 10 | brown | 10 smooth | 15 TOTAL- hue: irr.purple/ T- spots: irr.green | 1 | 0 | 1 |
| 18 | | | reshade | white | 3 | white | 3 | white | 3 | turquoise | 10 smooth | 15 | 0 | 0 | 0 |
| 19 | | grey | shade | brown* | 10 | brown* | 10 | brown* | 10 | brown | 10 smooth | 15 TOTAL- hue: irr.purple | 1 | 0 | 0 |
| 20 | | | sun | brown* | 10 | clear | 2 | clear | 2 | brown | 10 smooth | 15 MANTLE- hue: irr.purple | 1 | 0 | 0 |
| 21 | | | reshade | white | 3 | white | 3 | white | 3 | turquoise | 10 smooth | 15 | 0 | 0 | 0 |
| 22 | | black | shade | brown | 10 | brown | 10 | brown | 10 | brown | 10 smooth | 15 | 0 | 0 | 0 |
| 23 | | | sun | brown* | 10 | brown* | 10 | brown* | 10 | brown | 10 smooth | 15 TOTAL- spots: irr.green | 1 | 0 | 1 |
| 24 | | | reshade | white | 3 | white | 3 | white | 3 | turquoise | 10 smooth | 15 | 0 | 0 | 0 |
| 25 | | white | shade | brown | 10 | brown* | 10 | brown | 10 | brown | 10 smooth | 15 ARMS- bands: brown, clear | 0 | 1 | 0 |
| 26 | | | sun | brown** | 10 | brown* | 10 | brown | 10 | brown | 10 smooth | 15 MANTLE- hue: irr.purple/ M- spots: irr.green/ ARMS- bands: clear, brown | 1 | 1 | 1 |
| 27 | | | reshade | brown** | 10 | brown* | 10 | brown | 10 | brown | 10 smooth | 15 MANTLE- hue: irr.purple/ M- spots: irr.green/ ARMS- bands: clear, brown | 1 | 1 | 1 |
| 28 | | control | shade | brown* | 10 | brown* | 10 | brown* | 10 | brown | 10 smooth | 15 TOTAL- spots: irr.green | 1 | 0 | 1 |
| 29 | | | sun | brown* | 10 | brown* | 10 | brown* | 10 | brown | 10 smooth | 15 MANTLE & WEB-hue: irr.purple/ ARMS- bands: brown, clear | 1 | 1 | 0 |
| 30 | | | reshade | white | 3 | white | 3 | white | 3 | turquoise | 10 smooth | 15 | 0 | 0 | 0 |

O5 (*O.bocki*)

| | background | foreground | lighting | color | | | | | | | | texture | pattern | iridescence | pattern | spotting |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | mantle | | arms | | web | | eyes | | | color | | | |
| 1 | white | green | shade | brown* | 10 | brown* | 10 | brown* | 10 | brown | 10 | smooth | 15 TOTAL- spots: clear | 0 | 0 | 1 |
| 2 | | | sun | brown** | 10 | brown** | 10 | brown** | 10 | brown | 10 | smooth | 15 TOTAL- spots: white/ TOTAL- hue: irr.purple | 1 | 0 | 1 |
| 3 | | | reshade | brown | 10 | clear | 2 | clear | 2 | brown | 10 | smooth | 15 | 0 | 0 | 0 |
| 4 | | grey | shade | brown | 10 | brown* | 10 | brown | 10 | brown | 10 | smooth | 15 ARMS- bands: clear, brown | 0 | 1 | 0 |
| 5 | | | sun | brown* | 10 | brown** | 10 | brown* | 10 | brown | 10 | smooth | 15 TOTAL- hue: irr.purple/ ARMS- bands: clear, brown | 1 | 1 | 0 |
| 6 | | | reshade | brown* | 10 | brown** | 10 | brown* | 10 | brown | 10 | smooth | 15 TOTAL- hue: irr.purple/ ARMS- bands: clear, brown | 1 | 1 | 0 |
| 7 | | black | shade | brown | 10 | brown* | 10 | brown | 10 | brown | 10 | smooth | 15 ARMS- bands: clear, brown | 0 | 1 | 0 |
| 8 | | | sun | brown** | 10 | brown** | 10 | brown** | 10 | brown* | 10 | smooth | 15 TOTAL- hue: irr.purple/ TOTAL- spots: irr.green/ EYES- tint: irr.green | 1 | 0 | 1 |
| 9 | | | reshade | brown** | 10 | brown** | 10 | brown** | 10 | brown* | 10 | smooth | 15 TOTAL- hue: irr.purple/ TOTAL- spots: irr.green/ EYES- tint: irr.green | 1 | 0 | 1 |
| 10 | | white | shade | brown | 10 | brown* | 10 | clear | 2 | brown | 10 | smooth | 15 ARMS- bands: clear, brown | 0 | 1 | 0 |
| 11 | | | sun | brown* | 10 | clear | 2 | clear | 2 | brown | 10 | smooth | 15 MANTLE- hue: irr.purple | 1 | 0 | 0 |
| 12 | | | reshade | brown* | 10 | clear | 2 | clear | 2 | brown | 10 | smooth | 15 MANTLE- hue: irr.purple | 1 | 0 | 0 |
| 13 | | control | shade | brown* | 10 | brown* | 10 | brown* | 10 | brown | 10 | smooth | 15 TOTAL- hue: irr.purple/ TOTAL- spots: clear | 1 | 0 | 1 |
| 14 | | | sun | brown* | 10 | brown* | 10 | brown* | 10 | turquoise | 11 | smooth | 15 TOTAL- spots: clear | 0 | 0 | 1 |
| 15 | | | reshade | brown | 10 | brown* | 10 | clear | 2 | brown | 10 | smooth | 15 ARMS- bands: clear, brown | 0 | 1 | 0 |
| 16 | black | green | shade | brown* | 10 | brown* | 10 | brown* | 10 | brown | 10 | smooth | 15 MANTLE- hue: irr.purple/ ARMS- bands: clear, brown/ WEB- spots: irr.green | 1 | 1 | 1 |
| 17 | | | sun | brown* | 10 | brown* | 10 | brown* | 10 | brown | 10 | smooth | 15 TOTAL- hue: irr.purple/ TOTAL- spots: clear | 1 | 0 | 1 |
| 18 | | | reshade | brown* | 10 | light brown* | 9 | brown | 10 | brown | 10 | smooth | 15 MANTLE- spots: clear/ ARMS- bands: clear, brown | 0 | 1 | 1 |
| 19 | | grey | shade | brown** | 10 | brown** | 10 | brown** | 10 | brown* | 10 | smooth | 15 TOTAL- hue: irr.purple/ TOTAL- spots: irr.green/ EYES- tint: irr.green | 1 | 0 | 1 |
| 20 | | | sun | brown* | 10 | brown* | 10 | brown* | 10 | brown* | 10 | smooth | 15 MANTLE- hue: irr.purple/ EYES- tint- green | 1 | 0 | 0 |
| 21 | | | reshade | brown | 10 | clear | 2 | brown | 10 | brown | 10 | smooth | 15 | 0 | 0 | 0 |
| 22 | | black | shade | brown* | 10 | clear | 2 | brown* | 10 | brown | 10 | smooth | 15 MANTLE- hue: irr.purple/ WEB- spots: irr.green | 1 | 0 | 1 |
| 23 | | | sun | brown** | 10 | brown | 10 | brown** | 10 | brown | 10 | smooth | 15 MANTLE & WEB- hue: irr.purple/ M & W- spots: irr.green | 1 | 0 | 1 |
| 24 | | | reshade | brown | 10 | brown* | 10 | brown | 10 | brown | 10 | smooth | 15 ARMS- bands: clear, brown | 0 | 1 | 0 |
| 25 | | white | shade | white | 10 | white | 3 | white | 3 | blue | 12 | smooth | 15 | 0 | 0 | 0 |
| 26 | | | sun | brown* | 10 | brown* | 10 | clear* | 2 | turquoise | 11 | smooth | 15 TOTAL- hue: irr.purple | 1 | 0 | 0 |
| 27 | | | reshade | white | 10 | white | 3 | white | 3 | blue | 12 | smooth | 15 | 0 | 0 | 0 |
| 28 | | control | shade | brown* | 10 | brown* | 10 | brown* | 10 | brown | 10 | smooth | 15 TOTAL- hue: irr.purple | 1 | 0 | 0 |
| 29 | | | sun | brown* | 10 | brown* | 10 | brown* | 10 | brown | 10 | smooth | 15 TOTAL- spots: irr.green | 1 | 0 | 1 |
| 30 | | | reshade | clear* | 10 | clear* | 2 | clear* | 2 | blue | 12 | smooth | 15 TOTAL- spots: irr.green | 1 | 0 | 1 |

J1 (*O. bocki*)

| | background | foreground | lighting | color | | | | | | | texture | | pattern | iridescence | pattern | spotting |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | mantle | | arms | | web | | eyes | | | color | | | |
| 1 | white | green | shade | brown* | 10 | brown* | 10 | brown* | 10 | brown | 10 | smooth 15 | TOTAL-spots: brown | 0 | 0 | 1 |
| 2 | | | sun | brown | 10 | brown* | 10 | clear | 2 | brown | 10 | smooth 15 | ARMS-bands: brown, clear | 0 | 1 | 0 |
| 3 | | | reshade | brown | 10 | brown* | 10 | clear | 2 | brown | 10 | smooth 15 | ARMS-bands: brown, clear | 0 | 1 | 0 |
| 4 | | grey | shade | brown | 10 | brown* | 10 | brown | 10 | brown | 10 | smooth 15 | ARMS-bands: brown, clear | 0 | 1 | 0 |
| 5 | | | sun | brown* | 10 | clear | 2 | clear | 2 | brown | 10 | smooth 15 | MANTLE- spotted: clear | 0 | 0 | 1 |
| 6 | | | reshade | clear | 2 | clear | 2 | clear | 2 | turquoise | 11 | smooth 15 | | 0 | 0 | 0 |
| 7 | | black | shade | brown* | 10 | brown | 10 | brown | 10 | brown | 10 | smooth 15 | MANTLE- spotted: irr.green | 1 | 0 | 1 |
| 8 | | | sun | brown* | 10 | clear* | 2 | clear* | 2 | brown | 10 | smooth 15 | TOTAL- spots: irr. Green | 1 | 0 | 1 |
| 9 | | | reshade | clear | 2 | clear | 2 | clear | 2 | turquoise | 11 | smooth 15 | | 0 | 0 | 0 |
| 10 | | white | shade | brown | 10 | clear* | 2 | clear | 2 | turquoise | 11 | smooth 15 | ARMS- spots: irr.green | 1 | 0 | 1 |
| 11 | | | sun | brown | 10 | brown | 10 | brown | 10 | brown | 10 | smooth 15 | | 0 | 0 | 0 |
| 12 | | | reshade | brown | 10 | brown | 10 | brown | 10 | turquoise | 11 | smooth 15 | | 0 | 0 | 0 |
| 13 | | control | shade | brown | 10 | brown | 10 | brown | 10 | brown | 10 | smooth 15 | | 0 | 0 | 0 |
| 14 | | | sun | brown | 10 | brown | 10 | brown | 10 | brown | 10 | smooth 15 | | 0 | 0 | 0 |
| 15 | | | reshade | clear | 2 | clear | 2 | clear | 2 | brown | 10 | smooth 15 | | 0 | 0 | 0 |
| 16 | black | green | shade | clear* | 2 | clear* | 2 | clear* | 2 | turquoise | 11 | smooth 15 | TOTAL- spots: irr. Green | 1 | 0 | 1 |
| 17 | | | sun | brown* | 10 | clear* | 2 | clear | 2 | brown | 10 | smooth 15 | MANTLE- spots: irr.green/ ARMS- bands: brown, clear | 1 | 1 | 1 |
| 18 | | | reshade | brown* | 10 | brown* | 10 | brown* | 10 | brown | 10 | smooth 15 | TOTAL- spots: irr. Green | 1 | 0 | 1 |
| 19 | | grey | shade | brown | 10 | clear | 2 | clear | 2 | brown | 10 | smooth 15 | | 0 | 0 | 0 |
| 20 | | | sun | brown* | 10 | brown* | 10 | brown* | 10 | turquoise | 11 | smooth 15 | TOTAL- spots: irr. Green | 1 | 0 | 1 |
| 21 | | | reshade | brown* | 10 | brown* | 10 | brown* | 10 | turquoise | 11 | smooth 15 | TOTAL- spots: irr. Green | 1 | 0 | 1 |
| 22 | | black | shade | clear* | 2 | clear | 2 | clear | 2 | turquoise | 11 | smooth 15 | MANTLE- spots: brown | 0 | 0 | 1 |
| 23 | | | sun | brown | 10 | clear | 2 | clear | 2 | brown | 10 | smooth 15 | | 0 | 0 | 0 |
| 24 | | | reshade | brown | 10 | clear | 2 | clear | 2 | brown | 10 | smooth 15 | | 0 | 0 | 0 |
| 25 | | white | shade | clear* | 2 | clear* | 2 | clear* | 2 | turquoise | 11 | smooth 15 | TOTAL- spots: irr. Green | 1 | 0 | 1 |
| 26 | | | sun | brown | 10 | clear | 2 | clear | 2 | brown | 10 | smooth 15 | | 0 | 0 | 0 |
| 27 | | | reshade | clear | 2 | clear | 2 | clear | 2 | turquoise | 11 | smooth 15 | | 0 | 0 | 0 |
| 28 | | control | shade | brown | 10 | clear | 2 | clear | 2 | brown | 10 | smooth 15 | | 0 | 0 | 0 |
| 29 | | | sun | brown | 10 | brown | 10 | brown | 10 | turquoise | 11 | smooth 15 | | 0 | 0 | 0 |
| 30 | | | reshade | clear | 2 | clear | 2 | clear | 2 | brown | 10 | smooth 15 | | 0 | 0 | 0 |

J2 (*O.bocki*)

| | background | foreground | lighting | color mantle | | arms | | web | | eyes | | texture | | pattern color | iridescence | pattern | spotting |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | white | green | shade | brown | 10 | brown* | 10 | brown | 10 | brown | 10 | smooth | 15 | ARMS- spots: irr.green | 1 | 0 | 1 |
| 2 | | | sun | light brown* | 9 | light brown* | 9 | light brown* | 9 | brown | 10 | smooth | 15 | TOTAL- spots: irr.green | 1 | 0 | 1 |
| 3 | | | reshade | light brown* | 9 | light brown* | 9 | light brown* | 9 | brown | 10 | smooth | 15 | TOTAL- spots: irr.green | 1 | 0 | 1 |
| 4 | | grey | shade | brown | 10 | clear*** | 2 | brown | 10 | brown | 10 | smooth | 15 | ARMS- bands: brown,clear | 0 | 1 | 0 |
| 5 | | | sun | brown | 10 | clear*** | 2 | brown | 10 | brown | 10 | smooth | 15 | ARMS- bands: brown,clear | 0 | 1 | 0 |
| 6 | | | reshade | brown | 10 | clear*** | 2 | brown | 10 | brown | 10 | smooth | 15 | ARMS- bands: brown,clear | 0 | 1 | 0 |
| 7 | | black | shade | brown | 10 | clear | 2 | clear | 2 | turquoise | 11 | smooth | 15 | | 0 | 0 | 0 |
| 8 | | | sun | clear | 2 | clear | 2 | clear | 2 | turquoise | 11 | smooth | 15 | | 0 | 0 | 0 |
| 9 | | | reshade | clear | 2 | clear | 2 | clear | 2 | turquoise | 11 | smooth | 15 | | 0 | 0 | 0 |
| 10 | | white | shade | clear | 2 | clear | 2 | clear | 2 | brown | 10 | smooth | 15 | | 0 | 0 | 0 |
| 11 | | | sun | clear | 2 | clear | 2 | clear | 2 | brown | 10 | smooth | 15 | | 0 | 0 | 0 |
| 12 | | | reshade | clear | 2 | clear | 2 | clear | 2 | brown | 10 | smooth | 15 | | 0 | 0 | 0 |
| 13 | | control | shade | clear | 2 | clear* | 2 | clear | 2 | brown | 10 | smooth | 15 | ARMS- bands: brown,clear | 0 | 1 | 0 |
| 14 | | | sun | brown | 10 | brown | 10 | brown | 10 | brown | 10 | smooth | 15 | | 0 | 0 | 0 |
| 15 | | | reshade | brown | 10 | brown | 10 | brown | 10 | brown | 10 | smooth | 15 | | 0 | 0 | 0 |
| 16 | black | green | shade | brown | 10 | brown* | 10 | clear | 2 | brown | 10 | smooth | 15 | ARMS-bands: brown, clear | 0 | 1 | 0 |
| 17 | | | sun | brown | 10 | brown* | 10 | clear | 2 | brown | 10 | smooth | 15 | ARMS-bands: brown, clear | 0 | 1 | 0 |
| 18 | | | reshade | light brown | 9 | light brown | 9 | light brown | 9 | brown | 10 | smooth | 15 | | 0 | 0 | 0 |
| 19 | | grey | shade | brown | 10 | clear | 2 | clear | 2 | turquoise | 11 | smooth | 15 | | 0 | 0 | 0 |
| 20 | | | sun | brown* | 10 | brown* | 10 | brown* | 10 | brown | 10 | smooth | 15 | TOTAL- hue: irr.purple | 1 | 0 | 0 |
| 21 | | | reshade | clear | 2 | clear* | 2 | clear | 2 | brown | 10 | smooth | 15 | ARMS -bands: brown | 0 | 1 | 0 |
| 22 | | black | shade | brown | 10 | white* | 3 | white* | 3 | turquoise | 11 | smooth | 15 | TOTAL- spots: irr.green | 1 | 0 | 1 |
| 23 | | | sun | brown** | 10 | brown* | 10 | brown** | 10 | brown | 10 | smooth | 15 | MANTLE & WEB- hue: irr.purple/ TOTAL- spots: irr.green | 1 | 0 | 1 |
| 24 | | | reshade | brown | 10 | clear | 2 | clear | 2 | brown | 10 | smooth | 15 | | 0 | 0 | 0 |
| 25 | | white | shade | brown | 10 | white* | 3 | white* | 3 | turquoise | 11 | smooth | 15 | TOTAL- spots: irr.green | 1 | 0 | 1 |
| 26 | | | sun | brown | 10 | brown | 10 | brown | 10 | brown | 10 | smooth | 15 | | 0 | 0 | 0 |
| 27 | | | reshade | brown | 10 | brown | 10 | brown | 10 | brown | 10 | smooth | 15 | | 0 | 0 | 0 |
| 28 | | control | shade | brown | 10 | white* | 3 | white* | 3 | turquoise | 11 | smooth | 15 | TOTAL- spots: irr.green | 1 | 0 | 1 |
| 29 | | | sun | brown | 10 | brown* | 10 | brown | 10 | brown | 10 | smooth | 15 | ARMS- bands: clear, brown | 0 | 1 | 0 |
| 30 | | | reshade | light brown* | 9 | light brown* | 9 | light brown* | 9 | brown | 10 | smooth | 15 | TOTAL- spots: irr.green | 0 | 0 | 1 |

J3 (*O.bocki*)

| | background | foreground | lighting | color mantle | | arms | | web | | eyes | | texture | | pattern color | iridescence | pattern | spotting |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | white | green | shade | brown | 10 | brown | 10 | brown | 10 | brown | 10 | smooth | 15 | | 0 | 0 | 0 |
| 2 | | | sun | brown* | 10 | brown | 10 | brown | 10 | brown | 10 | smooth | 15 | MANTLE- spots: darker brown | 0 | 0 | 1 |
| 3 | | | reshade | light brown | 9 | light brown | 9 | light brown | 9 | brown | 10 | smooth | 15 | | 0 | 0 | 0 |
| 4 | | grey | shade | clear* | 2 | clear | 2 | clear | 2 | brown | 10 | smooth | 15 | MANTLE- spots: darker brown | 0 | 0 | 1 |
| 5 | | | sun | light brown | 9 | light brown | 9 | light brown | 9 | brown | 10 | smooth | 15 | | 0 | 0 | 0 |
| 6 | | | reshade | brown* | 10 | brown | 10 | brown | 10 | brown | 10 | smooth | 15 | MANTLE- spots: irr.green | 1 | 0 | 1 |
| 7 | | black | shade | brown | 10 | clear* | 2 | clear | 2 | turquoise | 11 | smooth | 15 | ARMS -spots:irr.green | 1 | 0 | 1 |
| 8 | | | sun | brown* | 10 | brown* | 10 | brown* | 10 | brown | 10 | smooth | 15 | TOTAL- spots: white | 0 | 0 | 1 |
| 9 | | | reshade | brown | 10 | light brown | 9 | brown | 10 | brown | 10 | smooth | 15 | | 0 | 0 | 0 |
| 10 | | white | shade | clear* | 2 | clear* | 2 | clear* | 2 | turquoise | 11 | smooth | 15 | TOTAL- spots: irr.green | 1 | 0 | 1 |
| 11 | | | sun | brown | 10 | brown* | 10 | brown | 10 | brown | 10 | smooth | 15 | ARMS- bands: irr.green | 1 | 1 | 1 |
| 12 | | | reshade | brown | 10 | clear* | 2 | clear | 2 | brown | 10 | smooth | 15 | ARMS: dipped: brown | 0 | 3 | 0 |
| 13 | | control | shade | light brown* | 9 | clear* | 2 | light brown* | 9 | brown | 10 | smooth | 15 | TOTAL- spots: irr.green | 1 | 0 | 1 |
| 14 | | | sun | brown | 10 | brown* | 10 | brown* | 10 | brown | 10 | smooth | 15 | W & A- spots: irr.green | 1 | 0 | 1 |
| 15 | | | reshade | clear* | 2 | clear* | 2 | clear* | 2 | brown | 10 | smooth | 15 | TOTAL- spots: irr.green | 1 | 0 | 1 |
| 16 | black | green | shade | brown | 10 | brown | 10 | brown | 10 | brown | 10 | smooth | 15 | | 0 | 0 | 0 |
| 17 | | | sun | brown* | 10 | brown* | 10 | brown* | 10 | brown | 10 | smooth | 15 | TOTAL- spots: irr.green | 1 | 0 | 1 |
| 18 | | | reshade | brown* | 10 | brown* | 10 | brown* | 10 | brown | 10 | smooth | 15 | TOTAL- spots: irr.green | 1 | 0 | 1 |
| 19 | | grey | shade | brown* | 10 | clear | 2 | clear | 2 | brown | 10 | smooth | 15 | MANTLE- spots: irr.green | 1 | 0 | 1 |
| 20 | | | sun | brown | 10 | brown | 10 | brown* | 10 | brown | 10 | smooth | 15 | WEB- hue: purple | 1 | 0 | 0 |
| 21 | | | reshade | brown | 10 | brown | 10 | brown* | 10 | brown | 10 | smooth | 15 | WEB- hue: purple | 1 | 0 | 0 |
| 22 | | black | shade | brown | 10 | brown | 10 | brown | 10 | brown | 10 | smooth | 15 | | 0 | 0 | 0 |
| 23 | | | sun | brown* | 10 | brown | 10 | brown* | 10 | brown | 10 | smooth | 15 | MANTLE & WEB- hue: irr.purple | 1 | 0 | 0 |
| 24 | | | reshade | brown** | 10 | brown* | 10 | brown** | 10 | brown | 10 | smooth | 15 | MANTLE & WEB- hue: irr.purple/ TOTAL- spots: irr.green | 1 | 0 | 1 |
| 25 | | white | shade | white* | 3 | white* | 3 | white* | 3 | turquoise | 11 | smooth | 15 | TOTAL- spots: irr.green | 1 | 0 | 1 |
| 26 | | | sun | brown* | 10 | white** | 3 | white** | 3 | turquoise | 11 | smooth | 15 | TOTAL- spots: irr.green/ hue: irr.purple | 1 | 0 | 1 |
| 27 | | | reshade | brown* | 10 | white** | 3 | white** | 3 | turquoise | 11 | smooth | 15 | TOTAL- spots: irr.green/ hue: irr.purple | 1 | 0 | 1 |
| 28 | | control | shade | brown | 10 | clear* | 2 | clear | 2 | blue | 12 | smooth | 15 | ARMS- dipped: brown | 0 | 3 | 0 |
| 29 | | | sun | brown | 10 | brown* | 10 | brown | 10 | brown | 10 | smooth | 15 | ARMS- bands: clear, brown | 0 | 1 | 0 |
| 30 | | | reshade | brown | 10 | brown* | 10 | brown | 10 | brown | 10 | smooth | 15 | ARMS- bands: clear, brown | 0 | 1 | 0 |

J4 (*O.bocki*)

| | background | foreground | lighting | color | | | | | | texture | | pattern | iridescence | pattern | spotting |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | mantle | | arms | | web | | eyes | | | color | | | |
| 1 | white | green | shade | brown | 10 | brown* | 10 | brown | 10 | brown | 10 | smooth 15 | ARMS- bands: clear, brown | 0 | 1 | 0 |
| 2 | | | sun | brown | 10 | brown* | 10 | brown | 10 | brown | 10 | smooth 15 | ARMS- bands: clear, brown | 0 | 1 | 0 |
| 3 | | | reshade | light brown | 9 | light brown* | 9 | light brown | 9 | brown | 10 | smooth 15 | ARMS- bands: clear, brown | 0 | 1 | 0 |
| 4 | | grey | shade | light brown | 9 | light brown | 9 | light brown | 9 | blue | 12 | smooth 15 | | 0 | 0 | 0 |
| 5 | | | sun | brown* | 10 | brown** | 10 | brown* | 10 | brown | 10 | smooth 15 | TOTAL- spots: irr.green/ ARMS- bands: clear, brown | 1 | 1 | 1 |
| 6 | | | reshade | brown | 10 | clear* | 2 | brown | 10 | brown | 10 | smooth 15 | ARMS- dipped: brown | 0 | 3 | 0 |
| 7 | | black | shade | brown* | 10 | clear* | 2 | brown* | 10 | brown | 10 | smooth 15 | TOTAL- spots: irr.green | 1 | 0 | 1 |
| 8 | | | sun | brown | 10 | brown* | 10 | brown | 10 | brown | 10 | smooth 15 | ARMS- bands: clear, brown | 0 | 1 | 0 |
| 9 | | | reshade | white | 3 | white | 3 | white | 3 | blue | 12 | smooth 15 | | 0 | 0 | 0 |
| 10 | | white | shade | clear | 2 | clear | 2 | clear | 2 | blue | 12 | smooth 15 | | 0 | 0 | 0 |
| 11 | | | sun | brown | 10 | brown* | 10 | brown | 10 | blue | 12 | smooth 15 | ARMS- bands: clear, brown | 0 | 1 | 0 |
| 12 | | | reshade | brown | 10 | clear | 2 | clear | 2 | blue | 12 | smooth 15 | | 0 | 0 | 0 |
| 13 | | control | shade | brown | 10 | brown | 10 | brown | 10 | blue | 12 | smooth 15 | | 0 | 0 | 0 |
| 14 | | | sun | brown | 10 | brown* | 10 | brown | 10 | blue | 12 | smooth 15 | ARMS- bands: clear, brown | 0 | 1 | 0 |
| 15 | | | reshade | brown | 10 | clear | 2 | clear | 2 | blue | 12 | smooth 15 | | 0 | 0 | 0 |
| 16 | black | green | shade | brown | 10 | clear* | 2 | clear | 2 | brown | 10 | smooth 15 | ARMS- spots: irr.green | 1 | 0 | 1 |
| 17 | | | sun | brown | 10 | brown | 10 | brown | 10 | brown | 10 | smooth 15 | | 0 | 0 | 0 |
| 18 | | | reshade | brown | 10 | brown | 10 | brown | 10 | brown | 10 | smooth 15 | | 0 | 0 | 0 |
| 19 | | grey | shade | brown* | 10 | brown** | 10 | brown | 10 | brown | 10 | smooth 15 | MANTLE-spots: irr.green/ ARMS- bands: clear brown | 1 | 1 | 1 |
| 20 | | | sun | brown* | 10 | clear* | 2 | brown* | 10 | turquoise | 11 | smooth 15 | TOTAL- spots: irr.green | 1 | 0 | 1 |
| 21 | | | reshade | brown* | 10 | clear* | 2 | brown* | 10 | turquoise | 11 | smooth 15 | TOTAL- spots: irr.green | 1 | 0 | 1 |
| 22 | | black | shade | brown* | 10 | clear* | 2 | brown* | 10 | turquoise | 11 | smooth 15 | TOTAL- spots: irr.green | 1 | 0 | 1 |
| 23 | | | sun | brown* | 10 | clear* | 2 | brown* | 10 | turquoise | 11 | smooth 15 | TOTAL- spots: irr.green | 1 | 0 | 1 |
| 24 | | | reshade | brown* | 10 | clear* | 2 | brown* | 10 | turquoise | 11 | smooth 15 | TOTAL- spots: irr.green | 1 | 0 | 1 |
| 25 | | white | shade | clear* | 2 | clear* | 2 | clear* | 2 | turquoise | 11 | smooth 15 | TOTAL- spots: irr.green | 1 | 0 | 1 |
| 26 | | | sun | brown | 10 | brown | 10 | brown | 10 | brown | 10 | smooth 15 | | 0 | 0 | 0 |
| 27 | | | reshade | brown | 10 | brown | 10 | brown | 10 | brown | 10 | smooth 15 | | 0 | 0 | 0 |
| 28 | | control | shade | brown | 10 | brown** | 10 | brown | 10 | brown | 10 | smooth 15 | ARMS- spots: irr.green/ A- bands: clear, brown | 1 | 1 | 1 |
| 29 | | | sun | brown | 10 | brown* | 10 | brown | 10 | brown | 10 | smooth 15 | ARMS- bands: clear, brown | 0 | 1 | 0 |
| 30 | | | reshade | brown* | 10 | clear* | 2 | clear* | 10 | brown | 10 | smooth 15 | TOTAL- spots: irr.green | 1 | 0 | 1 |

J5 (*O.bocki*)

| | background | foreground | lighting | color | | | | | | texture | | | pattern color | iridescence | pattern | spotting |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | mantle | | arms | | web | | eyes | | | | | | |
| 1 | white | green | shade | brown | 10 | clear | 2 | clear | 2 | brown | 10 | smooth | 15 | 0 | 0 | 1 |
| 2 | | | sun | brown* | 10 | clear* | 2 | clear | 2 | turquoise | 11 | smooth | 15 MANTLE- spots: irr.green/ ARMS- bands: clear, brown | 1 | 1 | 0 |
| 3 | | | reshade | white | 3 | white | 3 | white | 3 | brown* | 10 | smooth | 15 EYES: tint: green | 0 | 0 | 1 |
| 4 | | grey | shade | brown* | 10 | brown* | 10 | brown* | 10 | turquoise | 11 | smooth | 15 TOTAL- spots:white | 0 | 0 | 1 |
| 5 | | | sun | brown* | 10 | brown* | 10 | brown* | 10 | turquoise | 11 | smooth | 15 TOTAL- spots:white | 0 | 0 | 1 |
| 6 | | | reshade | brown* | 10 | brown* | 10 | brown* | 10 | turquoise | 11 | smooth | 15 TOTAL- spots:white | 0 | 0 | 1 |
| 7 | | black | shade | brown* | 10 | brown* | 10 | brown* | 10 | brown | 10 | smooth | 15 TOTAL- spots:white | 0 | 0 | 1 |
| 8 | | | sun | brown* | 10 | brown* | 10 | brown | 10 | turquoise | 11 | smooth | 15 MANTLE- spots: irr.green/ ARMS- bands: clear, brown | 1 | 1 | 1 |
| 9 | | | reshade | brown* | 10 | brown* | 10 | brown | 10 | turquoise | 11 | smooth | 15 MANTLE- spots: irr.green/ ARMS- bands: clear, brown | 1 | 1 | 1 |
| 10 | | white | shade | clear* | 2 | clear* | 2 | clear* | 2 | turquoise | 11 | smooth | 15 TOTAL- spots: irr.green | 1 | 0 | 1 |
| 11 | | | sun | brown** | 10 | brown** | 10 | brown* | 10 | brown | 10 | smooth | 15 TOTAL- hue: irr.purple/ MANTLE & WEB- spots: irr.green/ ARMS- bands: clear, brown | 1 | 1 | 1 |
| 12 | | | reshade | clear* | 2 | clear* | 2 | clear* | 2 | turquoise | 11 | smooth | 15 TOTAL- spots: irr.green | 1 | 0 | 1 |
| 13 | | control | shade | brown | 10 | clear | 2 | brown | 10 | brown | 10 | smooth | 15 | 0 | 0 | 0 |
| 14 | | | sun | brown** | 10 | brown** | 10 | brown** | 10 | turquoise | 11 | smooth | 15 TOTAL- spots: irr.green/ TOTAL- hue: irr.purple | 1 | 0 | 1 |
| 15 | | | reshade | clear* | 2 | clear* | 2 | clear* | 2 | turquoise | 11 | smooth | 15 TOTAL- spots: irr.green | 1 | 0 | 1 |
| 16 | black | green | shade | brown | 10 | brown* | 10 | brown | 10 | brown | 10 | smooth | 15 ARMS- bands: clear, brown | 0 | 1 | 0 |
| 17 | | | sun | brown** | 10 | brown | 10 | brown | 10 | brown | 10 | smooth | 15 MANTLE- spots: irr.green/ MANTLE- hue: irr.purple | 1 | 0 | 1 |
| 18 | | | reshade | clear* | 2 | clear | 2 | clear | 2 | brown | 10 | smooth | 15 MANTLE- spots: irr.green | 1 | 0 | 1 |
| 19 | | grey | shade | brown* | 10 | clear | 10 | brown* | 10 | brown* | 10 | smooth | 15 MANTLE & WEB- spots: irr.green/ EYES- tint: green | 1 | 0 | 1 |
| 20 | | | sun | brown** | 10 | brown | 10 | brown** | 10 | brown | 10 | smooth | 15 MANTLE & WEB- spots: irr.green/ MANTLE & WEB- hue: irr.purple | 1 | 0 | 1 |
| 21 | | | reshade | light brown** | 9 | light brown | 9 | light brown** | 9 | brown | 10 | smooth | 15 MANTLE & WEB- spots: irr.green/ MANTLE & WEB- hue: irr.purple | 1 | 0 | 1 |
| 22 | | black | shade | brown** | 10 | brown** | 10 | brown** | 10 | brown | 10 | smooth | 15 TOTAL- hue: irr.purple/ TOTAL: spots: irr.green | 1 | 0 | 1 |
| 23 | | | sun | brown | 10 | clear | 2 | clear | 2 | brown | 10 | smooth | 15 | 0 | 0 | 0 |
| 24 | | | reshade | light brown* | 9 | light brown* | 9 | light brown* | 9 | brown | 10 | smooth | 15 TOTAL- spots: irr.green | 1 | 0 | 1 |
| 25 | | white | shade | brown | 10 | brown | 10 | brown | 10 | brown | 10 | smooth | 15 | 0 | 0 | 0 |
| 26 | | | sun | clear* | 2 | clear* | 2 | clear* | 2 | brown | 10 | smooth | 15 TOTAL- spots: irr.green | 1 | 0 | 1 |
| 27 | | | reshade | brown | 10 | clear | 2 | brown | 10 | brown | 10 | smooth | 15 | 0 | 0 | 0 |
| 28 | | control | shade | brown | 10 | brown | 10 | brown | 10 | brown | 10 | smooth | 15 | 0 | 0 | 0 |
| 29 | | | sun | brown* | 10 | brown* | 10 | brown* | 10 | turquoise | 11 | smooth | 15 TOTAL- hue: irr.purple | 1 | 0 | 0 |
| 30 | | | reshade | clear* | 2 | clear* | 2 | clear* | 2 | turquoise | 11 | smooth | 15 TOTAL- spots: irr.green | 1 | 0 | 1 |

J6 (*O.cyanea* )

| | background | foreground | lighting | color | | | | | | texture | | pattern | iridescence | pattern | spotting |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | mantle | | arms | | web | | eyes | | | color | | | |
| 1 | white | green | shade | creamy yellow* | 6 | creamy yellow** | 6 | creamy yellow* | 6 | brown | 10 | smooth | 15 TOTAL- stoney: black, white, brown/ ARMS- outline: brown | 0 | 0 | 1 |
| 2 | | | sun | yellow* | 7 | yellow* | 7 | yellow* | 7 | brown | 10 | shaggy | 14 TOTAL- stoney: black, white, brown | 0 | 0 | 1 |
| 3 | | | reshade | brown* | 10 | brown* | 10 | brown* | 10 | brown | 10 | shaggy | 14 TOTAL- stoney: black, white, brown | 0 | 0 | 1 |
| 4 | | grey | shade | cream | 4 | cream | 4 | cream | 4 | brown | 10 | shaggy | 14 | 0 | 0 | 0 |
| 5 | | | sun | brown | 10 | brown | 10 | brown | 10 | brown | 10 | shaggy | 14 | 0 | 0 | 0 |
| 6 | | | reshade | brown | 10 | brown | 10 | brown | 10 | brown | 10 | shaggy | 14 | 0 | 0 | 0 |
| 7 | | black | shade | white | 3 | white | 3 | white | 3 | brown | 10 | shaggy | 14 | 0 | 0 | 0 |
| 8 | | | sun | brown | 10 | brown | 10 | brown | 10 | brown | 10 | shaggy | 14 | 0 | 0 | 0 |
| 9 | | | reshade | white | 3 | white | 3 | white | 3 | brown | 10 | shaggy | 14 | 0 | 0 | 0 |
| 10 | | white | shade | creamy yellow* | 6 | creamy yellow** | 6 | creamy yellow* | 6 | brown | 10 | smooth | 15 TOTAL- stoney: black, white, brown/ ARMS- outline: brown | 0 | 0 | 1 |
| 11 | | | sun | brown* | 10 | brown* | 10 | brown* | 10 | brown | 10 | smooth | 15 TOTAL- spots: white | 0 | 0 | 1 |
| 12 | | | reshade | brown* | 10 | beige* | 5 | beige | 5 | brown | 10 | smooth | 15 ARMS- spots: white | 0 | 0 | 1 |
| 13 | | control | shade | cream | 4 | cream | 4 | cream | 4 | brown | 10 | shaggy | 14 | 0 | 0 | 0 |
| 14 | | | sun | cream* | 4 | cream* | 4 | cream* | 4 | brown | 10 | shaggy | 14 TOTAL- rings: brown | 0 | 2 | 0 |
| 15 | | | reshade | yellow | 7 | yellow | 7 | yellow | 7 | brown | 10 | smooth | 15 | 0 | 0 | 0 |
| 16 | black | green | shade | cream* | 4 | cream* | 4 | cream* | 4 | brown | 10 | smooth | 15 TOTAL- stoney: black, white, brown | 0 | 0 | 1 |
| 17 | | | sun | olive yellow* | 8 | olive yellow* | 8 | olive yellow* | 8 | brown | 10 | shaggy | 14 TOTAL- stoney: black, white, brown | 0 | 0 | 1 |
| 18 | | | reshade | cream | 4 | cream | 4 | cream | 4 | brown | 10 | shaggy | 14 | 0 | 0 | 0 |
| 19 | | grey | shade | creamy yellow* | 6 | creamy yellow** | 6 | creamy yellow* | 6 | brown | 10 | shaggy | 14 TOTAL- stoney: black, white, brown | 0 | 0 | 1 |
| 20 | | | sun | olive yellow* | 8 | olive yellow* | 8 | olive yellow* | 8 | brown | 10 | shaggy | 14 TOTAL- stoney: black, white, brown | 0 | 0 | 1 |
| 21 | | | reshade | cream* | 4 | cream* | 4 | cream* | 4 | brown | 10 | shaggy | 14 TOTAL- stoney: black, white, brown | 0 | 0 | 1 |
| 22 | | black | shade | olive yellow* | 8 | olive yellow* | 8 | olive yellow* | 8 | brown | 10 | smooth | 15 TOTAL- stoney: black, white, brown | 0 | 0 | 1 |
| 23 | | | sun | olive yellow** | 8 | olive yellow** | 8 | olive yellow** | 8 | brown | 10 | shaggy | 14 TOTAL- stoney: black, white, brown/ ARMS- spots: irr.green | 1 | 0 | 1 |
| 24 | | | reshade | white | 3 | white | 3 | white | 3 | brown | 10 | shaggy | 14 | 0 | 0 | 0 |
| 25 | | white | shade | olive yellow* | 8 | olive yellow* | 8 | olive yellow* | 8 | brown | 10 | shaggy | 14 TOTAL- spots: white | 0 | 0 | 1 |
| 26 | | | sun | beige* | 5 | beige* | 5 | beige* | 5 | brown | 10 | shaggy | 14 TOTAL- stoney: black, white, brown/ ARMS- spots: irr.green | 1 | 0 | 1 |
| 27 | | | reshade | cream* | 4 | cream* | 4 | cream* | 4 | brown | 10 | shaggy | 14 TOTAL- spots: white | 0 | 0 | 1 |
| 28 | | control | shade | beige | 5 | beige | 5 | beige | 5 | brown | 10 | smooth | 15 | 0 | 0 | 0 |
| 29 | | | sun | cream | 4 | cream | 4 | cream | 4 | brown | 10 | shaggy | 14 | 0 | 0 | 0 |
| 30 | | | reshade | yellow | 7 | yellow | 7 | yellow | 7 | brown | 10 | shaggy | 14 | 0 | 0 | 0 |

J7 (*O.cyanea* )

| | background | foreground | lighting | color | | | | | texture | | pattern | iridescence | pattern | spotting |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | mantle | | arms | web | eyes | | | color | | | |
| 1 | white | green | shade | yellow* | 7 | yellow* | 7 yellow* | 7 brown | 10 | smooth | 15 TOTAL- spots: white | 0 | 0 | 1 |
| 2 | | | sun | olive yellow* | 8 | olive yellow | 8 olive yellow* | 8 brown | 10 | smooth | 15 TOTAL- spots: white | 0 | 0 | 1 |
| 3 | | | reshade | olive yellow* | 8 | olive yellow | 8 olive yellow* | 8 brown | 10 | smooth | 15 TOTAL- spots: white | 0 | 0 | 1 |
| 4 | | grey | shade | white* | 3 | white* | 3 white* | 3 brown | 10 | shaggy | 14 TOTAL- stoney: white, black, brown | 0 | 0 | 1 |
| 5 | | | sun | cream* | 4 | cream* | 4 cream* | 4 brown | 10 | shaggy | 14 TOTAL- stoney: white, black, brown | 0 | 0 | 1 |
| 6 | | | reshade | cream* | 4 | cream* | 4 cream* | 4 brown | 10 | shaggy | 14 TOTAL- stoney: white, black, brown | 0 | 0 | 1 |
| 7 | | black | shade | yellow* | 7 | yellow* | 7 yellow* | 7 brown | 10 | shaggy | 14 TOTAL- stoney: white, black, brown/ MANTLE- rings: white | 0 | 2 | 1 |
| 8 | | | sun | yellow* | 7 | yellow* | 7 yellow* | 7 brown | 10 | shaggy | 14 TOTAL- spots: white | 0 | 0 | 1 |
| 9 | | | reshade | yellow* | 7 | yellow* | 7 yellow* | 7 brown | 10 | shaggy | 14 TOTAL- spots: white | 0 | 0 | 1 |
| 10 | | white | shade | yellow | 7 | yellow | 7 yellow | 7 brown | 10 | smooth | 15 | 0 | 0 | 0 |
| 11 | | | sun | brown* | 10 | brown* | 10 brown* | 10 brown | 10 | smooth | 15 TOTAL- spots: white | 0 | 0 | 1 |
| 12 | | | reshade | yellow* | 7 | yellow* | 7 yellow* | 7 brown | 10 | smooth | 15 TOTAL- spots: brown | 0 | 0 | 1 |
| 13 | | control | shade | white | 3 | white | 3 white | 3 brown | 10 | shaggy | 14 | 0 | 0 | 0 |
| 14 | | | sun | white* | 3 | white* | 3 white* | 3 brown | 10 | shaggy | 14 TOTAL- ring: brown | 0 | 2 | 0 |
| 15 | | | reshade | yellow | 7 | yellow | 7 yellow | 7 brown | 10 | smooth | 15 | 0 | 0 | 0 |
| 16 | black | green | shade | yellow* | 7 | yellow* | 7 yellow* | 7 brown | 10 | smooth | 15 TOTAL- spots: white | 0 | 0 | 1 |
| 17 | | | sun | white* | 3 | white | 3 white | 3 brown | 10 | shaggy | 14 MANTLE- bands: brown | 0 | 1 | 0 |
| 18 | | | reshade | cream | 4 | cream | 4 cream | 4 brown | 10 | shaggy | 14 | 0 | 0 | 0 |
| 19 | | grey | shade | yellow | 7 | yellow | 7 yellow | 7 brown | 10 | rough | 13 | 0 | 0 | 0 |
| 20 | | | sun | olive yellow* | 8 | olive yellow | 8 olive yellow* | 8 brown | 10 | shaggy | 14 TOTAL- stoney: white, black, brown | 0 | 0 | 1 |
| 21 | | | reshade | white* | 3 | white* | 3 white* | 3 brown | 10 | shaggy | 14 TOTAL- stoney: white, black, brown | 0 | 0 | 1 |
| 22 | | black | shade | brown* | 10 | brown* | 10 brown* | 10 brown | 10 | smooth | 15 TOTAL- stoney: white, black, brown | 0 | 0 | 1 |
| 23 | | | sun | yellow* | 7 | yellow* | 7 yellow* | 7 brown | 10 | shaggy | 14 TOTAL- stoney: white, black, brown/ MANTLE- rings: white | 0 | 2 | 1 |
| 24 | | | reshade | brown | 10 | brown | 10 brown | 10 brown | 10 | smooth | 15 | 0 | 0 | 0 |
| 25 | | white | shade | cream* | 4 | cream* | 4 cream* | 4 brown | 10 | shaggy | 14 TOTAL- stoney: white, black, brown | 0 | 0 | 1 |
| 26 | | | sun | yellow* | 7 | yellow* | 7 yellow* | 7 brown | 10 | shaggy | 14 TOTAL- spots: white | 0 | 0 | 1 |
| 27 | | | reshade | white | 3 | white | 3 white | 3 brown | 10 | shaggy | 14 | 0 | 0 | 0 |
| 28 | | control | shade | yellow* | 7 | yellow* | 7 yellow* | 7 brown | 10 | shaggy | 14 TOTAL- stoney: white, black, brown/ MANTLE- rings: white | 0 | 2 | 11 |
| 29 | | | sun | brown | 10 | brown | 10 brown | 10 brown | 10 | shaggy | 14 | 0 | 0 | 0 |
| 30 | | | reshade | brown* | 10 | brown | 10 brown | 10 brown | 10 | shaggy | 14 MANTLE- rings: brown | 0 | 2 | 0 |

J8 (*O.cyanea*)

| | background | foreground | lighting | color mantle | | arms | | web | | eyes | | texture | | pattern color | iridescence | pattern | spotting |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | white | green | shade | cream* | 4 | cream** | 4 | cream* | 4 | brown | 10 | shaggy | 14 | TOTAL- ring: brown/ MANTLE- spots: white | 0 | 2 | 1 |
| 2 | | | sun | cream* | 4 | cream** | 4 | cream* | 4 | brown | 10 | smooth | 15 | TOTAL- ring: brown/ MANTLE- spots: white | 0 | 2 | 1 |
| 3 | | | reshade | white* | 3 | white* | 3 | white* | 3 | brown | 10 | smooth | 15 | TOTAL- rings: brown | 0 | 2 | 0 |
| 4 | | grey | shade | cream* | 4 | cream* | 4 | cream* | 4 | brown | 10 | smooth | 15 | TOTAL- rings: brown | 0 | 2 | 0 |
| 5 | | | sun | beige* | 5 | beige* | 5 | beige* | 5 | brown | 10 | smooth | 15 | TOTAL- rings: brown | 0 | 2 | 0 |
| 6 | | | reshade | white | 3 | white | 3 | white | 3 | brown | 10 | smooth | 15 | | 0 | 0 | 0 |
| 7 | | black | shade | cream | 4 | cream | 4 | cream | 4 | brown | 10 | smooth | 15 | | 0 | 0 | 0 |
| 8 | | | sun | beige | 5 | beige* | 5 | beige | 5 | brown | 10 | shaggy | 14 | ARMS- spots: black | 0 | 0 | 1 |
| 9 | | | reshade | cream | 4 | cream | 4 | cream | 4 | brown | 10 | smooth | 15 | | 0 | 0 | 0 |
| 10 | | white | shade | beige | 5 | beige | 5 | beige | 5 | brown | 10 | shaggy | 14 | | 0 | 0 | 0 |
| 11 | | | sun | cream* | 4 | cream** | 4 | cream* | 4 | brown | 10 | smooth | 15 | TOTAL- ring: brown/ MANTLE- spots: white | 0 | 2 | 1 |
| 12 | | | reshade | brown | 10 | brown | 10 | brown | 10 | brown | 10 | shaggy | 14 | | 0 | 0 | 0 |
| 13 | | control | shade | cream* | 4 | cream* | 4 | cream* | 4 | brown | 10 | shaggy | 14 | TOTAL- spots: white | 0 | 0 | 1 |
| 14 | | | sun | brown* | 10 | brown* | 10 | brown* | 10 | brown | 10 | shaggy | 14 | TOTAL- stoney: black, white, brown | 0 | 0 | 1 |
| 15 | | | reshade | cream | 4 | cream | 4 | cream | 4 | brown | 10 | smooth | 15 | | 0 | 0 | 0 |
| 16 | black | green | shade | cream | 4 | cream | 4 | cream | 4 | brown | 10 | shaggy | 14 | | 0 | 0 | 0 |
| 17 | | | sun | cream | 4 | cream | 4 | cream | 4 | brown | 10 | shaggy | 14 | | 0 | 0 | 0 |
| 18 | | | reshade | white | 3 | white | 3 | white | 3 | brown | 10 | shaggy | 14 | | 0 | 0 | 0 |
| 19 | | grey | shade | yellow* | 7 | yellow* | 7 | yellow* | 7 | brown | 10 | shaggy | 14 | TOTAL- spots: white | 0 | 0 | 1 |
| 20 | | | sun | olive yellow | 8 | olive yellow | 8 | olive yellow | 8 | brown | 10 | smooth | 15 | | 0 | 0 | 0 |
| 21 | | | reshade | olive yellow* | 8 | olive yellow* | 8 | olive yellow* | 8 | brown | 10 | shaggy | 14 | TOTAL- spots: white | 0 | 0 | 1 |
| 22 | | black | shade | brown | 10 | brown | 10 | brown | 10 | brown | 10 | shaggy | 14 | | 0 | 0 | 0 |
| 23 | | | sun | beige | 5 | beige | 5 | beige | 5 | brown | 10 | shaggy | 14 | | 0 | 0 | 0 |
| 24 | | | reshade | olive yellow | 8 | olive yellow | 8 | olive yellow | 8 | brown | 10 | shaggy | 14 | | 0 | 0 | 0 |
| 25 | | white | shade | olive yellow* | 8 | olive yellow* | 8 | olive yellow* | 8 | brown | 10 | shaggy | 14 | TOTAL- spots: white | 0 | 0 | 1 |
| 26 | | | sun | cream* | 4 | cream* | 4 | cream* | 4 | brown | 10 | smooth | 15 | TOTAL- spots: white | 0 | 0 | 1 |
| 27 | | | reshade | cream | 4 | cream | 4 | cream | 4 | brown | 10 | shaggy | 14 | | 0 | 0 | 0 |
| 28 | | control | shade | yellow* | 7 | yellow | 7 | yellow | 7 | brown | 10 | smooth | 15 | MANTLE- rings: brown | 0 | 2 | 0 |
| 29 | | | sun | yellow* | 7 | yellow | 7 | yellow | 7 | brown | 10 | smooth | 15 | MANTLE- rings: brown | 0 | 2 | 0 |
| 30 | | | reshade | yellow** | 7 | yellow* | 7 | yellow* | 7 | brown | 10 | smooth | 15 | TOTAL- spots: white/ MANTLE- rings: brown | 0 | 2 | 1 |

# Prey selectivity of the nocturnal planktivore, *Myripristis* spp. at different light intensities.

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ABSTRACT. Past studies of size selective predation by visual-feeding planktivorous fish have shown nocturnal predators to be more discriminating than their diurnal counterparts, preying only on the larger plankton in the water column. However, it is not known whether this selectivity represents predator feeding efficiency or inability to see smaller plankton. This study compared prey selection by the nocturnal planktivore, *Myripristis* spp. at two different light intensities. Predation by *Myripristis* on four planktonic organisms of different sizes was tested by subsampling a plankton population in an aquarium before and after inhabitation by two fish for twenty-four hours. Four trials each were run in a dark tank into which minimum light was allowed and in a light tank, which was illuminated for the duration of the fish's habituation. Both the light and the dark experiments displayed the same results: A significant difference in pre and post experimental plankton populations was found for the two larger organisms; little or no predation occurred on the smaller plankton. Thus, results support the hypothesis that nocturnal planktivores of the genus *Myripristis* actively select larger prey. However, other factors such as plankton behavior, plankton escape and defense mechanisms, and predator/prey encounter rates should be considered before definitive conclusions can be made. An alternative explanation for this study's findings is offered: The visual adaptations that allow nocturnal planktivores to detect prey in dim light sacrifice the visual acuity that allow them to detect small zooplankters, thus making it impossible for these fish to prey on smaller plankton.

## Introduction

Our oceans are filled with minute organisms, scarcely visible to the naked eye, called plankton. Plankton provides the foundation for a complex web that is part of a productive marine environment. Planktivorous fish are some of the many predators that rely on these tiny creatures for sustenance. Planktivores have developed features specially adapted for dining on microscopic prey. Diurnal planktivores have a modified jaw that allows them to capture tiny, motile prey in the open ocean. Nocturnal planktivores are further adapted for detecting these creatures in dim light, possessing exceptionally large eyes. However, nocturnal planktivores are more discriminating than their diurnal counterparts, preying only on larger plankton.

Studies examining the gut contents and feeding behavior of the nocturnal planktivore, Myripristis spp. found these fish to prey on plankton 2 mm. or greater in length (Dee and Parrish 1994; Hobson and Chess 1978). Conventional wisdom among the scientific community is that these findings are evidence of a preference for larger prey. A 1997 study done by Fraser and Metcalf offers an alternative explanation to the widespread belief that fish actively select the largest organisms available to them. Fraser and Metcalf tested the feeding efficiency of juvenile Atlantic salmon in relation to light intensity. They found that foraging efficiency of juvenile salmon is high at high light intensities, ranging from daylight to those equivalent to dawn or dusk, but drops markedly at lower levels of illumination; even under the best night conditions (full moon and clear sky), predatory success is only 35% of diurnal efficiency. Less-than-ideal conditions (overcast sky or no moon) can reduce feeding efficiency to 10% of optimal. Fish were unable to find or capture drifting prey in complete darkness. This study is an attempt to answer the question, does light intensity play a role in dictating the feeding behavior of nocturnal planktivores?

Subsequent to this study, the author discovered a 1991 article postulating that adaptations for nighttime hunting that increase visual sensitivity sacrifice visual acuity, making it impossible for nocturnal planktivores to see smaller prey (Sale 1991). This theory offers an alternate explanation for the findings of this study.

## Materials and Methods

### *Plankton*

Plankton used as prey in this study was collected in late October through mid-November, 1998. A 200 μm, cone-shaped standard plankton net towed behind a skiff was the method of collection. All tows were done in Cooks Bay, Moorea. Cooks Bay is located on the north end of the island of Moorea (17° 30'S 143° 50'W). I conducted all experiments in the Gump Station laboratories, located on the west shore of Cooks

Bay. Tows were done between twilight and midnight. Sorokin (1995) showed that zooplankton density by day is one to two orders less than at night because of migration to the bottom by most planktonic organisms. My own observations of daytime tows supported this assertion. Furthermore, the only plankton I found in any significant number during daytime tows were gastropod veligers, which also compose a large portion of the nighttime plankton population. I therefore concluded that tows done only at night sufficed to collect a representative plankton population. Approximately seven liters of plankton water was collected at each tow. However, seasonal changes in current, climate, moonlight and wind within the bay caused natural variation and fluctuations in the composition of the plankton collected. Earlier studies found plankton samples to vary according to method, place and time of collection (Sorokin 1995).

Preliminary examination of plankton collected during several tows in early October found only four types of plankton in numbers large enough to compose a significant portion of the fish's diet. These were: mysid shrimps, (Mysidae, 2-4 mm.), calanoid copepods, (Copepoda, 1-3 mm.), ostracods, (Cypridinida, 300-600 μm), and gastropod veligers, (Gastropoda, 200-500 μm). Based on these observations, I included only these four plankton guilds in my recorded data.

*Myripristis spp.*

I chose the fish *Myripristis* spp. (Holocentridae) as my representative nocturnal planktivore (Allen and Robertson 1994), and is commonly known as the Soldierfish. *Myripristis* is the dominant nocturnal planktivore in Cooks Bay (Graber personal observation during nighttime snorkels). *Myripristis* possess disproportionately large eyes, characteristic of nocturnal planktivores (Sale 1991). Studies done by Dee and Parrish (1993) on the gut contents of *Myripristis amaena* found that plankton represents a substantial portion of this fish's diet. Fish were line-caught off the Gump Station dock and kept in the Gump display tank until needed for the experiments.

*Experimental Set-Up*

Two, 46 liter glass aquariums were set up side by side in the Gump Station wet lab. Approximately 4.5 liters of plankton water collected on tows was added to each aquarium, then diluted with 20 liters of sea water, filtered with a 200μm sieve. An aerator pump was used to oxygenate the aquarium water.

*Subsampling*

A 4.5 mL vial was used to sample the in-situ plankton populations. The diameter of the vial was 1.5 cm; in order to eliminate the possibility of sampling bias due to the small opening, I fashioned a cardboard funnel to the top of the vial, 5 cm in diameter. A length of fishing wire was tied around the vial. The vial was dropped into the aquarium, allowed to sink to the bottom, then reeled in with the fishing line. Before each sample was taken, I stirred the aquarium water in order to distribute randomly the resident plankton. Each sample was then poured into another vial to be transported back to the dry lab. Samples were replaced after analysis.

Each sample was poured into a petri dish, and examined under a dissecting microscope at 13 power magnification, except when higher power was necessary for identification. I recorded the number of each of the four organisms present per sample. I included dead plankton in my counts; any plankton organism present represented uneaten prey. The vials and petri dish were cleaned and dried between each count to avoid counting the same organism twice. Transport vials were also examined to account for plankton stuck to the bottom or sides. Twenty-four subsamples were taken from each of the control and experimental tanks. After obtaining my pre-experiment plankton counts, I placed two *Myripristis* in the experimental aquarium. Different fish were used for each trial in each experiment. All fish were 15-20cm. in length. The fish were left in the aquarium for 24 hours. After removing the fish, I re-sampled the plankton population in each aquarium and recorded plankton present.

*Experiments*

I ran 2 experiments, with 4 trials each. My first experiment was intended to test feeding behavior and prey selection by *Myripristis* in a dark environment. I wrapped each aquarium in aluminum foil in order to obscure all light penetration. The top of the aquarium was kept open during the sampling procedure, but covered for the duration of the experiment. A small amount of light penetrated the aquarium along the bottom edges and through the hole made by the aerator tube. I allowed this under the premise that complete darkness never occurs in *Myripristis'* natural environment.

My second experiment was designed to test predation by *Myripristis* when given ample light. The aquariums were kept open; illumination was provided by daylight (during daylight hours), an overhead fluorescent light, and a 60W incandescent table lamp, set between the control and

experimental aquariums. All lights were kept on for the course of the experiment.

*The Control*

The control tank was subject to the same parameters and sampling methods as the experimental tank, except that no fish were added to the control aquarium. I calculated mean, standard deviation and standard error on the 24 control subsample numbers of each planktonic organism. I used a two-tailed student's t-test to determine a 95% confidence interval for the pre-experiment plankton population. My post-experiment mean for my control fell within this 95% confidence interval in every trial for both experiments, thus ensuring that changes in the plankton population within the experimental tank was due to predation by *Myripristis*.

**Results**

The control was used only to validate experimental results. Plankton population in all control experiments remained stable within a 95% confidence interval. Therefore, results are reported on changes in the experimental in-situ plankton populations only.

The results from the four trials in the dark and light aquariums respectively, were combined; a new mean, standard deviation and standard error was found for each data set. A one-tailed t-test compared the total count of individual plankton eaten for each of the pre and post-experimental populations of mysids, copepods, ostracods, and veligers showed a significant change in the mysid and copepod populations; ostracod and veliger populations remained stable. (Figures 1 and 2) These results were consistent in both light and dark experiments.

**Discussion**

The results demonstrate that *Myripristis* spp. does not change prey selectivity at different light intensities. Results for this study support the hypothesis that *Myripristis* actively selects larger plankton, demonstrating predatory efficiency by maximizing food benefit per amount of capture energy exerted (Bergon et al. 1996). Further evidence for this comes from the Dee and Parrish study (1994). They found that the guts of *Myripristis* contained no identifiable prey if captured during the late morning through early afternoon. The only prey available during daytime hours are plankton smaller than 1 mm (Sorokin 1995; Dee and Parrish 1994). Dee and Parrish concluded that *Myripristis* was therefore not feeding on the smaller zooplankters.

Fish behavior is not the only possible factor in prey selection. Plankton vary not only in size, but in social behavior, swimming speed, color, and migration patterns. Studies done on prey selection by fish found prey size selectivity to be influenced by physiological (visual ability, swimming speed), biological (predator and prey size) and environmental (light intensity, turbidity) factors (Luo et al. 1996). Plankton availability, conspicuousness, and ease in capture likely play a role in what gets eaten.

An examination of the gut contents of *Myripristis* found a significant portion to consist of plankton that migrates up into the water column at night (Dee and Parrish 1994). These fish have also been observed foraging extensively well above the bottom (Dee and Parrish 1994; Graber personal observation). Mysids and copepods migrate vertically on a diel schedule, rising into the water column at night to feed (Sorokin 1995). My own experience with these zooplankters supports these observations. I found mysids and copepods to be active swimmers, tending to reside in the upper layers of the water in the aquariums. On the other hand, I observed that veligers tended to sink to the bottom of the tanks unless agitated. Ostracods also preferred the upper strata of the water column, but the exceptional speed of this zooplankter could explain its avoidance of predation (Graber personal observation).

Color can affect relative vulnerability of various zooplankters as well. Other studies on planktivory have shown fish to select plankton that is more heavily pigmented (Sale 1991). Several species of plankton are highly visible through their pigmented parts, such as eyes or gut contents, thus making them easy targets in dim light. However, color did not appear to be a factor in this study. Veligers were the most heavily pigmented organism, and mysids the most transparent (Graber personal observation), yet mysids were the preferred prey of *Myripristis*.

Sale (1991) offers an alternative explanation for my results and the findings of the studies cited in this paper. Sale argues that nocturnal planktivores prey only on large zooplankton because of an inability to see smaller ones. Most reef fish that rely on vision for nighttime hunting have sacrificed visual acuity for visual sensitivity, which limits their ability to see smaller objects (Allen et al. 1973). In a study on nocturnal fish vision, Sale (1991) found that visual detection of prey likely depends more on maximizing sensitivity and on motion detection than on high visual resolution. Allen et al. (1973) observed

nocturnal planktivores to have a lower cone density than their diurnal counterparts, prompting these scientists to claim that visual acuity is most likely higher in diurnal fishes than in nocturnal species.

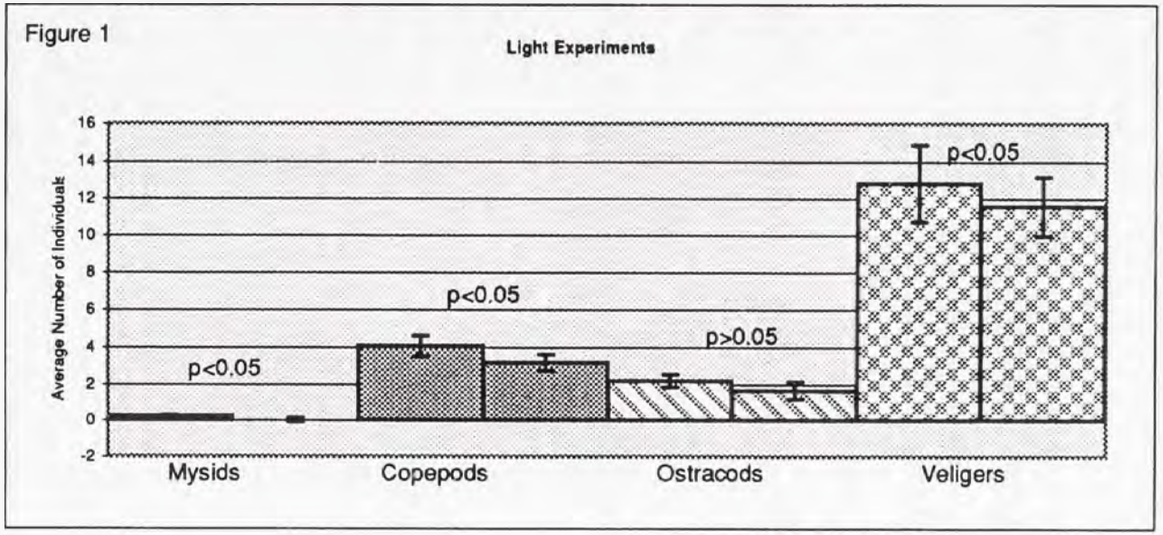
Further support for this argument comes from an examination of planktivore morphology. Most diurnal planktivores have a small, upturned mouth and highly protrusible jaw (Sale 1991). Scientists argue about whether this feature is used to create a suction, which draws prey into the cavity or if the protrusion is used to bring the jaws more quickly to the prey (Sale, 1991). Nevertheless, there is little argument that this feature is an adaptation for fish needing to capture small, motile organisms in the open water. Studies have shown that diurnal planktivores feed on the small (<1 mm.) zooplankters that swim in the water column during the day (Sale 1991). Nocturnal planktivores lack the protrusible jaw of their diurnal counterparts. Sale (1991) argues that the difference in morphology between the temporal guilds represents a lack of selection for features that permit a diet of smaller prey; predators that feed by sight would have no use for mechanisms that accommodate prey too small for them to see.

**Acknowledgements**

I would like to acknowledge the TAs and professors of the 1998 Moorea class. I also want to thank Julio Gutierrez for taking me on countless plankton tows, Miles Zajaczkowski for inventing helpful gadgets, Brooke Weaver for teaching me the ins and outs of Excel graphs, my father, David Graber, for his patience, time and advice, and the rest of the Moorea class for good conversation, great company, and lots of laughs.

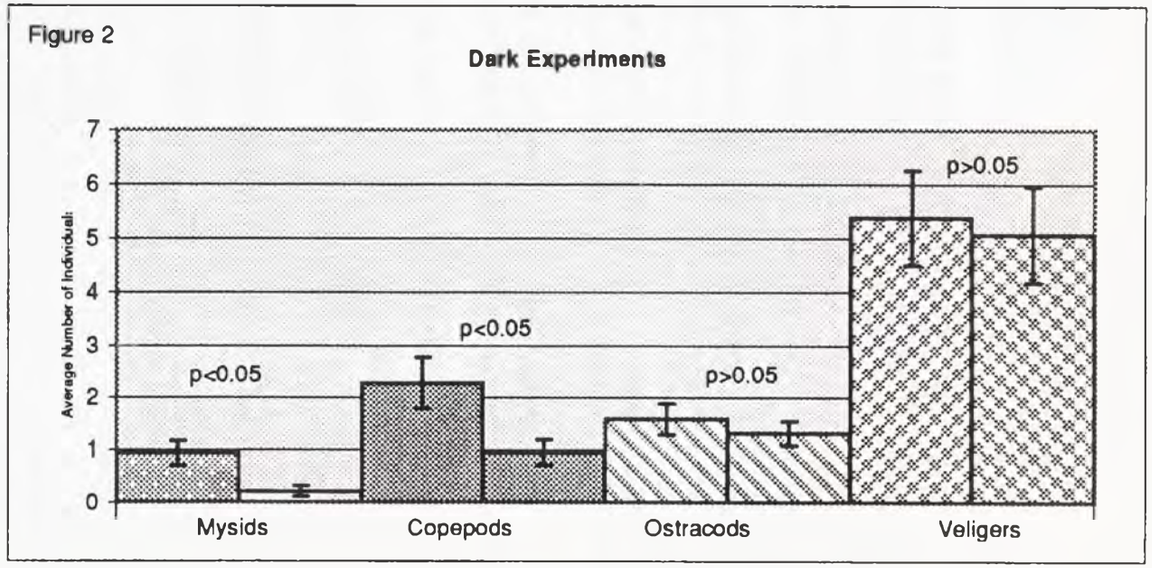
Results from the combined total of the four light-experiment trials. The fir bar for each organism represents pre-experimental mean and 95% confidence interval; the second bar is the post experimental mean and confidence interval.

Figure 1




Results of the dark-experiment trials. The first bar for each organism shows pre-experiment mean and 95% confidence interval; the second bar represents the same for the post experimental populations.

Figure 2



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# Distribution, Prevalence and Host-Size Relationships Of Gill and Stomach Parasites in Four Tropical Pelagic Fish

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ABSTRACT. In this study, stomach and gill parasites of *Katsuwonus pelamis*, *Sphraena barracuda*, *Acanthocybium solandri*, and *Coryphaena hippurus* were analyzed for distribution, prevalence and relationships between fish size and their parasites. Stomach length was used an indicater for fish size. 45% of *K. pelamis* were infected with an average of 1.43 unidentified stomach digenetic trematodes (blood flukes), and there were no significant relationships between size of fish and weight of parasite. 100% of S. barracuda were infected with an average of 2.23 stomach digenetic trematodes, and 84% of *A. solandri* were infected with an average of 1.54 stomach digenetic trematodes. Both species of fish shared the same parasite, *Hirundella ventricosa*, and showed significant relationships between size of fish and parasite weight. Two species of flukes were found in *C. hippurus*, one gill parasite was *Bathyctyle coryphanae*, and the second was an unidentified stomach digenetic trematode. The nematode *Anasakis simplex* was also found in the stomach. *C. hippurus* showed significant relationships between size of fish and diversity of parasites present. The results indicate that fish size is strongly correlated with the intensity and frequency of parasites in all fish studied, except *K. pelamis*. This may be explained by (1) mechanisms of host or parasites (2) growth of parasites with the host over its life, or (3) accumulation of parasites over time.

## Introduction

Marine parasites are probably the least known group of organisms (Rhode 1993), in spite of their ecological, economic, and public health importance (Hargis 1985, Kinne 1990, Sindermann 1966, 1990). Most of what is known about them consists largely with taxonomy and life cycles of fish parasites (Grabda 1991), and in the tropic even this is often unknown because of the diversity of fish present (Rhode 1993). The present state of knowledge on the subject is at its most elementary levels, but the complexity of parasite-host relationships are as intricate as food webs described by ecologists (Williams and Williams 1996). Many parasites display life cycles with at least three intermediates, and this can often be compounded with other factors that make them very difficult study organisms.

Authors have long argued the effects of parasites on their hosts, and a concise general answer still does not exist. Experiments on the "goodness" of parasitism has shown that the host often benefits from the parasite by increasing in size or receiving deficient vitamins and enzymes (Holmes 1986). Several species of parasites are known to be commensals, living on the bacteria and detritus in the gut under certain conditions (Rhode 1982). These interactions are the most poorly understood aspects of the relationship between host and parasite.

Other studies have shown parasites to be responsible for mass moralities, reduction of reproductive organs, disease and skeletal abnormalities (Rhode 1993). It is estimated that one-fifth to one-half of all fishery resources is loss to disease, and an unknown number of which may be caused by interactions with parasites.

Parasitologists have long tried to understand the relationship between the size of a host and its parasite. Many studies have shown an increase in intensity of infections in relation to host size (Amin 1985). However, the broad range of host and parasites makes a complex puzzle, and each relationship must be examined individually.

In this study, I sampled *Katsuwonus pelamis* (bonito), *Sphraena barracuda* (barracuda), *Acanthocybium solandri* (wahoo), and *Coryphaena hippurus* (mahimahi) to determine the distribution and prevalence of stomach and gill parasites. No oceanic collections of parasites from these fish near Moorea have been published. I present evidence that host size can play an important role in determining the intensity and frequency of parasites, and give possible explanations for the occurrence.

## Materials and Methods

Collections for this study were taken October 3through November 17, 1998 from the South Pacific Ocean in the waters surrounding the Island of Moorea (149'50 W, 17'30 S), French Polynesia. The average mean temperature for the surface of the open ocean in Moorea during the collection time was 26.6'C. All specimens were collected by local professional fishermen using hook and line, with exception of *C. hippurus* which was often taken with throwing spears.

All fish were positively identified, and the stomach was measured to the nearest millimeter and used an indicator for the size of the fish. Gills, stomach contents and linings were all examined for parasites. Individuals species of parasites were identified, weighed and counted for each specimen. Parasites were preserved in 5% formalin in seawater, cleared in glycerin and identified according to descriptions in Williams and Williams (1996) and assistance of Dr. Mike Moser.

*Data Analysis*

Data was pooled by host species and checked for normal distributions using Shapiro-Wilk test for normality. Prevalence was calculated as the number of host species infected divided by the number of hosts examined (Williams and Jones 1994). The mean parasite weight in each species of host was compared using one way ANOVA and all pairs were tested with a Tukey-Kramer HSD adjustment (JMP 1996), using confidence intervals <.05. Comparing total mass of parasites was useful as an indicator to identify which species of fish carried the largest parasite load.

To show trends in host size to mass of parasite, simple linear regressions were performed using stomach length (x-axis) to parasite weight (y-axis) for each species of fish. Species of fish were calculated separately to show individual trends within populations and because of variability of stomach length when compared interspecifically.

A t-test was performed to compare the mean stomach length of infected fish vs. uninfected fish in *K. pelamis* to illustrate any difference in size.

*C. hippurus* was the only fish in which more than one species of parasite was observed, and a simple linear regression was done using stomach length of *C. hippurus* (x-axis) to diversity of parasites (Y-axis). One way ANOVA was performed to compare the diversity of parasites present in three stomach length size classes of *C. hippurus* and all pairs were compared with a Tukey-Kramer HSD adjustment, using confidence intervals <.05. Stomach size classes were divided into big (over 25cm), medium (18-25cm), n and small (under 18cm).

## Results

*Distribution and Prevalence*

Information was collected on five different types (species or species complexes) of parasites from four fish. A summary of the raw data is given in Table 1.

45% of 121 *K. pelamis* were infected with an average of 1.43 parasites. The parasite was an unidentified digenetic trematode (unknown 1).

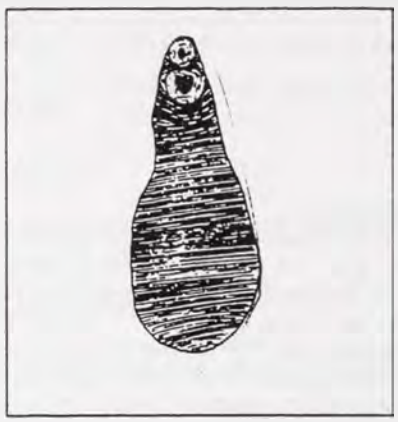

Figure 1: A stomach fluke, *Hirundella vetricosa*

100% of the S. barracuda sampled were infected with an average of 2.23 stomach flukes, identified as *Hirundella ventricosa*. *A. solandri* shared the same fluke, *H. ventricosa*, exhibiting an 84% infection rate out of 13 fish sampled, with an average of 1.54 parasites.

The 39 *C.hippurus* used in the study shared no parasites with other fish. Infection rates were 100%, with an average of 48.7 parasites per fish. A gill fluke was identified as *Bathycotyle coryphaenae*. A second digenetic trematode was found attached to the wall of the stomach and was unidentified (unknown 2). One species of nematode, *Anasakis simplex*, was in the stomach contents, lining and adjacent flesh.

To better understand the load of parasites interspecifically, one-way ANOVA was used to compare the mean parasite weight in each fish. Mean parasite weights per species of fish were shown to be significantly different from one another (df=3, F=419.86, and P<.001). Using pairwise comparisons with a Tukey-Kramer adjustment, all pairs still differed from each other, except *A. solandri* and *C. hippurus*. In Table 1, the mean parasite weight for each fish is given.

*Parasite-Host Size Relationships*

Simple linear regressions showed a high correlation between host stomach size and parasite weight in *S. Barracuda* and *A. solandri*, both fish shared the same stomach parasite *H. ventricosa*. In these two cases size explained 61% and 55% of the variance respectively (in both P<.001). Figures 2 and 3 illustrate the relationship. No significance in length of stomach to weight of parasites was found in the case of *K. pelamis* ($r^2$=.04, and P=.146) or *C. hippurus*. ($r^2$=.26, and P=.008)

(a)

(b)

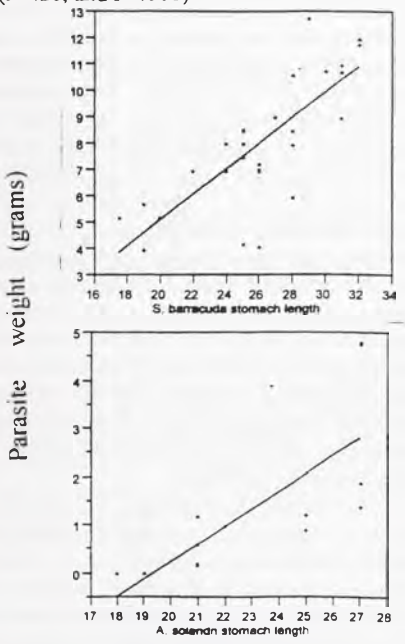


Figure 2: Effects of fish size on parasite mass of *(a) S. barracuda* and *(b)A. solandri*.

To explore whether any difference existed between a *K. pelamis* infected and non-infected fish, I performed a t-test. The results indicated that there was no significant difference in size between the two classes of fish (F=.03, and P=0.86).

In *C. hippurus* a second trend was observed, in which the diversity of parasites increased as a function of the size of the stomach length. A simple linear regression showed that size explained 54% of the variance associated with diversity of parasites present. One way ANOVA showed that the diversity of parasites present in three different size classes were significantly different from each other, and all pairwise combinations were also significantly different from one another as shown in Figure 3.

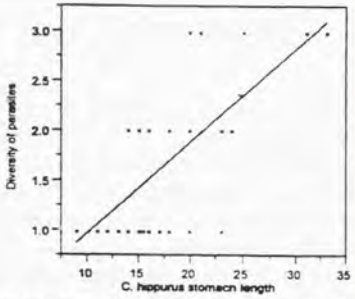


Figure 3: Effect of size on diversity of parasites in *C. hippurus*

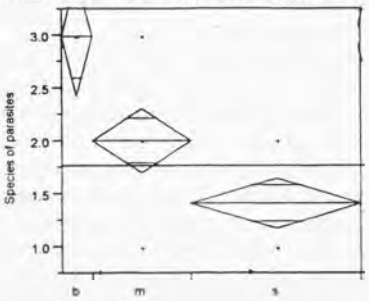


Figure 4: (a) *C. hippurus* diversity of parasites per size class. (Big=b, medium=m, and small)

Most commonly, the parasite that was found in *C. hippurus* when fish stomach length was smallest (below 18 cm) was stomach digenetic trematode 2 (Gutierrez, J. pers. obsev. 1998). Fish that were above 18cm were often infected with either the gill fluke *Bathycotyle coryphaenae* or nematode *Anasakis simplex*, and fish with stomach lengths above 25 cm usually were infected with all three.

| Host | Parasite | Prevalence | Mean Parasite Weight (grams) | # of fish sampled |
|---|---|---|---|---|
| *A. solandri* | *H. ventricosa* | 84% | 1.39 g ± 0.23 | 13 |
| *C. hippurus* | *B. coryphaenae*, *A. simplex*, and digenetic trematode 2 | 100% | 1.06 g ± 0.13 | 39 |
| *K. pelamis* | digenetic trematode 1 | 45% | 0.37 g ± .07 | 121 |
| *S. barracuda* | *H. ventricosa* | 100% | 7.98 g ± 0.15 | 30 |

Table 1: Illustrates key points of hosts.

**Discussion**

In addition to describing distribution and prevalence of parasites on four pelagic hosts, this study set out to define the effects of fish size on its parasites. Results indicated that in the case of *S. barracuda* and *A. solandri* the weight of their parasite, *H. ventricosa*, increases as fish size increases. This data is slightly compounded because it describes intensity and frequency of parasites, but it allows for speculation on some of the mechanisms that could control this relationship.

Flukes are believed to be permanent parasites in most marine fishes (Williams and Williams 1996). This could possibly suggest that *H. ventricosa* is a permanent resident in *S. barracuda* and *A. solandri*, and the mass of parasites present increases with fish size. The pairwise comparison of mean parasite weight in *S. barracuda* and *A. solandri* were shown to be significantly different from one another. Although this study does not include average weight of fish, it was been shown (Williams and Williams 1996) that *S. barracuda* is on average 20 lbs heavier than *A. solandri*. This data also shows that size of fish can have a direct impact on its parasites, however additional factors may be affecting the outcome. Another common explanation parasitologists have used to explain such relationships is that parasites accumulate over time. For these two hosts, this would indicate that older and larger fish consume more food and more intermediate hosts than smaller conspecific hosts, and therefore harbor more parasites. It is not known when *H. ventricosa* begins to parasitize the final host, and this information is critical to confirm or deny either idea. High infection rates do suggest that almost all fish are exposed to the parasite at some point in their life history.

Williams and Williams (1996) also suggest that there may be some mechanism of the host or parasite that regulates number and size. The idea that the processes leading to a predictable parasite burden in relation to fish size are density-dependent. Brown (1986) gives evidence on experimental primary and superimposed infections of hosts with various dosages of parasites that indicate density-dependent establishment reached high levels partly dependent on host size. Additionally, he advised that the size of parasites themselves seemed to have an influence. Caution is needed when attempting to interpret density dependent effects within a parasite population as the results of intraspecific competition. Immune reaction intensities elicited from the host invariably depends on the density of parasites, which reflects an active reaction by the parasites environment. No experimental studies on density-dependence and natural populations of marine fish parasites have been published.

Low infection rates and no significant difference in parasitized and non-parasitized fish characterized this study's findings on *K. pelamis*. The absence or presence of parasites indicated that transmission may represent stochastic occurrence over time, and is not related to fish size. In a study defining the parasites throughout the Pacific of *K. pelamis*, Lester (1986) suggested that the rate of parasite infections could change dramatically from school to school. No evidence is known on longevity

Of schools or life of digenetic trematode 1, but it is possible that the data represents different populations of fish with varying exposure to a parasite. Probably the most critical information that is needed to understand how schooling could affect parasite transmission is the life of the school. Lester (1986) suggests that they could stay together from a day to years, so concrete answers are not known.

Although no significance was observed in the relationship of fish size to parasite mass, a second trend was documented in which diversity of the parasite infra community increased as the size of *C. hippurus* increased. This trend may also be explained by an idea put forth earlier, accumulation of parasites over time.

Alternatively, Williams and Williams (1996) propose that at least one species, *Bathycotyle coryphanae*, only infects the largest *C. hippurus*. This could possibly be explained by an immunity that smaller fish retain and larger ones do not. Noisi and Maillard (1980) describe a similar trend in the fish *Sparus aurata,* which exhibit younger fish lacking parasites until a size of 25cm is reached. However, this may be bound up in other factors that change as a fish grows older, such as feeding and sexual behavior (Rhode 1993).

The inter- and intra- specific relationship of parasites within a host have often been described as 'exploitation' or 'interference' (Dobson 1985). In the case of a large *C. hippurus*, the joint use of the host species by three parasites would be understood as exploitation. Factors that allow competing species of parasites to co-exist is the independent aggregations of distribution within the host. *C. hippurus*'s parasites were found in such a distribution, with one species found in the gill, another mixed among the stomach contents, and a third attached to the inner wall of the stomach. Further experimental tests are needed to assess the importance of competition and partitioning of resources in determining the structure of such complex parasite infra communities.

One of the great difficulties with sampling natural populations of fish for parasites is that hosts that are infected to the point of mortality are almost never found. It is possible that smaller *C. hippurus* that become infected with all three species of parasites, do not survive and are never collected.

This study represents preliminary efforts to understand parasite host relationships in the tropics. I offer some explanations for the trends seen, however the answers are still not known. A number of the factors discussed could be responsible for the relations seen in fish size to their parasites. Research that would be most effective in further defining this relationship would use natural populations as well as laboratory manipulations. Some studies have attempted to recreate the internal environment of the host in the laboratory. Although this may be especially difficult for pelagic fish when trying to recreate pressure and temperature that could be experienced in the deep ocean, as well as the internal conditions of a fish.

There remains an enormous amount of research left to be done on parasites in the tropics. Some of the most exciting applications of parasites with pelagic fish are as biological tags, to help track migrations and intermixing of different populations. Many parasites still have undefined life cycles, and much debate still exists over such topics as host specificity.

**Acknowledgements**

I would like to that thank all the instructors of the course, especially Jere, Amy and Virgina- all of whom demonstrated the true nature of a teacher and a scientist to me. I indebted to my parents for affording me the opportunity to pursue all my dreams. I give special thanks to Dr. Mike Moser, for his guidance and assistance in identifying many of my parasites. To the good men and profeesional fishermen of Moorea, Pascual, Joe and Jacque who gave all my samples, shared their catch, and showed how to catch the big fish.

Finally, I would like to thank all my classmates for a great Halloween, many beautiful moments that will never again pass, and their friendships.

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# Distribution and abundance of two gastropods (*Melanoides tuberculata* and *Thiara granifera*) in taro (*Colocasia esculenta*) plantations in Moorea, French Polynesia

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ABSTRACT.

This study compared the relative distribution and abundance of *Melanoides tuberculata* and *Thiara granifera* in lowland / wet taro (*Colocasia esculenta)* plantations in Moorea, French Polynesia. Microhabitat and food preferences were studied both in the field and in the laboratory. *M. tuberculata* was found to feed primarily on algae and to prefer coarse sand substrates and stagnant waters. In contrast *T. granifera* fed on lettuce in laboratory tests, and preferred fine sand substrates and flowing water. *M. tuberculata* was found in highest densities in the iron and channel taro plantations, while highest densities of *T. granifera* were found in the channel without taro and the channel taro plantation.

## 1. Introduction

*Colocasia esculenta* ( red taro) is a staple food crop throughout much of the world including, French Polynesia (Wang 1983). Because of the methods by which taro is cultivated, plantations create unique habitats for freshwater organisms. In this study, the two dominant organisms found in these environments were the snails *Melanoides tuberculata* and *Thiara granifera* (Figure 2). Although I have found no previous literature about these snails living naturally in this specific environment, *M. tuberculata* has been introduced into *C. esculenta* plantations for biological control purposes and found not to survive very well (Pointier et al, 1993).

*M. tuberculata* and *T. granifera* are burrowing snails completing their reproductive life cycles in the freshwater environment. *M. tuberculata* is both viviparous and parthenogenic (Bij De Vaate et al. 1994). *M. tuberculata* was the focus of the study because it serves as the first intermediate host for the human liver fluke *Opisthorchis sinensis* (Dundee and Paine, 1977) . *Opisthorchis sinensis* is transmitted from the snail to a fish, which serves as the second intermediate host, and is then transmitted to humans through consumption of raw fish. Although *Opisthorchis sinensis* has not yet reached French Polynesia, estimates have been set for its possible arrival late in the twenty-first century (B. Salvat as communicated by V. Resh). The arrival of this parasite poses potentially serious health risks to those working in these plantations.

This study was designed to suggest preliminary methods of reducing numbers of *M. tuberculata* from taro plantations, by looking at the distribution, abundance and biological characteristics of this species.

## 2. Materials and Methods

### *2.1 Site Selection*

Field data was collected in September through November 1998 on Moorea, French Polynesia. There were a total of six sampling sites, including three different types of taro plantations, two freshwater streams, and one human made channel without taro present. The total number of snails was counted, and the first 100 snails encountered were measured for a site quality analysis. Abiotic factors were also analyzed including flow rate at each site, and dominant for each individual sample. The six sites are described as follows:

1. Channel Taro Plantation
   This plantation is located in a small valley on the north west side of the island (between PK 20 and PK 21), approximately 10meters up the single dirt road that runs through the valley (Figure 1). Within the plantation channels have been cut around taro beds, which are raised above the natural topography. An adjoining stream, less than 100 m away feeds the channels. Water flow is constantly

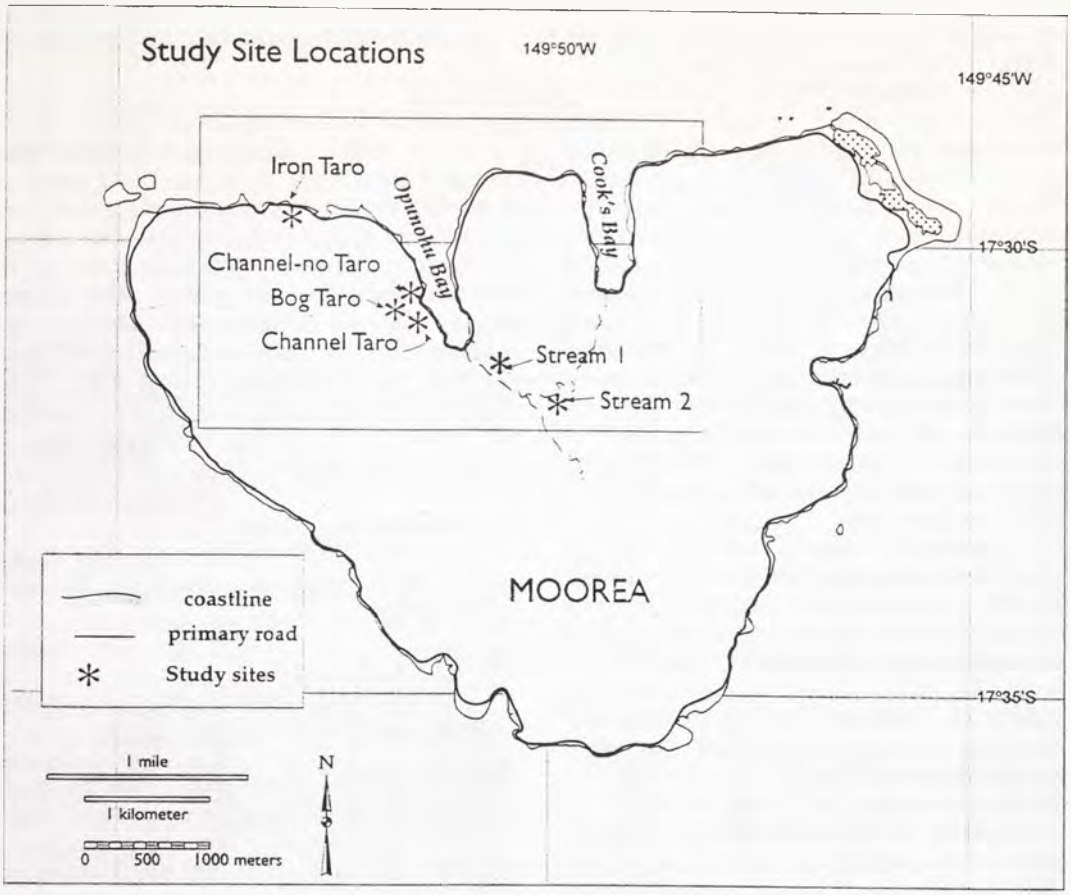



**Figure 1.** Study site locations, Moorea French Polynesia

**Figure 2.** Study organisms: *Melanoides tuberculata* (top), *Thiara granifera* (bottom)

maintained in bordering channels, however, water in inner channels remains stagnant.

2. Iron Taro Plantation
   This plantation is also located on the north west side of the island (between PK 22 and PK 23) alongside the main road (Figure 1). Similar to site 1, channels have been cut around taro beds, which are raised above the natural topography of the area. The beds are lined by corrugated iron siding, which appear to have left iron oxide residue in the soil and water of the channels. Soil in this plantation was dark gray in color and smelled of sulfur when disturbed, suggesting anoxic conditions. Channels are fed by a stream, which is approximately 0.5 km away. There was no detectable water flow within the channels.
3. Bog Taro Plantation
   This plantation is located in the same valley as site #1 approximately 100m farther up the dirt road (Figure 1). It is unlike sites 1 and 2 in that no channels are cut through the plant beds. Instead the entire plantation is flooded with water fed by a natural spring within the plantation. Although the soil is constantly moist the water level is highly variable within the plantation.
4. Stream #1
   Stream site #1 is located in the Opunohu Valley approximately 0.5km upstream from the Opunohu Bay. It is approximately 100m away from the road that runs through the Opunohu valley. The canopy is dominated by Tahitian chestnut (*Inocarpus fagifer)* and hibiscus (*Hibiscus tiliaceus*).
5. Stream #2
   Stream site #2, also located in the Opunohu Valley, is approximately 1.5 km upstream from the Opunohu Bay. A break in the sampling area occurs where the stream runs through a culvert under a road bridge. The dominant vegetation surrounding the stream was Tahitian chestnut (*Inocarpus fagifer*) and hibiscus (*Hibiscus tiliaceus*).
6. Man made channel – no Taro
   This site, also located in the same valley as sites 1 and 3, runs parallel to site 1 approximately 5 meters away from the outer channel of the plantation. The channel is comparable in width and depth to the channels in sites 1 and 2, however there is a constant flow of water through the channel, fed by the same natural spring that feeds site #3.

*2.2 Collection and Sorting*

Twenty 0.05m$^3$ sediment samples were taken randomly from each of the six sites using an aluminum corer. Approximate flow rate was measured by time it took a stick to float down a set distance. Samples were taken back to the laboratory and sorted using three sieves (2.0mm, 500µm, 250µm) to determine the dominant sediment size for each sample. Snails were removed from sediment, their shell length measured for site quality comparison (Figure 3), and stored in a running freshwater tank for laboratory experiments.

*2.3 Laboratory Experiments*

Snails stored in freshwater tanks were used in various experiments to determine biological characteristics.

*2.3.1 Substrate preference*

Fifteen snails were placed in the center of the tank, equidistant from four

different substrate choices (rocks, pebbles, coarse sand, and fine sand) placed in each corner. Snails were left for a period of 24 hours, after which time the number of snails in each distinct substrate was counted. The experiment was repeated four times, each time changing the samples of the substrate and rotating its location in the tank. *M. tuberculata* and *T. granifera*, were first tested in isolation, then with both species in the same tank.

*2.3.2 Food Preference*

Fifteen snails were placed in the center of the tank, with three different food choices (algae, detritus, and lettuce or bok choy[1]) placed in three of the four corners. The fourth corner was left empty. Snails were left for 24 hours, after which time the number of snails in each corner was counted. Experiment was repeated four times, with food samples changed and their location in the tank rotated each time. Both *M.*

*tuberculata* and *T. granifera* were tested in isolation.

*2.3.3 Clustering*

[1] Depending on availability

| | M. tuberculata | T. granifera |
|---|---|---|
| Iron Taro | 291±156.0 | 0 |
| Channel Taro | 41±26.9 | 129.8±160.2 |
| Channel- no taro | 0 | 943±217.1 |
| Bog Taro | 0 | 0 |
| Stream #1 | 4±0.5 | 98.8±15.3 |
| Stream #2 | 0 | 0 |

**Table 1** Abundance of two gastropods at six sites Moorea, French Polynesia

Fifteen snails (*M. tuberculata*) were placed in the center of the tank. Twenty-four hours later number of snails
in each corner was counted. The experiment was repeated four times.

*2.4 Data Analysis*

The mean number of snails per cubic meter and corresponding confidence intervals were computed for all field sites to determine significance of macrohabitat preferences observed in the field. Flow data collected in the field was regressed against number of gastropods to demonstrate the influence of velocity on snail abundance. The first hundred snails encountered at each site were measured for length and regressed against number of snails as an indication of site quality. A Chi- squared analysis was used to determine relative significance of microhabitat preferences observed in laboratory experiments.

**3. Results**

*3.1 Abundance*

*M. tuberculata* was found to be more abundant ($p \leq 0.05$) in the iron taro plantation (291.0± 156.0 individuals/$m^3$) than in the channel taro plantation (41 ± 26.9 individuals/$m^3$)(Table 1). It was found in significantly smaller numbers in the stream transect #1 (4± 0.5individuals/$m^3$) than in either of the preceding two sites. *M. tuberculata* completely absent from the bog taro plantation, stream transect #2, and the channel without taro.

*T. granifera* was found in higher numbers ($p \leq 0.05$) in the channel without taro (943.8 ± 217.1 individuals/$m^3$ ) than in the channel taro plantation (129.8± 160.2 individuals/$m^3$) significantly lower numbers were found in stream transect #1 (98.8±15.3 individuals/$m^3$ ) than in either of the two aforementioned sites. *T. granifera* was completely absent from the iron taro plantation, the bog taro plantation, and stream transect #2.

*3.2 Factors influencing Microdistribution*

Microhabitat differences were observed both in the field and the laboratory to determine how they influence the distribution of gastropods.

Physical factors such as flow, substrate, and food preference were studied as well as the tendency to cluster or disperse. Site quality was also analyzed for each species under the assumption that larger mean shell length is an indication of higher site quality.

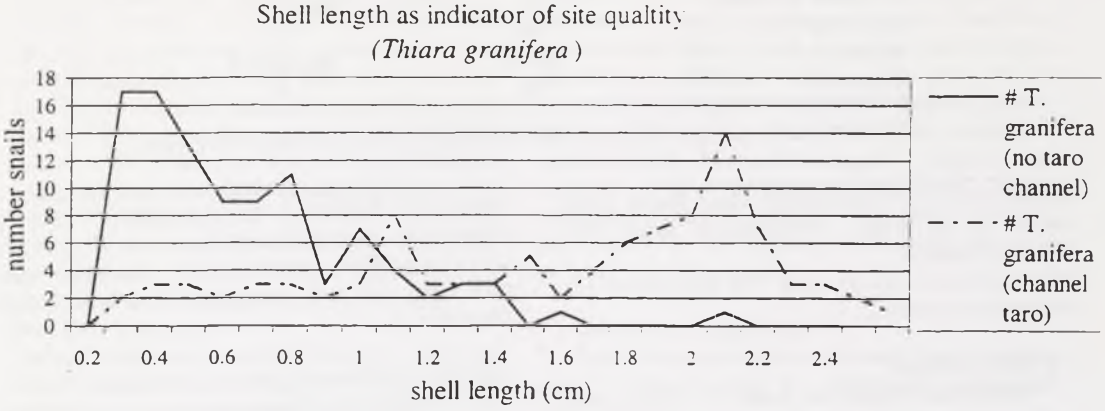
3.2.2 *Flow*

Flow rates taken in the field were plotted against number of snails found (Figure 3). The numbers of *M. tuberculata* peak in stagnant water (0 m/sec), whereas the highest incidence of *T. granifera* occurs at a flow rate of 0.11 m/sec. Numbers of *M. tuberculata* remain close to zero when any flow is present, whereas populations of *T. granifera* seem to be present throughout the range of flow encountered in this study.

3.2.3 *Substrate Preference*

Field data shows a clear substrate preference for both species of gastropods (Figure 4). The majority of *M. tuberculata* sampled (53%) were found in substrates dominated by coarse sand, whereas the majority of *T. granifera* were found (53%) in fine sand dominated substrates. Both *M. tuberculata* and *T. granifera* showed a secondary preference for pebble dominated substrates (24% and 34% respectively). *M. tuberculata* did not show much of a preference between fine sand and rock (13% and 10%

respectively), and was completely absent from substrates dominated by detritus. Similarly, *T.*



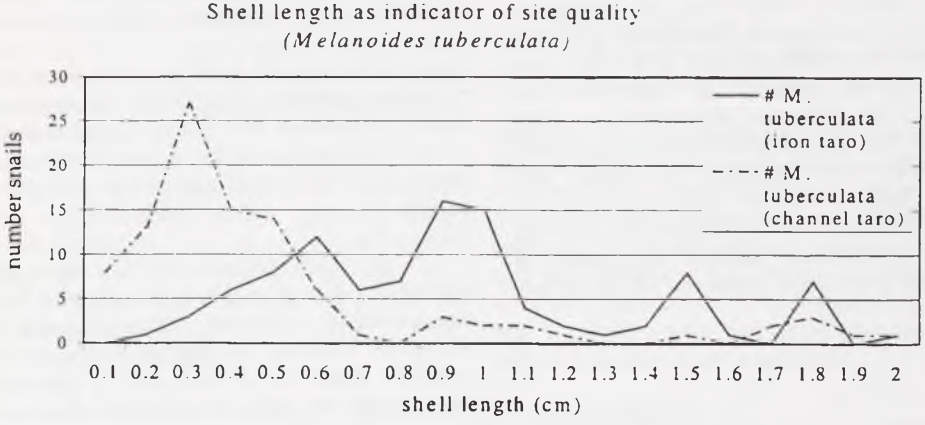




**Figure 3.** Site quality comparisons

*granifera* did not show much preference between coarse sand and rock (6% and 5% respectively), however was found in small numbers (2%) in substrates dominated by detritus.

Laboratory experiment results for *M. tuberculata* support the trend observed in the field. *M. tuberculata* showed a significant (p= 0.05) substrate preference for coarse sand both when isolated and when in the same tank as *T. granifera*. Corresponding with field observations, when isolated in the laboratory *T. granifera* also showed preference for fine sand However when placed in the same tank as *M. tuberculata* the snail showed preference for silt.

3.2.4 *Food preference*

In laboratory food preference studies *M. tuberculata* showed a significant ($p \leq 0.05$) preference for algae over detritus or lettuce / bok choy. *T. granifera* showed preference for lettuce/ bok choy.

3.2.5 *Tendency to cluster vs. disperse*

No significant results were found for clustering tendencies in *M. tuberculata*.

*3.2.5 Snail shell length*

Average *M. tuberculata* shell length in the iron taro plantation was found to be 0.954cm whereas average shell length in the channel taro plantation was 0.499cm.

Average *T. granifera* shell length in the channel without taro was 0.572cm and 1.4cm in the channel taro plantation.

3.3 ***Other organisms found***

*3.3.1 Iron Taro Plantation*

- *Chironomus* larvae (approx. 125)[1]

*3.3.2 Channel- no Colocasia Esculenta*

- *Hyradinia Piscolede* (approx. 3)
- Freshwater shrimp

*3.3.3 Stream Transect #1*

- *Neretina turrita*
- *Clithon spinosa*

**4. Discussion**

The high numbers of *M. tuberculata* found in the iron taro plantation correspond with trends found in laboratory experiments. Although all four substrate types (rock, pebble, coarse sand and fine sand) were evenly distributed throughout the plantation, *M. tuberculata*'s preference for coarse sand and aversion for rocky substrates was observed. 51% of the snails were found in samples dominated by coarse sand while only 12% were found in rocky samples. These results concur with Liu and Resh's findings (1997) for smaller substrate preference observed in the Opunohu River. This substrate selectivity accounts for the large deviation from the mean ($\mu$= 291 individuals/$m^3$, $\sigma$ = 346.9) calculated for this site. This clustering appears to be related to substrate and food preferences as opposed to behavioral tendencies as laboratory experiments did not show any significant clustering trend in the absence of these variables. However, the small scale of the experiment may also explain these results. Perhaps a larger tank (> .25$m^2$ base) would have given different results on this account.

The complete absence of *T. granifera* at this site is not related to substrate preference, as fine sand is present at this site. The absence of water flow is the probable explanation as only 8% of *T. granifera* sampled in this study were found in stagnant water. In contrast 91% of *M. tuberculata* were found in these areas of zero flow. This preference for stagnant water is most likely related to food source availability as other studies have found *M. tuberculata* in areas of extremely high flow such as the faces of waterfalls (Resh et al. 1988). In laboratory experiments *M. tuberculata* showed a preference for algae which perhaps grows best in areas of stagnant water (Pentecost 1984 , Round 1965).

This trend may also explain the complete absence of *M. tuberculata* from the channel without taro. The constant water flow along the length of the channel ($\mu$ = 0.11 m/sec) , and minimal rocky substrate (15% of samples taken), make algal growth difficult, and thus food source absent. The absence of coarse sand in this channel may also explain the dearth of *M. tuberculata*. Previous studies have also found that *M. tuberculata* prefers areas where flow is minimal (Dundee and Paine, 1977). The dominance of fine sand (85%) and constant water flow ($\mu$ = 0.11m/sec) at the site may explain the extremely high numbers of *T. granifera* (943.8 ± 217.1 individuals/ $m^3$), as these results correspond to laboratory experimental data as well as trends found in previous studies (Liu and Resh 1997). Additionally, the high numbers of *T. granifera* present at this site suggest that the colonization of these channels is independent of the presence of *Colocasia esculenta*.

*T. granifera* was also present in stream transect #1, where the average flow rate was 0.232 m/sec and the substrate was divided among small rocks (25%), pebbles (35%), coarse sand (30%) and fine sand (10%). Despite the various choices of substrate at this location no preference was observed, as snails were fairly evenly distributed along the transect. *M. tuberculata* was present in much lower frequencies (4 ± 0.47 individuals/ $m^3$) presumably due to the heavy flow rate again preventing sufficient algal growth to support a viable population. Although previous studies found similar population numbers for *M. tuberculata* (Liu and Resh 1997) at comparable distances upstream, a second stream sampling

[1] Also found to be associated with *M. tuberculata* by Dundee and Paine (1977)

was done to assure all possible habitat preferences in the plantations were duplicated in the streams.

Stream transect #2 was chosen to include both areas of flow and stagnant water. As expected, in areas of measurable flow *M. tuberculata* was again absent from the transect. However, it was also absent from areas of stagnant water where 60% samples taken were composed mainly of coarse sand. These results may be explained by environmental stress, as *T. granifera* was also completely absent from this transect. The transect runs along the border of a dry/upland taro plantation where pesticide and fertilizer runoff may render the area an unfavorable habitat. Additionally, a portion of the stream is culverted under a road possibly hindering migration to the site.

*M. tuberculata* and *T.granifera* were also completely absent from the bog taro plantation. Again, although the water was completely stagnant and the dominant substrate was a mixture of coarse and fine sand, environmental stress may be reason neither freshwater species can survive here. The water level at this site was highly variable, and much of time the plantation was completely drained. Neither *M. tuberculata* nor *T. granifera* are tolerant of desiccation (Pointier, 1993 and personal observation) which may explain the absence of both species at this site.

The channel taro plantation seemed to be a suitable habitat for both species of snails. Coarse and fine sand were both present at the site (65% and 35% respectively), and areas of both flow and stagnant water were present. Algal mats were observed floating in the stagnant water and *M. tuberculata* were often found feeding on the mats in samples taken back to the laboratory. Populations of both species were patchy throughout the plantation, which would account for the large deviations from the mean calculated for each species (129 ± 365.5 *T. granifera*/ $m^3$ and 41 ± 61.4 *M. tuberculata*/ $m^3$). Congruous with laboratory experiments most of the *M. tuberculata* (91%) were found in samples dominated by coarse sand and most *T. granifera* (85%) were found in samples dominated by fine sand. No correlation was found between location of either species and presence or absence of flow, possibly because food availability was not a limiting factor at this site.

Based on the assumption that the larger the average shell length the better the site quality, relative site quality comparisons were made for each species (Figure 3). The average shell length was calculated and compared for *M. tuberculata* at the iron and channel taro plantations, and for *T. granifera* at the channel without taro and the channel taro plantation. Results suggest a density dependant relationship between shell length and number of snails for *T. granifera*, as the site where the snails were most abundant (channel without taro) had a lower average shell length. The higher average shell length at the channel taro plantation, however, suggests an overall better site quality. In contrast, *M. tuberculata* site quality is currently not density dependant, as the site with the highest number of snails also had the largest average shell length, and thus the better site quality.

## 14. Conclusion

Plantations of *Colocasia esculenta* evidently provide a suitable habitat for both *Melanoides tuberculata* and *Thiara granifera*. Populations are not a problem at this time as the snails do not appear to be pest species. *T. granifera* in particular does not pose any threat however, as intermediate host for the human liver fluke *Opisthorchis sinensis M. tuberculata's* colonization of these plantations may pose serious health risks in the future. Preventative measures should be taken to minimize and eventually eliminate populations from these habitats. Although more research is needed, based on this study, possible methods of minimizing numbers would be to increase water flow through the channels, as well as increasing substrate size. Additionally, periodic draining of the channels may provide enough stress in order to render the plantations an unsuitable habitat.

## Acknowledgments

Thank you to all of the GSI's, involved with the class for all of your long hours, advise, tolerance and card playing. Thanks also to all of the professors involved in the course, especially to Vince Resh, for your much appreciated vested interest, and to Jere Lipps for helping this project get off the ground. Lastly, thanks to my field buddies for jumping in the mud with me without rubber boots.

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# Suggestions for management of *Trochus niloticus* stocks based on size-selection by people who collect the marine snail for its meat

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ABSTRACT. In Moorea, French Polynesia, the size preferences of people who collect *Trochus niloticus* for meat may have implications for management of *Trochus* stocks. Comparisons between the size-class distributions of *Trochus Niloticus* collected by people for meat and available live populations in fished areas suggest that some collectors selectively choose larger sizes, some have no size preferences, and none adhere to the minimum and maximum size restrictions set by the government. Interviews with seventeen collectors corroborated these results. A model was constructed to illustrate the potential effects of three types of *Trochus* collectors on the reproductive potential of a fished population. The three types of collectors were 1) a collector who removed *Trochus* only within legal size limits 2) a collector who was indiscriminate in her size-selection 3) a collector who selectively chose larger sizes. The model predicts that the law-abiding collector would have the least negative impact, and the large-size-preferring collector would have the greatest negative impact on a *Trochus* population's reproductive potential. Factors that might affect collectors' size-preferences include the size-class structures and densities of fished populations. Another potential factor is collectors' personal conservation concerns. Five of the collectors interviewed said they collect larger *Trochus* and leave the small to ensure a future *Trochus* supply. This stewardship strategy is incoherent with the strategy for *Trochus* conservation employed by the government. If collection of *Trochus* for meat were extensive enough, successful management of *Trochus* stocks might require that people collecting *Trochus* for meat abide by the size restrictions set by the government. These collectors might be encouraged to follow governmental size-limits if they were to sell the shells they acquire. People who collect *Trochus* for meat collect more often and at a smaller scale than those who collect *Trochus* for its shell, and usually discard the shells they collect to avoid incriminating themselves during long closed seasons. If managers were to allow longer periods in which quotas for *Trochus* collection could be met, people who collect *Trochus* for meat might be encouraged to sell the shells they acquire, and thus select *Trochus* within the industrially preferred size limits set by the government.

## Introduction

*Trochus Niloticus*, also commonly known as the tropical topshell and troca, is a large marine gastropod found on intertidal and subtidal reefs throughout the Tropical Pacific (Hahn 1993). *Trochus* shell supplies raw material to several industries, including the button and furniture industries, and is an important export commodity for many Pacific Island nations (Barnuhaddin 1997). *Trochus* shell is also a resource for home industries, and its meat is a food item in many Pacific countries.

The collection of *Trochus* requires little capital investment and is relatively easy, as *Trochus* are conspicuous, sedentary organisms that can be collected by walking on intertidal reefs or by diving in subtidal areas. This relative accessibility means that *Trochus* collection can benefit a broad spectrum of people. It also contributes to *Trochus* stocks' vulnerability to overexploitation.

Overexploitation of a fishery often leads not only to a reduction in overall population levels, but also to a reduction in the mean size of the fished population. The recruitment potential of a population can be affected not only by the level of catch, but also by what sizes are caught. As with many other organisms, the fecundity of Trochus increases exponentially with size (Hahn 1993). A decrease in larger size classes within a *Trochus* population may affect the populations' reproductive potential.

Studies that have examined size-selectivity in *Trochus* collection have primarily considered how the industrial quality of *Trochus* shells affects the size preferences of people collecting for the shell market (Amos 1997). Few studies have examined the size preferences of people who collect *Trochus* for meat. The lack of attention on this subject probably reflects the fact that the pressure on *Trochus* populations from people collecting for meat is lower in most areas than is the pressure from collection for the shell market. In areas

where meat collection is extensive enough, perhaps due to proximity to population centers, the numbers and sizes of *Trochus* collected might affect the recruitment potential of a given *Trochus* population. This may particularly hold true on a local scale. Studies have shown that *Trochus* are dependent on local recruitment, as their larvae are viable for only 3-4 days (Amos 1997).

This study was conducted on Moorea in French Polynesia. In response to overexploitation of the pearl oyster in French Polynesia at the beginning of this century, *Trochus niloticus* was introduced to French Polynesia in 1957. Sizable populations of *Trochus* have since established throughout the islands (Dr. Manuel Jarillo personal interview).

In Moorea, the sale of *Trochus* shell and its use in home industries are sources of supplementary income for islanders. *Trochus* meat also provides a source of income and subsistence for islanders. The introduction of *Trochus* served not only to augment a diminishing mother-of-pearl source, but also a diminishing food-source, another marine gastropod, the Maoa *(Turbo setosus).* The Maoa has become increasingly rare and *Trochus* now often replaces it in traditional meals. Though it is illegal to collect and sell *Trochus* meat during closed seasons, these activities appear to be common.

In this study, I was not able to determine how extensively *Trochus* is collected for meat in Moorea, nor was I able to obtain information on the overall stock of *Trochus* on the island. I was thus not able to examine what the overall impacts that people collecting *Trochus* for meat might have on the viability of *Trochus* stocks on the island.

The purpose of this study was to elucidate how these impacts might be shaped by collectors' size preferences, and how management policy might encourage more conservation-friendly size selection by *Trochus* collectors. This was accomplished by investigating the following questions:

1) Do people who collect *Trochus* for meat select particular sizes?
2) How might collectors' size preferences affect the reproductive potential of *Trochus* populations?
3) What are some of the factors that affect their size preferences?

**Materials and Methods**

To determine whether people exhibit size preference when collecting *Trochus* for meat, I employed two approaches. I interviewed seventeen collectors and asked them if they select particular sizes when collecting. I also compared the sizes of human-collected shells with those of live *Trochus* in the area from which the collected *Trochus* were taken. I used vernier calipers to measure the maximum basal diameters of collected and live Trochus.

*Finding measurable collected shells*

To compare the sizes of collected and live *Trochus.* I first had to find and measure shells that had been collected by people for meat. By observing people collecting *Trochus*, by finding collections of shells, and by asking *Trochus* collectors about their collecting practices, I determined three general areas in which I might find shell collections: 1) near barrier reefs 2) near or on shore and 3) at private residences.

A common collection method is to travel by canoe to a barrier reef, collect *Trochus* from the reef, remove the meat while in the canoe, and dump the shells into the ocean. Some collectors discard the shells near or on shore. While collectors rarely bring shells home, I discovered that some people do so in order to decorate their gardens or homes. To improve my ability to identify human-collected shells, I examined the markings people made on *Trochus* shells, and asked collectors how they remove meat from shells.

Finding collected shells in barrier reef areas was complicated by several factors. For one, it was time-consuming to examine large areas under water. I also found that people make markings on shells that can resemble markings left by peeling predators such as crabs and by octopus who drill holes in shells. People sometimes discard shells in heaps that can resemble collections left by octopus beside their dens. I also observed people discarding shells irregularly around the back reef. In this situation, one person collected *Trochus* and handed them to people seated in a canoe. Those in the canoe removed the meat from the *Trochus* and threw the shells from the canoe as they followed the swimming collector around the reef.

It might have been possible to accompany *Trochus* collectors and measure the shells they collected. I did not obtain such an opportunity, in part, because people were wary of implicating

themselves in illegal activities by allowing me to directly observe them collecting.

Not all the shells I found were measurable. Some people remove meat from *Trochus* by smashing the shells with a hammer. I found it infeasible to measure shells receiving such a treatment to the degree of accuracy that I needed.

*Site Descriptions*

I searched for human-collected shells at the back reef and fore reef area east and west of Cook's Bay, and at the back reef South of Temae public beach, where I had observed *Trochus* collection and been told that collection is common (Map 1). Another area in which I searched for shells was near and on-shore along the section of coast between the public beach at Temae and Aroa Point. I searched in this area because I had spotted collections of shells there previously. I also considered it likely that people bring shells ashore in this area because the barrier reef where *Trochus* predominate is accessible by walking along this section of coast. Another method I used to search for human-collected shells was simply to ask people if they knew of any such collections. I found human-collected *Trochus* shells at three sites:

Site 1 I gained access to a collection of *Trochus* that had been collected for meat at Opunohu Bay. These shells were used to decorate a garden. I measured one assemblage of shells that had been collected five to ten years before the time of this study according to the owner of the collection. I also measured shells that had been collected one month prior to the time of this study. I found no significant difference between the size-class structures of the five-year-old and one-month-old assemblages, and they were grouped together in my analysis.

According to the owner of the shell collection, several people collected the shells from a fringing reef on the West side of the mouth of Opunohu Bay. At this reef, I measured 30 live individuals in a 200m x 30m area to obtain a sample of the available live population in the area of collection.

Site 2 I found a collection of shells at the back reef offshore of the town of Maharepa. I had some reason to suspect that these *Trochus* might have been preyed upon by octopus, but it is most probable that this collection was human derived for the following reasons: One, the shells were found in a heap. Although octopus have been known to create conglomerations of shells outside their dens, the most likely octopus predator of *Trochus* in Moorea, *Cyanea*, has not been observed to create such collections (Forsythe and Hanlon, 1997); Two, the holes in the shells were similar in size to the holes found in a known human-derived collection of shells; Three, an octopus would have been of an improbable size to have drilled holes the size of those found on these shells.

At this site, I measured a sample of live *Trochus* on the back reef near the spot where I found the collection of shells. I measured 59 *Trochus* in a 150m x 10m area.

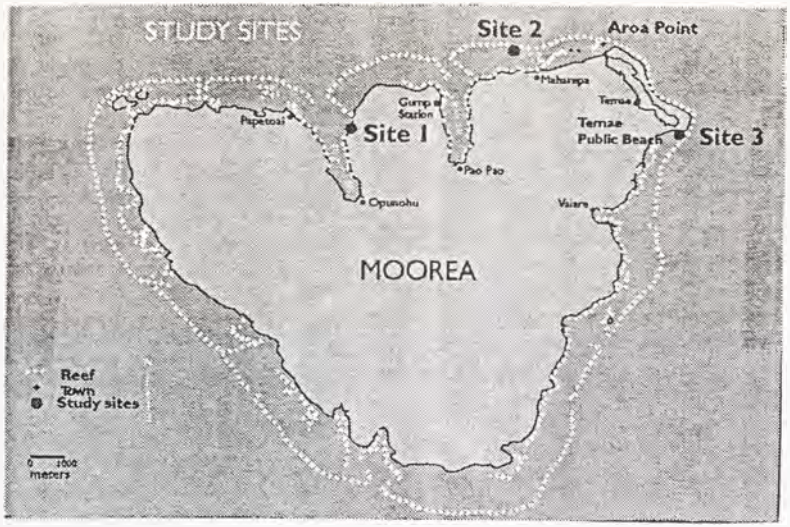
Site 3 At Temae public beach, I measured five shell assemblages that I found near a floating platform and at other near-shore areas. According to nearby residents, the shells had been collected for meat consumption and had been there for at most five months. A storm that occurred five months ago apparently washed away other assemblages. Residents informed me that the shells had been collected from the back reef just South of the public beach. At this back reef, I measured 56 live *Trochus* in a 250m x 10m area.

*Measuring live Trochus*

When measuring the live samples at the various sites, I thoroughly searched a sizable portion of the area of collection until I had measured at least 30 *Trochus*. I might have obtained a more representative sample of the size distribution of the living population had I measured Trochus along transects placed randomly in the entire collection areas of the three sites. The areas I searched represented large enough portions of the areas of collection to yield a fairly representative sample of the live population.

*Interviewing Trochus collectors*

The seventeen *Trochus* collectors I interviewed consisted of friends and acquaintances of mine, as well as people I approached on the street in Maharepa and at Temae near Site 3. It would have been interesting to interview somebody who I could directly connect with I was unable to do so. I asked the interviewees a pre-determined set of questions, and recorded their answers and any




**Map 1.** Study sites on Moorea, French Polynesia

other information they provided in a notebook. Most of the people I approached were willing to answer my questions but some were suspicious that I might turn them in to authorities for illegal collection activities.

*Data Analysis*

I compared the size-class frequencies of collected and live *Trochus* from each site to determine if the collected shells displayed a different size-class distribution than the available live population. Here let me note that I refer to the live samples as the available live population (what the collectors had to choose from), but if the live samples represent the residual live population (what was left after collection), the comparison between size frequencies to determine size preferences still holds true.

I grouped the size measurements into four size-classes to allow an adequate number of measurements in each size class. For each site, I used the overall proportion of the number of live to the number of collected shells to determine the expected number of live and collected *Trochus* in a given size class if the sizes were distributed evenly among size classes. I then calculated a chi-squared statistic with two df to determine if the observed distribution among size classes deviated from an even distribution among size classes. I graphed the proportion of the percent frequencies of live to collected *Trochus* in each size class to visually determine if the proportions of live and collected *Trochus* demonstrated a trend over size classes.

*Modeling the effects of size-selectivity*

My examination of size-preferences suggested that some collectors selectively choose larger sizes and some show no preference for particular sizes. To illustrate how *Trochus* collectors' size preferences might affect the reproductive potential of a *Trochus* population, I created a model to compare the impacts of three types of collectors: a law- abiding, a non-selective, and a large-size-biased collector. I estimated oocyte production for different sizes of *Trochus*, and compared how each type of collector might affect the oocyte production of a *Trochus* population.

In this model, the fished *Trochus* population affected by the three types of collectors reflected the size-frequency distribution of the live *Trochus* that were measured at the three sites. I grouped the live *Trochus* into three size-classes: below the legal size limit from 6.5 to 8cm; within the legal limits of 8-11cm; and above the legal limit from 11-13cm. I then removed ten percent of the *Trochus* population as the three types of collectors would.

To mimic a law-abiding collector, I removed only sizes that fell within the legal limits set by the government. To mimic a non-selective collector, I removed sizes in proportion to their frequencies in the population. To mimic a large-size-biased collector, I selectively removed larger sizes in the same proportions as was demonstrated by the most extreme example of large-size selectivity at Site 2. At this site, 56% of the collected shells fell in the range above the maximum size limit, 44% fell within legal limits,

and none fell below the minimum legal size limit. I then compared the percent loss in oocyte production among the three scenarios.

Previous studies have shown that *Trochus* oocyte production increases with size (Hahn 1993). To estimate oocyte production in the different size classes, I assumed oocyte production to be proportional to the volume of the digestive-gonadal complex. I estimated this volume by following a plan of the prosobranch body that was conceptualized by Dr. David Lindberg. In this plan, the prosobranch body is conceived as a coiled cone. The height of the cone is the length of the spiraled coil encompassing the prosobranch body. The area of the base of the cone is approximated as a circle with a radius equal to the average of the length and width of the shell aperture. The digestive-gonadal complex is estimated to begin at half the cone's height. (Figure 1)

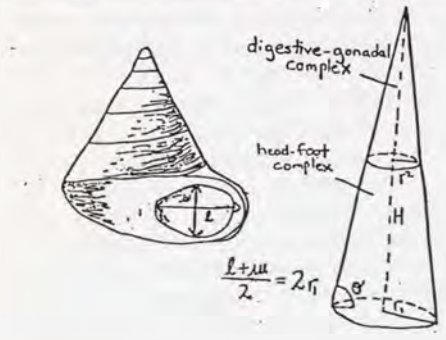



**Figure 1.** Conceptualized Prosobranch body plan (after Lindberg)

I used measurements from a *Trochus* specimen to estimate relationships between basal diameter, the height of the coiled cone, and the area of the shell aperture. I assumed that the relationships between these three measurements was representative of any *Trochus* shell. The angle between a cross-section of the cone and the side of a cone was thus consistent for different sizes of *Trochus*. Using this angle and the height of the coiled cone, I computed a radius of the cone encompassing the digestive-gonadal complex, and estimated the volume of this cone for each size-class. I used an exponential average to determine an average volume for each size class. I assumed the oocyte content of the digestive-gonadal complex to be 70%. This value was taken from the maximum gonadal index that was determined in a study on *Trochus niloticus* fecundity conducted in Indonesia (Pradina et. al 1997). In this study, the gonadal index was measured as (gonad area/total conical area of the digestive-gonadal complex) x 100%.

A reference to a study by Heislinga (1981) stated that a 12cm *Trochus* female has the potential to contribute 14 times more eggs annually than does a 6cm female (Hahn 1993). I converted these findings into an exponential relationship between basal diameter and egg production and compared this relationship to that which I calculated. The relationship I calculated is within 4 percent of that found by Heislinga. Unfortunately, I was unable to obtain this study to examine what methods were used by Heislinga to estimate the size to egg production relationship.

The model I constructed only attempts to illustrate how collectors' size-selectivity might affect the reproductive potential of *Trochus* populations. This model assumes that oocyte production is a measure of reproductive potential. The model does not account for a myriad of biological and environmental factors that can amplify or dampen the effects of lost oocyte production on a population's level of recruitment (Power 1996). For example, the effects of lost oocyte production on recruitment might be dampened if the survival of young *Trochus* is increased by decreased density of conspecific juveniles.

## Results

### *Size-preferences of Trochus Collectors*

At Site 1, I found that the collected and live shells did not differ significantly in size-class distribution. At Sites 2 and 3, the size distribution of collected and live *Trochus* differed significantly for $p<.05$. At Sites 2 and 3, the proportions of live to collected *Trochus* in each size class showed that the live *Trochus* predominated in the smaller size classes and the collected shells predominated in the larger size-classes. At Site 2, this trend was more extreme than at Site 3 (Figures 2 and 3). The results of the live vs. collected comparisons at the three sites suggest that some collectors exhibit no size-selectivity and some prefer larger *Trochus* to differing degrees.

The results of the size comparisons between live and collected *Trochus* corresponded to what I was told in the interviews. Of 17 collectors I interviewed, 10 said they select bigger *Trochus* and 7 indicated that they had no preference for particular sizes.

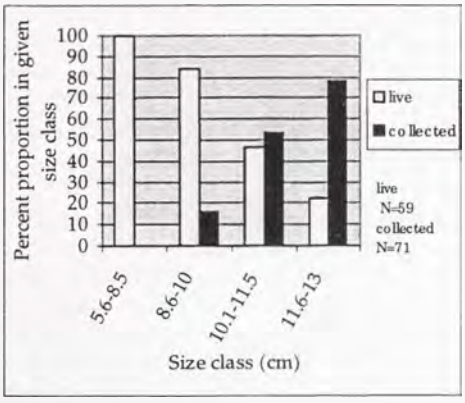



**Figure 2.** Site 2: Proportion of live and collected *Trochus* in each of four size classes.

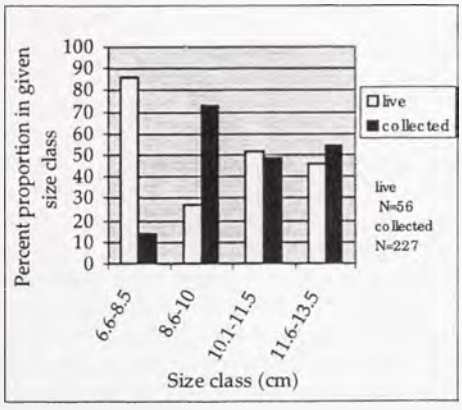



**Figure 3.** Site 3: Proportion of live and collected *Trochus* in each of four size classes.

*Modeling the effects of size-selectivity*

The model I constructed to illustrate the potential effects of different types of collectors on the oocyte production of a *Trochus* population suggests that the large-size-biased collector is likely to cause the greatest decrease in oocyte production, followed by the unselective collector, with the law-abiding collector causing the smallest reduction in a population's oocyte production. Compared to the effects of the law-abiding collector, oocyte production would decrease by ~31% more if a population were subjected to the effects of an unselective collector, and by ~69% more subject to a large-sized-biased collector (Figure 4).

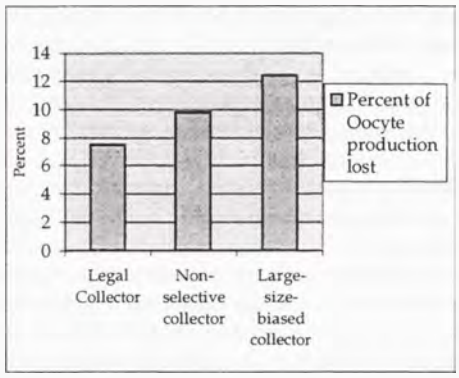



**Figure 4.** Comparison of oocyte production lost with extraction of 10% of population by law-abiding, unselective, and large-size-biased collector.

## Discussion

Both the size comparison between live and collected *Trochus* at each site, and what I was told in the interviews indicate that some collectors select larger *Trochus*, and some collectors have no preference for particular sizes. What are some of the reasons people might select larger sizes or show no size preference when collecting?

### *Factors affecting collector's size preferences*

*Government Regulations*

The results of the interviews and the examinations of collected shells suggest that people who collect *Trochus* for meat do not follow the size restrictions stipulated by the government. When *Trochus* are collected for their shells, it is probable that the size restrictions set by the government are more closely followed than when *Trochus* is collected for meat. The sale of *Trochus* shell is monitored and penalties for violations are severe. Also, the maximum size limit is likely to be heeded by people collecting for the shell market because the upper size limit set by the government corresponds to the maximum size preferred by shell buyers.

The collection of *Trochus* for meat is difficult to monitor, as it occurs more often and at a smaller scale than does collection for the shell market, and because the meat can be collected and the shells discarded in relative privacy in the ocean. The government's communication of size restrictions to smaller-scale collectors appears to be rather unsuccessful. None of the *Trochus* collectors I interviewed knew the minimum and maximum size restriction set by the government. The size preferences of those who collect *Trochus* for meat are thus most probably influenced by factors other than government regulations.

*Maximizing meat gained for effort expended*

Some collectors told me that they select larger *Trochus* simply because they have more meat. This is an obvious reason to prefer larger sizes, but the amount of meat that a certain size *Trochus* provides does not necessarily explain the entire motivation behind a collector's preferences for larger sizes. It would seem that a collector would not just want to maximize the amount of meat she collects, but the amount of meat she collects for the effort she expends. If it takes a lot more time for a collector to find a bigger organism, then the extra meat larger *Trochus* provide might not justify the extra effort expended to selectively choose larger *Trochus*.

The frequency with which a particular size of *Trochus* occurs within a population can be seen to be a good indication of how much time would be required to find a *Trochus* of that size. In the size-class distribution I measured for all the samples of live *Trochus*, the second to smallest size class occurs more frequently than the largest size class. To see if a collector would nevertheless maximize her meat gained for effort expended in the two larger size classes, I estimated the amount of meat gained per effort expended when collecting from each size class.

I assumed that the meat a *Trochus* provides is proportional to the volume of its head-foot complex, the portion most likely to be consumed. To estimate the volume of the head-foot complex for a given size, I used the prosobranch body plan outlined in the 'Methods' section. I assumed that the lower half of the coiled cone represents the head-foot complex. I then multiplied the frequency of *Trochus* in each size class by the volume of meat provided by a *Trochus* of that size. I assumed that for a given quantity of meat collected, a collector would optimize her efforts in the size classes where the frequency of meat was greatest. Figure 5 illustrates that a collector would optimize her efforts if she chose *Trochus* in the two largest size classes.

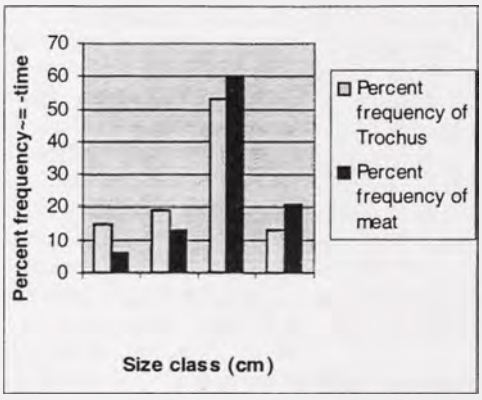



**Figure 5**. Schematic representation of meat gained for effort expended.

Figure 5 does not account for yet another factor that might influence one's size selectivity when collecting an organism for meat. The time it takes to find an organism of a particular size depends not only on how frequently that organism appears in the population, but also on the density of the population in the area of collection. If densities are lower, and it takes more time to find any organism at all, it is more likely that the extra meat a larger organism would provide would not warrant the extra time spent searching for that organism. Table 1 shows that collectors' degrees of size-selectivity at the three sites corresponds to the densities of Trochus found at the three sites, with greater size preference corresponding to higher densities. The density of *Trochus* in an area may affect the degree to which people select larger sizes.

**Table 1.** Size preference as related to *Trochus* density

| Degree of large- size preference demonstrated by collectors | Density of *Trochus* |
|---|---|
| Site 1- None | .005 *Trochus*/m^2 |
| Site 2- Medium | .022 *Trochus*/m^2 |
| Site 3- High | .039 *Trochus*/m^2 |

*Stewardship Considerations*

Though the size-class structure of a *Trochus* population and the density of *Trochus* in an area may affect collectors' size preferences, it may not be terribly illustrative to think of collectors as primarily meat-for-effort maximizers. Along with other considerations, collectors' stewardship sentiments may primarily affect what sizes they select. Five collectors I interviewed said that they prefer to take larger *Trochus* and leave the small to ensure a future *Trochus* supply.

### *Implications of collectors' size-selectivity for management of Trochus on Moorea*

The model I constructed illustrates how the selective removal of larger Trochus might potentially reduce the reproductive potential of a population more than the non-size-selective removal of *Trochus*. I have already discussed how the size-class structure of a population and the densities of a population in a given area may affect collectors' size-preferences. These factors may have implications for management in that they might help predict what sizes would be removed by people collecting *Trochus* for meat in a given area, and thus what collectors' impacts may be on the reproductive potential of a given *Trochus* population.

I also mentioned that a collector's stewardship sentiments might primarily affect her size preferences. It may be that the viable management of *Trochus* may depend on bringing collectors' stewardship considerations and size preferences more in line with the size restriction strategy employed by the government. The model I constructed to compare the effects of three types of collectors illustrates that a collector who selects *Trochus* within legal size limits might have a lower negative impact on the reproductive potential of a *Trochus* population than a collector who is unselective or preferentially chooses larger sizes.

The stewardship approach some collectors claimed to follow consisted of selecting large *Trochus* and leaving the small to ensure a future *Trochus* supply. This stewardship strategy of only taking *Trochus* above a minimum size is inconsistent with the minimum and maximum size-restriction approach used by the government. If collection of *Trochus* for meat were extensive enough, the combined effect of added extraction and a preference for larger sizes among collectors' might interfere with the government's management strategy, which requires leaving the largest *Trochus* to contribute large quantities of gonads to the recruitment process.

Theoretically, *Trochus* fisheries could be regulated by a minimum size limit alone. This method is not widely used because the value of *Trochus* shell decreases with size. With heavy fishing pressure, the minimum size limit would have to be high at about 10-11cm (Amos 1997). The value of *Trochus* shell on the market seriously diminishes past a shell size of 11cm. At these sizes, the shell's industrial quality is reduced as it becomes riddled with holes made by boring organisms and as the shell's basal coil becomes fluted (Manuel Jarillo personal interview). Because collection of *Trochus* for the shell market is probably more extensive and of greater economic importance in Moorea than is the collection of *Trochus* for meat, the minimum and maximum size limits are a necessary strategy for *Trochus* conservation. How, then, might people who collect *Trochus* for meat be encouraged to collect within the legal size-limits?

Perhaps if more people who collect *Trochus* for meat were familiar with the government's size restriction strategy for conserving *Trochus*, they would be more likely to select allowable sizes of *Trochus*. Achieving better communication of the government's conservation measures to *Trochus* collectors is a complex undertaking that I will not address in the scope of this paper.

An additional way to influence collectors' size preferences might be to change the way in which permits for *Trochus* shell collection are distributed. At present, permits and quotas for shell collection are issued generally for a period of about a week, when the government estimates that stocks are plentiful enough to sustain an extraction defined by the quotas. Dr. Manuel Jarillo, of French Polynesia's Marine and Aquaculture Service has suggested perhaps a better strategy of issuing quotas and permits that is under review. He has recommended that collectors be permitted to fulfill their allowed quotas over longer periods. He has explained that the short collection periods of about a week can inconvenience people who often abandon their regular livelihoods to collect *Trochus*. As Dr. Jarillo also has elucidated, short collection periods result in the waste of large quantities of meat. There is not enough demand for meat to account for the boom that comes when permits for shell collection are issued.

When meat collection occurs more often at a smaller scale, the unused shells may also be seen to represent a waste. Collectors with whom I spoke said that they throw shells into the ocean to avoid being caught with incriminating evidence. These shells represent a lost income that collectors might have obtained from selling the shells. If quotas were allowed to be met gradually within longer periods, people collecting *Trochus* for meat might consider getting permits and selling the shells they otherwise would have discarded. This might encourage people collecting for meat to stay within the industrially preferred size limits set by the government.

## Conclusions

The model I constructed illustrates that *Trochus* collection within the legal size restrictions may have less negative impact on the reproductive potential of *Trochus* populations than collection with a preference for large sizes or with no size size-selectivity. Because people collecting *Trochus* for meat on Moorea appear to either prefer larger sizes or to collect unselectively, it may be vital to the successful management of *Trochus* stocks to bring collectors' size preferences more in line with the size restrictions set by the government. This might be achieved by lengthening the periods in which quotas for *Trochus* collection are met. With longer open seasons, people who collect *Trochus* for meat throughout the year might be encouraged to sell the shells they obtain, giving them an impetus to stay within the governmental size limits preferred by shell buyers.

Further research would be needed to establish the utility of these suggestions. Further study would be needed to determine if people who collect *Trochus* for meat would be interested in selling the shells they acquire. Whether or not *Trochus* collection for meat is extensive enough on Moorea to impact *Trochus* populations on the island would need to be examined to determine if *Trochus* management policy should take into account the size selectivity of *Trochus* meat collectors. Factors that might affect the demands placed by meat collection on *Trochus* stocks include economic conditions that influence islanders' dependence on local resources, the availability of other edible marine snails such as the Maoa and the introduced Burgaux (*Turbo marmoratus*), and trends in islanders' tastes. Further biological and ecological information on the recruitment process of *Trochus* populations would facilitate better understanding of how changes in populations' size-class structures might affect their reproductive potential.

## Acknowledgements

Many thanks to the Gump Research Station, to Professors Jere Lipps, David Stoddart, Vincent Resh, and David Lindberg, and to graduate student instructors Virginia Matzek, Tegan Churcher, and Amy Lesen for their outstanding efforts in facilitating an amazing learning experience. Special thanks to David Lindberg, station managers John and Debbie, and Virginia Rich for helping me see that my glass was not empty. Special thanks to Kevin Cooney, whose valour amid torrential currents was formidable. Many thanks to all my classmates whose kindness and support when what I had hoped would be a credential-building experience turned into a character-building experience I will never forget. Mauruuru to Tony and Haimiri for all your kindness.

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# THE SHALLOW-WATER SPONGES OF COOK'S BAY, MOOREA, FRENCH POLYNESIA: A SYSTEMATIC AND DISTRIBUTIONAL SURVEY

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**ABSTRACT.** We examined the shallow water sponge fauna of Cook's Bay, Moorea, French Polynesia. The purpose of our research was to provide a comprehensive species list as well as examine the distribution of shallow water sponges in Cook's Bay. Sponge specimens were measured and collected at six sites around the bay's perimeter. Substrate size and type, salinity, and temperature were measured at each site. Spicule preparations were made of each specimen in order to classify sponge species on the basis of distinct spicule composition. Thus, a catalog of 42 shallow water sponge species was compiled based on unique spicule and color morphologies. T-test analysis of species richness and abundance revealed significant differences ($p < 0.05$) between the exterior sites (sites 5 and 6) and the interior sites (sites 1 and 3) of the bay. Analysis of the data showed a correlation between the site location in the bay and species richness and abundance. In addition, data analysis shows that the amount of available rubble substrate correlates to sponge abundance.

## 1. Introduction

An urgent task biologists face today is to document the biological diversity of living species. One group of organisms of which we have limited knowledge is sponges (Phylum Porifera). It is estimated that only about one third of species in the sponge fauna have been identified and described (Hooper and Levi 1994). Sponge systematics are still debated, even as to order classification (Boury-Esnault & Rutzler 1984). This is partly caused by the lack of specialists in sponge biology. Sponges are reportedly the phylum with the smallest ratio of number of specialists to number of species (Winston 1988).

Additionally, knowledge of sponge distributions is far behind those of other benthic groups (molluscs, coelenterates, crustacea, echinoderms) and no single review of sponge distributions is available (Soest 1994). Studies thus far have focused on macrosponges but the greatest proportion of sponge species are thin encrusters (Bergquist 1994). Studies have shown a high level of endemism in sponges around islands, mostly due to the abundance of small, cryptic, encrusting species, especially on coral rubble (Hooper and Levi 1994). Furthermore, there are a limited number of observations of sponges regarding substrate cover, due to high variability among individual transects (Alcolado 1994). Only recently have sponges been considered as important indicators for environmental health. For example, sponges have been used as bio-indicators of organic pollutants in coral reefs (Alcolado 1994).

Few studies have examined shallow-water sponge faunas (Hooper and Levi 1994). Shallow-water sponge research is often complicated by the highly variable and stochastic shallow-water environments (Hooper and Levi 1994). While limited research is available on shallow-water sponges, particularly in French Polynesia, our purpose was to survey and compile a species list of the shallow-water sponges in Cook's Bay, Moorea, French Polynesia. Through field and laboratory observations we evaluated the following null hypotheses:

1. There is no difference in the richness or abundance of sponges from the exterior (closest to mouth of bay) to the interior (furthest from mouth of bay) of Cook's Bay.

2. There will be no difference in sponge richness or abundance with increased distance from shore.

3. There will be no difference in species richness or sponge abundance with variation in site depths.

4. Sedimentation will not correlate with species richness or sponge abundance around Cook's Bay.

5. There is no difference in species richness or sponge abundance with variation in substrate composition around Cook's Bay.

## 2. Materials and Methods

### *2.1 Site Selection*

Our study was conducted on the island of Moorea, French Polynesia in Cook's Bay, located in the north-east part of the island (Map 1). Fieldwork was conducted during October and November 1998 with further work and analysis at UC Berkeley. Cook's Bay is a moderately developed bay, surrounded by at least three hotels, two churches, and over 50 local residences. The bay is surrounded by a fringing coral reef and the mouth of the bay opens into a large lagoon that is encircled by a barrier reef. Preliminary surveys of Cook's bay provided evidence of the presence of shallow water sponges. Our study sites were selectively chosen based upon these surveys. We selected six sites with an even distribution around the bay's perimeter (Map 2). Substrate composition varied among sites and was adequately representative of the variation in substrate throughout the bay. The locations of the six sites were also chosen to represent a general location of the bay, namely, interior (sites 1 and 3), middle (sites 2 and 4), and exterior (sites 5 and 6).

### *2.2 Sampling Methods*

Our area of study was the perimeter of the bay, namely shallow water from depths of zero to one and a half meters. Data was collected at each site by positioning two transect lines perpendicular to shore, beginning five meters from the shoreline. These transects were fifteen meters long by one and a half meters wide. Each meter along the transect line was treated as a 1.5 x 1.0 meter quadrat and the entire area of the transect was scoured for sponges. Our six sites were chosen selectively, and the placement of the first transect at each site was arbitrary. The placement of the second transect line at each site was randomly chosen to be between 10 and 50 meters from the first transect and to serve as a replicate at each of our six sites. Preparation at each site included the measurement of physical parameters including temperature, salinity, depth, and sedimentation, and the set-up of the transects (Appendix I: data sheet). The depths at each meter, from 0-15 m, along the transect were recorded. The temperature and salinity at each site were measured in one day to avoid daily variation. Descriptions of the substrate composition of each quadrat were recorded as percent covers, and a brief description of the site's shoreline and aquatic habitats were noted. We recorded all of the sponge specimens along the transect line. Measurements taken included sponge size, substrate size and type, location along the transect, specimen color and morphology, and the location of the specimen on the substrate. Due to an overwhelming abundance of coral rubble in particular transects, we imposed a time limit of one hour per quadrat to ensure thorough and consistent examination of each transect. After completing our sample collection at each transect, two durable plastic sedimentation plates, with dimensions of 0.09 $m^2$ were placed for forty-eight hours at four and nine meters along the transect line to provide an average sedimentation percent cover. The average percent cover of thick sediment was used to compare relative sedimentation at each site.

### *2.3 Site Description*

**Site 1:**
This site was located at the southeast side of Cook's Bay (Map 2). The shoreline was rocky and the sediment silty and fine. The average percent cover of the sedimentation plate was 13.8%. This site was shallow with depths ranging from 0.50m to 0.70m. The general substrate composition was homogeneous, composed largely of coral rubble and fixed platform. Algal growth on substrate was noticeable at this site. The water temperature at this site was 29.5"C with a salinity reading of 38%.

**Site 2:**
This site was located on the north-east side of Cook's Bay (Map 2), directly across the bay from Gump Research Station. Site 2 was also shallow with depths ranging from 0.78m to 1.0m. The shoreline was moderately developed with a house

approximately 30m from the water. The substrate consisted mainly of sand, patchy rubble, and some sporadic coral heads, both live and dead. The water was almost as clear as Site 1,with a sedimentation plate percent cover of 14.5 %. The sediment was light and sandy. Here the water temperature was 29.5° C with a salinity of 38%.

**Site 3:**
This site was located on the west side of Cook's bay, near the second most northern nautical marker in the bay (Map 2). The coastline was lined with palm trees and the shore was sandy. This site was moderately deep, with a change in depth ranging from 0.30m to 1.5m. The sediment was coarse and composed of many gravel-sized pieces of rubble. Site 3 was composed primarily of sand with some small coral rubble. We measured an average sediment plate percent cover of 70% at Site 3. The temperature at Site 3 was 28.5° C with a salinity reading of 38%.

**Site 4:**
This site was located just south of Gump Research Station and across the bay from Site 2, on the west shore of Cook's Bay (Map 2). This site was composed entirely of gravel, cobble, and rocky rubble with small, intermittent patches of sand. The water was much clearer than Site 3, with an average sedimentation plate cover of 31%. The coast was lined with palm trees and coarse sediment. The depths range from 0.30m to 1.15m. Here the temperature was 28.5° C with a salinity reading of 38%.

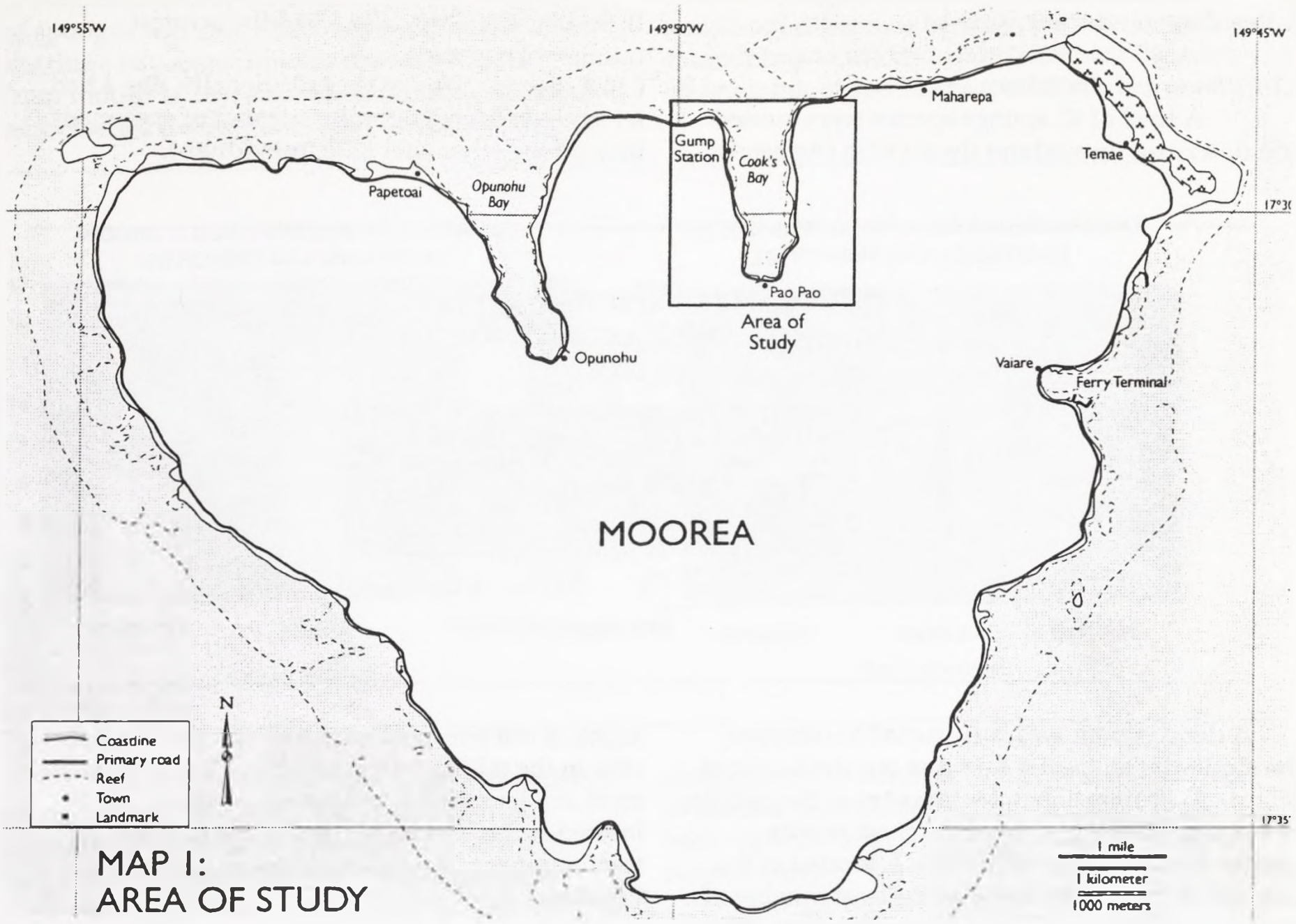
**Site 5:**
This site was located at the northern most end of the bay on the west shore (Map 2). Here the sediment was fine and silty, with a sedimentation plate cover of 57.5%. This site had an abundance of large fixed coral rubble and algae. A stand of trees at the water's edge shaded the shoreline and there was a large amount of sticks, seeds, and leaf litter in the water near shore, due to the overhanging trees and shrubs. Depths at this site ranged from 0.59m to 0.90m. The temperature was 28.5° C and the salinity reading was 38%.

**Site 6:**
This site was located at the north east side of Cook's Bay, north of the Cook's Bay Hotel(Map 2). Wave action was unusually low because this site sits in a lagoon area, between the shore and a wide stretch of coral reef platform. The sediment here was light and fine and the water fairly clear, with an average sedimentation plate cover of 51.3%. The shoreline was rocky and the transects consistently shallow, ranging in depth from 0.29m to 0.63m. The temperature here was 29° C and the salinity was 38%.

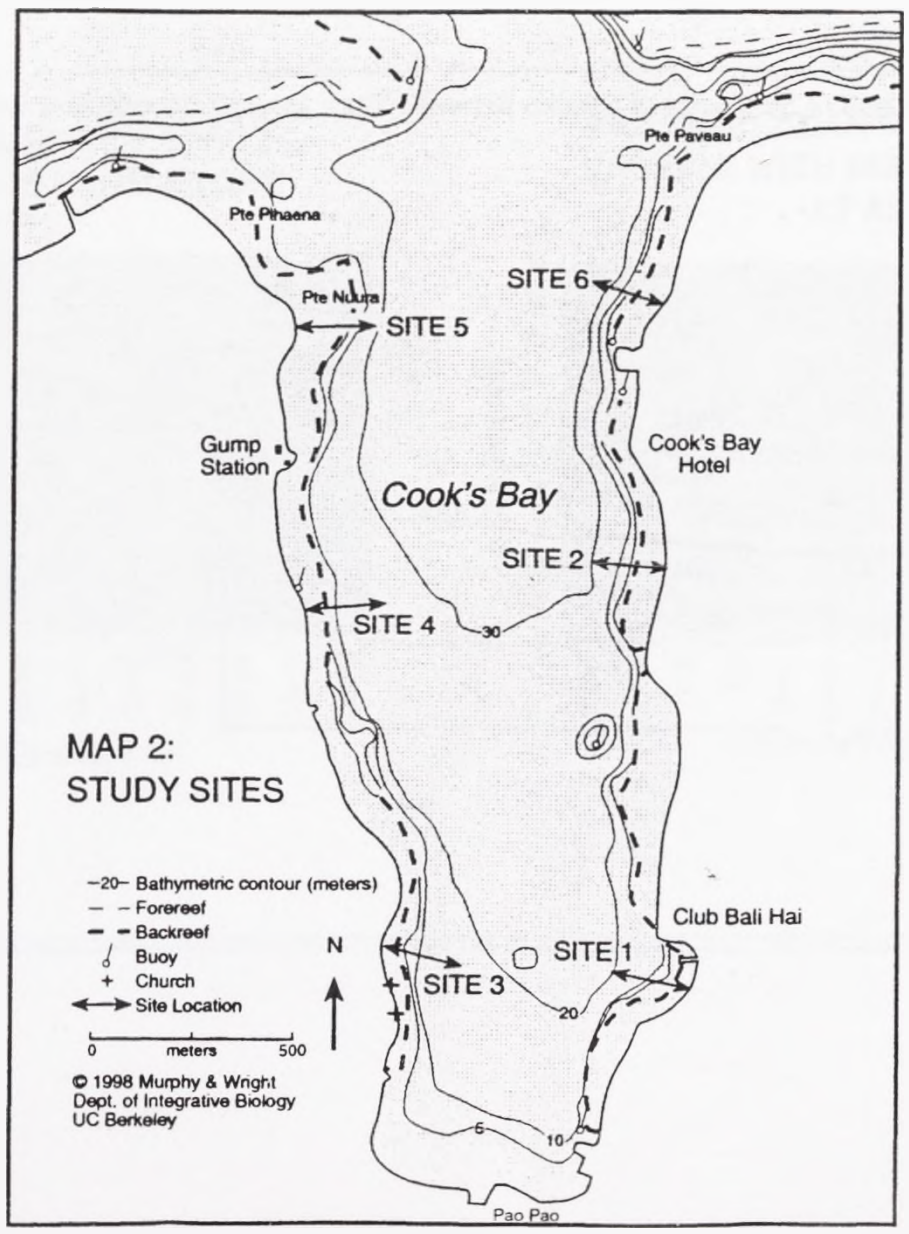
*2.4 Specimen Collection & Lab Techniques*

Shallow-water sponge specimens and their substrate were collected in the field for laboratory analysis. Specimens were removed using a razor blade and placed into vials, then preserved in a solution of 10% ethanol. To identify the collected specimens, samples of the organisms were mounted on microscope slides, and treated with bleach in order to isolate the spicules. These were examined using a compound microscope (Johannes and Stoddart 1978). Positive sponge identification was confirmed if spicules, which comprise the skeleton of many sponges, were evident after the bleach digestion. These mineral skeletons are also sometimes found in soft corals and tunicates. Preliminary surveying and sample collection aided in the identification of sponges. We were able to differentiate the sponges from other organisms based upon their morphologies, textures, and the effect of bleach digestion on their tissues. Our basis of species identification was defined by the distinct morphological composition of the spicules. Thus, only sponges with mineral skeletons, or spicules, were included in our species list. Spongin sponges were noted but not recorded because no positive identification could be made. If a specimen could be positively identified in the field then that specimen was not collected. Data was analyzed using t-tests, regression curves, Spearman's correlation matrix, and Jaccard's coefficient.

**Map 1.** Map of Study Area (Cook's Bay).




**Map 2.** Map of Study Sites in Cook's Bay.

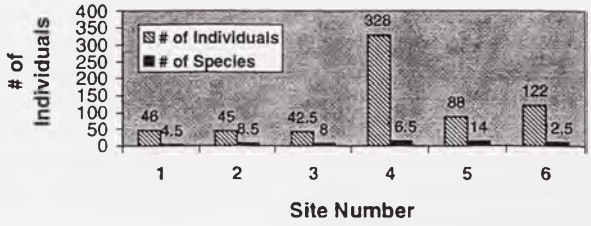


## 3. Results

### *3.1 Richness and Abundance*

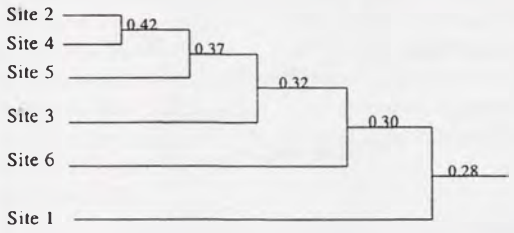
A total of 42 sponge species were located and described throughout the six sites (Appendix II: Species Catalog). Site 4 had the greatest number of species ( 16.5 species) (Figure 1). Additionally, Site 4 had an overwhelmingly greater number of specimens than all the other sites (328 individuals).

FIGURE 1:MEAN SPECIES RICHNESS AND SPONGE ABUNDANCE PER SITE




A dendrogram was constructed to compare the similarity in species found at our site locations (Figure 2). It shows that the two sites in the middle of the bay (Sites 2 & 4) have the most similar species compositions. While Site 1, located in the interior section of the bay, has the least number of species in common with the rest of the sites. This dendrogram reflects the similarity of species found at our site locations. It shows that the two sites in the middle of the bay (Sites 2 & 4) have the most similar species compositions. While Site 1, located in the interior section of the bay, has the least number of species in common with the rest of the sites.

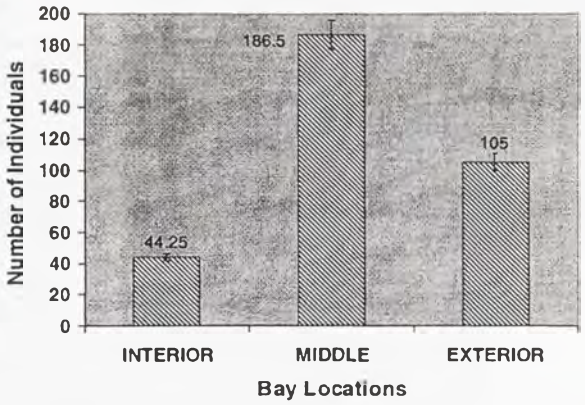
**FIGURE 2.** Dendrogram: Coefficient of Similarity of Species Between Sites. Jaccard's coefficient was used to construct the dendrogram.



A comparison of species richness and abundance of sponges was made between the sites of each of the three bay areas: interior (two sites furthest from mouth of bay, sites 1&3), middle (sites 2&4), and exterior (two sites closest to mouth of bay, sites 5&6) (Figures 3 and 4). T-tests revealed a significant difference between the interior and exterior bay locations in both number of species and number of specimens ($p<0.05$).

**FIGURE 3: MEAN SPECIES RICHNESS AT DIFFERENT BAY LOCATIONS**


**FIGURE 4: MEAN SPONGE ABUNDANCE AT DIFFERENT BAY LOCATIONS**




Number of species and sponge abundance were compared between each meter on the transect for all sites, also representing distance from shore (Figures 5and 6). The comparison demonstrates a trend showing that both number of species and number of individuals increases with distance from shore ($R^2$=0.6681, $R^2$=0.6698, respectively).

**FIGURE 5: AVERAGE NUMBER OF SPECIES VARYING WITH DISTANCE FROM SHORE AT ALL SITES**

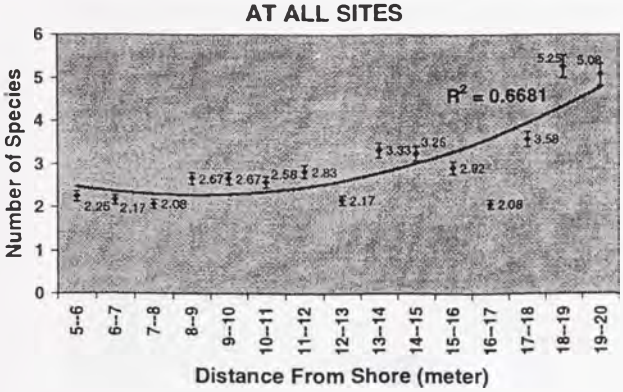
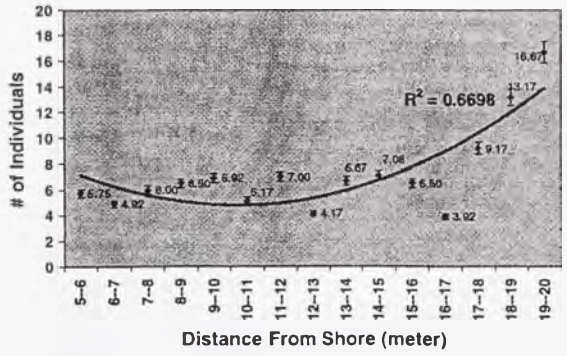



**FIGURE 6: MEAN SPONGE ABUNDANCE VARYING WITH DISTANCE FROM SHORE AT ALL SITES**



Additionally, depths of all sites were compared to number of species and number of individuals. Results suggest a trend for species richness and specimen abundance to be greater at middle-range depths (approximately between 0.51 and 0.8m) ($R^2$=0.7121, $R^2$= 0.7463, respectively) (Figures 7 and 8).

**FIGURE 7: AVERAGE NUMBER OF SPECIES AT ALL SITE DEPTHS**

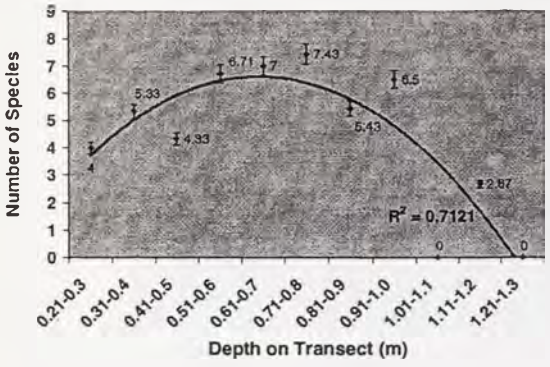
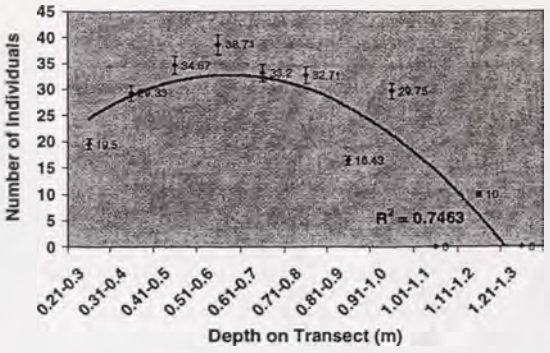



**FIGURE 8: MEAN SPONGE ABUNDANCE AT ALL SITE DEPTHS**




*3.2 Sedimentation*

A comparison between average sedimentation per site and number of species shows that Site 3 had the greatest average sedimentation percent cover (70%), but the second least number of species (Figure 9). Site 4 had the greatest number of species, but not the most nor the least sedimentation percent cover. Therefore, no strong correlation is apparent between sedimentation and number of species ($R^2$=0.0911). Additionally, when comparing the average sedimentation per site with sponge abundance, no strong trend is apparent demonstrating that sedimentation shows no strong correlation with sponge abundance ($R^2$=0.0074) (Figure 10).

**FIGURE 9: MEAN SEDIMENTATION PER SITE VERSUS NUMBER OF SPECIES**

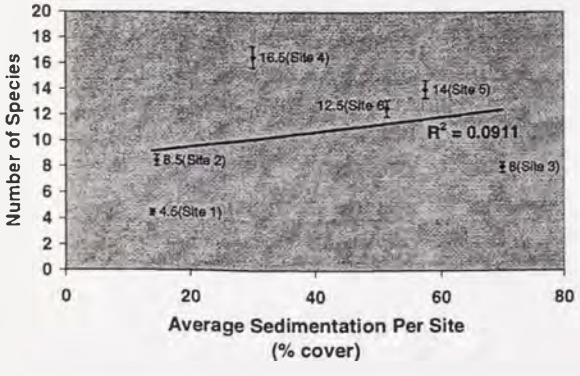
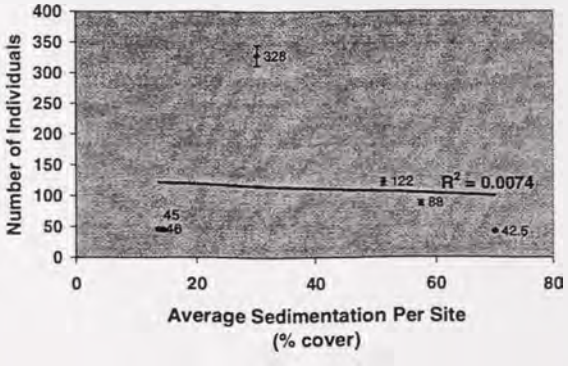
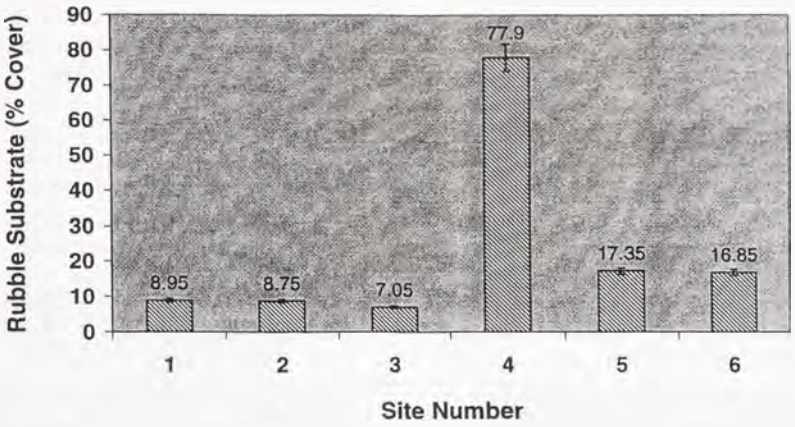



**FIGURE 10: MEAN SEDIMENTATION PER SITE VERSUS SPONGE ABUNDANCE**



Site 4 contained the greatest amount of coral rubble substrate (77.9%), while Site 3 had the least (7.05%) (Figure 11).

**FIGURE 11: MEAN PERCENT COVER OF RUBBLE SUBSTRATE AT EACH SITE**

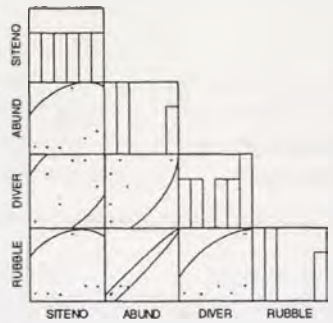



Data was analyzed using a Spearman correlation matrix which correlates the abundance of specimens with the amount of rubble that is available for them to grow on (Table 1). The value of 0.943 emphasizes the correlation of coral rubble, as available substrate for sponge growth, with sponge abundance. On the other hand, diversity does not strongly correlate with rubble abundance demonstrating that an increase in rubble most definitely affects sponge abundance but not necessarily diversity.

**Table 1.** Spearman Correlation Matrix correlating the abundance of sponges with the amount of available rubble substrate (represented as percent cover).

SPEARMAN CORRELATION MATRIX

| | SITE # | ABUNDANCE | DIVERSITY | RUBBLE (%) |
|---|---|---|---|---|
| SITE # | 1.000 | | | |
| ABUNDANCE | 0.600 | 1.000 | | |
| DIVERSITY | 0.522 | 0.551 | 1.000 | |
| RUBBLE | 0.543 | **0.943** | 0.696 | 1.000 |




A weak correlation was found between an increase in percent cover of rubble substrate (by site) and an increase in number of species ($R^2$=0.552) (Figure 12). This supports the Spearman correlation matrix (Table 1), showing that an increase in rubble does not necessarily correspond to an increase in species richness. However, a strong corrleation was found between an increase in percent cover of rubble substrate and an increase in sponge abundance ($R^2$= 0.9766) (Figure 13). This also supports the Spearman correlation matrix in that an increase in rubble clearly correlates with an increase in number of individuals found.

**FIGURE 12: AVERAGE NUMBER OF SPECIES VERSUS PERCENT COVER OF RUBBLE SUBSTRATE AT EACH SITE**

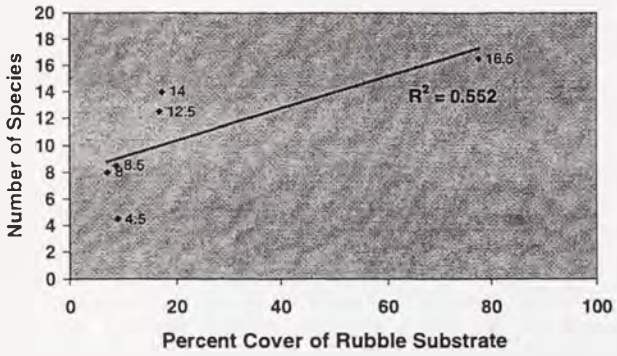
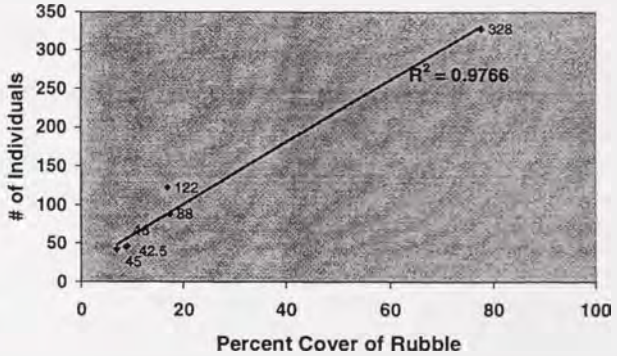



**FIGURE 13: MEAN SPONGE ABUNDANCE VERSUS PERCENT COVER OF RUBBLE SUBSTRATE AT EACH SITE**




## 4. Discussion

*4.1 Richness and Abundance*

The location in Cook's Bay influences the site's composition both in species richness and in sponge abundance. The T-test comparison of the sites at different bay locations shows a significant difference between the sites located at the interior (sites 1&3) and exterior (sites 5&6) in both species richness and sponge abundance. The exterior sites have the greatest average species richness. This may be due to parameters not measured in this study, such as nutrient flux. Nutrient flux could be greater at these sites due to their position at the mouth of the bay. Sponges are filter feeders, therefore increased current flow coupled with increased nutrient flux might provide an environment that is advantageous for sponge growth.

The interior sites have a substantially lower average of species richness and sponge abundance. Perhaps this could be due to the lack of nutrient flux because these sites are inside the bay. Current flow might be lower in the protected interior of the bay. Sponges, being sessile filter feeders, need a constant flow of water to survive. This portion of the bay might be too stagnant of an environment to sustain a high level of sponge diversity. In addition, sponges might be in competition for substrate with the high levels of algae growing at these sites. Perhaps the presence of a salinity gradient due to the influx of fresh water from surrounding streams also contributes to the decrease in sponge abundance and species richness.

been called sponges. However, we evaluated many specimens prior to the study in order to practice sponge identification and we felt confident in our ability to identify sponges. In addition, because we were limited in microscope equipment, viewing of spicules was only possible up to 40x magnification and smaller spicules may have been overlooked.

## 5. Conclusion

Field tests and analysis indicate the following conclusions:

1. 42 shallow-water sponge species were found in Cook's Bay, Moorea.
2. Location of sites in Cook's Bay influences species richness and sponge abundance.
3. Species richness and sponge abundance increases with distance from shore.
4. Species richness and sponge abundance are greatest at middle transect depth ranges.
5. Sedimentation shows no correlation with species richness or sponge abundance.
6. Sponge abundance increases with an increase in rubble substrate percent cover, while species richness is not necessarily correlated to an increase in rubble composition.

### *5.1 Further Studies*

Although any scientist focusing on the phylum Porifera may feel overwhelmed by the large number of species and abundance, sponge research during the past two decades has proven to be one of the most prolific sources of new natural products (Vos & Rutzler 1991). With such limited research available on sponges, sponge biology is virtually an untouched field. Exposure to the anatomy, morphology, and symbiont content of sponges will suggest new research topics in the areas of ecology, evolution, cell biology, and molecular biology to individuals interested in the structure and biosynthesis of new natural marine products of biomedical potential (Vos & Rutzler 1991). Sponges encompass an expansive realm of study, from which many topics can be pursued. In particular, our study provides a basic introduction to the sponges of Moorea and can be used as a foundation for future studies on the sponges of French Polynesia. An important factor that has been established as influential to sponge growth is light, namely ultra violet radiation (Stoddart and Johannes 1978). A study assessing light intensity, using an underwater light meter could provide crucial information concerning light and UV radiation on sponge growth. The affects of light exposure on the growth of shallow-water encrusting sponges could be monitored by overturning coral rubble to expose sponges growing underneath the rubble to light. Incorporating a water quality study and correlating this to sponge biomass and growth potential could provide an interesting perspective on sponge distribution, as well as on their tolerance for certain habitat conditions. Sponges could also be used as bio-indicators for organic pollutants. A comparison study of Cook's Bay, a moderately developed bay, to Opunohu Bay, a more pristine and undeveloped environment, might be useful for studying the effects of human influence on the biodiversity of surrounding waters as well as an interesting comparison study of sponge diversity and abundance. A broad spectrum of the sponge fauna present in French Polynesia, of which there have been few documented distribution studies, could be described by mapping the sponge distribution of the entire island of Moorea. Spongin sponges could also be included in future species catalogs as well as being an important component for a distribution study. Ultimately, identification of the sponge families and possibly genera could be evaluated in further French Polynesia systematic studies. Both the identification of spongin species as well as the determination of familial and generic names is vital for future research, however, would require additional equipment and resources in Moorea.

**Acknowledgements**

We would like to express our utmost appreciation and gratitude to Jere Lipps, David Lindberg, Vince Resh, and David Stoddart for making our time in Moorea unforgettable. Thank you for your hours of patience and enthusiasm! Amy Lesen, Tegan Churcher, and Virginia Matzek, where can we begin? The countless hours you devoted to us and your eternal encouragement and wisdom made all the difference. You all made our semester memorable, educational, and most of all, fun! Maruru Roa! We would also like to thank Allen Collins, our favorite sponge expert, for enlightening us with his facts and information about our favorite invertebrate-thank you so much for all of your time and help. Thank you Cherie Northon for donating your time and cartography expertise, we greatly appreciated it. Special thanks to John and Debbie for making the station a fantastic place! Last, but certainly not least, we would like to thank our classmates for always wearing a smile, for always willing to lend a hand, and certainly for always being ready for a good time!

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# APPENDIX II: SPECIES CATALOG

## Species A (see plate 1-figure1)

**Morphology and General Habitat Description**: Occurs in various shades of bright orange and yellow, as well as the most common color, an intermediary shade of bright orange yellow. An encrusting sponge found growing in amorphous patches on the underside, side, and top of loose and fixed coral rubble. Ostia, or pores are barely visible to the naked eye and the texture appears fairly smooth and elastic. Found at site locations 1 through 5 within the bay and occurred 157 times in high abundance.

**Spicule Composition**:

Two distinct spicules of same shape- some straight, some slightly curved

1. Subtylostyle-a monoaxon spicule (style) with one end pointed and the other with a slight swelling or 3-dimensional knob
   - some spicules are straight
   - range in length from 62.5-187.5 micrometers
2. Subtylostyle-a monoaxon spicule (style) with one end pointed and the other with a slight swelling or 3-dimensional knob
   - some spicules are curved
   - range in length from 62.5-187.5 micrometers

## Species B (see plate 1-figure 2)

**Morphology and General Habitat Description**: Occurs in a number of colors, namely grey-green, black-grey, and a yellow brown color. Specimens found growing in thick, clump-like encrusting patches on the underside of coral rubble. Surface texture is clathrate and appears porous due to visible ostia. Sponge B occurred 56 times, in sites 1,2,4,5, and 6 in moderately high abundance.

**Spicule Composition:**

Two distinct spicules of same shape-some straight, some slightly bowed

1. Fusiform oxea
   - approximately 62.5 micrometers in length
2. Curved oxea
   - approximately 62.5 micrometers in length

*Oxea Definition-a monoaxon spicule pointed at both ends; different types are distinguished by shape and tip morphology

## Species C (see plate 1-figure 3)

**Morphology and General Habitat Description**: Occurs in a clumpy encrusting form and assumes a red-orange color. Commonly found underneath various sizes of coral rubble. Found at sites 1, 2, and 5 in low abundance. Only 21 specimens found.

**Spicule Composition:**

Five spicules of distinct shape

1. Subtylostyle-a monoaxon spicule (style) with one end pointed and the other with a slight swelling or 3-dimensional knob
   - range in length from 187.5-250 micrometers
2. Anisochela-a chela with unequal ends
   - approx. 31 micrometers in length
3. Sigma- microsclere is in a C or S-shape
   - approx. 42 micrometers long
4. Arcuate chela-an isochela with a bow-shaped shaft and free alae
   - approx. 21 micrometers in length

5. Thin, small hooked spicule present, in shape similar to spicule 4
    - approx. 8 micrometers

## Species D (see plate 1-figure 4)

**Morphology and General Habitat Description**: Sponge is globular and smooth in texture. Occurs in mottled shades of grey and beige and appears to be ball shaped. Specimen is compressible to the touch. Found growing underneath coral rubble of various sizes. Found at site locations 5 and 6 in extremely low abundance. Only three specimens found.

**Spicule Composition:**

Three distinct spicules

1. Stronglyoxea- a fusiform oxea (monoaxon spicule) with one blunt end
    - approx. 500 micrometers long
2. Spheroxyaster-euaster (astrose microsclere) with a centrum that is more than one-third the total diameter.
    - approx. 16 micrometers
3. Tiny eustars that could not be photographed clearly under 40x magnification but were evident in the spicule prep.
    - approx. 8 micrometers

## Species E (see plate 2-figure 5)

**Morphology and General Habitat Description**: Occurs in shades of peach-brown and yellow-brown. Specimen is thin and encrusting, found growing under coal rubble in small irregular patches. Found at sites 1,4 and 6 in low abundance, occurring 22 times.

**Spicule Description**:

Four distinct spicules

1. Stronglyoxea- a fusiform oxea (monoaxon spicule) with one blunt end
    - range in size from 125-187.5 micrometers
2. Subtylostyle-a monoaxon spicule (style) with one end pointed and the other with a slight swelling or 3-dimensional knob
    - range in size from 83-125 micrometers
    - straight spicules
3. Subtylostyle-a monoaxon spicule (style) with one end pointed and the other with a slight swelling or 3-dimensional knob
    - range in size from 83-125 micrometers
    - slightly curved spicules
4. Verticillate-spicule ornamented by whorls
    - approx. 21 micrometers in length

## Species F (see plate 2-figure 6)

**Morphology and General Habitat Description**: Found in various colors ranging from light pink to purple, a shade of beige, as well as a translucent grey color. Extremely abundant in Cook's Bay and occurs in a variety of conditions. Morphological features of this sponge vary from thick, encrusting clumps to massive forms. Also found occurring in digitate morphs, with thin, finger-like projections. The pores are visible and the oscula are large(~5mm wide). Appears to be plastic and clathrate. Grows on the underside, top, and side of coral rubble, on logs, and found growing on large pieces of live coral. Found at all site location in the bay in unusually high abundance, 208 specimens found, and appears to have a very generalized habitat preference.

**Spicule Description:**

Two distinct spicule shapes noted

1. Fusiform oxea
   - approx. 83 micrometers in length
2. Curved oxea
   - approx. 83 micrometers in length

## Species G (see plate 3-figure 7)

**Morphology and General Habitat Description**: Found in translucent shades of beige and white. Occurs in thick encrusting layers on the underside of coral rubble. Ostia are highly visible and sponge has a crunchy and friable texture. Found only two specimens at sites 2 and 6 in extremely low abundance.
**Spicule Description:**
Five distinct spicules

1. Sigma- microsclere is in a C or S-shape
   - approx. 31 micrometers in length
2. Fusiform oxea-extremely thin
   - approx. 125 micrometers in length
3. Curved oxea-extremely thin
   - approx. 125 micrometers in length
4. Tiny cent-shaped sign spicule-too small to photograph clearly at 40x magnification
   - approx. 12.5 micrometers long
5. Curly, thin microsclere –hooked almost into a loop
   - approx. 21 micrometers in length

## Species H (see plate 3-figure 8)

**Morphology and General Habitat Description**: Occurs in shades of red, ranging from bright red-orange to a salmon color. Assumes an encrusting form and found growing in thin patches on the underside of coral rubble. Found 66 specimens located at sites 2,4, and 5 in moderate abundance.
**Spicule Description:**
Four distinct spicules

1. Toxa-bow-shaped microsclere
   - range in size from 16-31 micrometers
2. Subtylostyle-a monoaxon spicule (style) with one end pointed and the other with a slight swelling or 3-dimensional knob
   - knobs can be displaced along shaft-notice there are three distinct bumps
   - range in size from 167-187.5 micrometers
3. Stronglyoxea- a fusiform oxea (monoaxon spicule) with one blunt end
   - approx. 250 micrometers in length
   - note the slight curve of the shaft
4. Tiny shovel spicule
   - approx. 8 micrometers

## Species I (see plate 4-figure 9)

**Morphology and General Habitat Description**: Occurs in an orange-brown color, growing in thin, encrusting patches on the underside of coral rubble. Only one specimen found in Site 1.
**Spicule Description:**
Two distinct spicules

1. Tylostyle-a style with a globular swelling at the base

- approx. 187.5 micrometers in length

2. Oxyaster-euaster with free rays; centrum less than one-third the diameter of entire spicule
   - approx. 6 micrometers in length

## Species J (see plate 4-figure 10)

**Morphology and General Habitat Description**: Occurs as an encrusting form in a translucent light yellow color. Found growing on the underside of coral rubble. One specimen found only in Site 6.
**Spicule Description:**
Two distinct spicules- same shape, different sizes

1. Strongyloxea- a fusiform oxea (monoaxon spicule) with one blunt end
   - note length in comparison to Spicule 2
   - range in size from 167-250 micrometers
2. Strongyloxea- a fusiform oxea (monoaxon spicule) with one blunt end
   - much thinner than Spicule 1
   - range in size from 125-187.5 micrometers

## Species K (see plate 4-figure 11)

**Morphology and General Habitat Description:** Found in a burnt orange color and growing in a thin encrusting layer. Ostia are small and difficult to discern with the naked eye, surface has a punctuate appearance. Texture is smooth and has an elastic component. Found in moderate abundance, twenty-six times, at sites 2,3, and 4.
**Spicule Description:**
Four distinct spicules

1. Strongyloxea- a fusiform oxea (monoaxon spicule) with one blunt end
   - approx. 125 micrometers in length
2. Toxa-bow-shaped microsclere
   - approx. 31 micrometers long
3. Subtylostyle-a monoaxon spicule (style) with one end pointed and the other with a slight swelling or 3-dimensional knob. These knobs can be displaced along shaft.
   - range in size from 125-250 micrometers
4. Tiny cent-shaped sign spicules
   - approx. 8 micrometers long

## Species M (see plate 5-figure 12)

**Morphology and General Habitat Description:** Frequently occurs in Cook's Bay, in small distinct patches underneath coral rubble. Found in an opaque, white color with an abundance of tiny ostia that contribute to the porous appearance of this specimen. Found in the highest abundance, 262 specimens, at sites 2,3,4,5, and 6.
**Spicule Description:**
Two distinct spicules

1. Spheroxyaster-euaster (astrose microsclere) with a centrum that is more than one-third the total diameter
   - range from 12-16 micrometers in length
2. Truncaster-aster with crowded blunt rays
   - range from 12-16 micrometers in length

## Species N (see plate 5-figure 13)

**Morphology and General Habitat Description**: Occurs in a conspicuous shade of blue, as well as peach and brown colors, although seen most frequently in the blue hue. Found growing in thin, amorphous, encrusting layers on the underside of coral rubble. The texture is smooth and elastic, with a punctuate surface. Fifty-seven specimens found at site locations 2,4,5, and 6 in moderate to high abundance.
**Spicule Description**:
One distinct spicule- could be slightly bent

1. Some type of Subtylostyle-one end pointed and the other with a slight swelling or knob
    - note distinct spade shape of knob
    - range in size from 100-250 micrometers

## Species O (see plate 5-figure 14)

**Morphology and General Habitat Description**: Sponge has morphological similarities to the encrusting form of Sponge F. Both textures are plastic and clathrate, with a visible network of veins. Occurs in a characteristic blue-green color and has visible ostia, as well as noticeable oscula that are few in number. Found only at Site 6, in high abundance throughout each transect. Occurred a total of 62 times.
**Spicule Description**:
One distinct spicule

1. Curved oxea-note that these spicules are shorter in length than Sponge B & Sponge F
    - approx. 47 micrometers in length

## Species P (see plate 5-figure 15)

**Morphology and General Habitat Description**: Occurs in a light pink color in encrusting patches on the underside of coral rubble. Appearance is stringy and the texture is soft. Found at site locations 2,5, and 6 in low abundance. Only fifteen specimens found.

**Spicule Description**:
One distinct spicule

1. Tornote-a straight, iso-diametric, diactinal megasclere with conical or mucronate extremities
    - range in size from 21-62 micrometers

## Species Q (see plate 6-figure 16)

**Morphology and General Habitat Description**: Occurs in a dark orange color on the underside of coral rubble in thin encrusting layers. Generally small in size. Texture is smooth, with a punctuate surface. Found in sites 2 and 4 in fairly low abundance, occurring twenty-three times.
**Spicule Description**:
Five distinct spicules

1. Blunt oxea
    - approx. 167 micrometers in length
2. Toxa-bow-shaped microsclere
    - range in size from 31-83 micrometers
3. Sigma- microsclere is in a C or S-shape
    - approx. 62 micrometers long
4. Anisochela-a chela with unequal ends
    - approx. 31 micrometers long

5. Arcuate chela-an isochela with a bow-shaped shaft and free alae
    - approx. 16 micrometers in length

## Species R (see plate 6-figure 17)

**Morphology and General Habitat Description**: Occurs in a deep purple color and is a species of encrusting sponge, growing in thin patches underneath coral rubble. Surface is uniquely velvety and smooth. Found at sites 2,3, and 4 in fairly low abundance. Only twelve specimens found.
**Spicule Description**:
Three distinct spicules

1. Curved oxea
    - approx. 83 micrometers in length
2. Spheraster-an euaster with short rays and a thick centrum; the diameter of the centrum exceeds the length of the rays
    - range in size from 12-16 micrometers
3. Three-dimensional spiky sphere-spikes are thin and straight
    - range in size from 12-16 micrometers

## Species S (see plate 7-figure 18)

**Morphology and General Habitat Description**: Noticeably glutinous and thinly encrusting. Found in a yellow brown color on the underside of coral rubble. Found only at Site 2 in extremely low abundance. Found only three times.
**Spicule Description:**
Six distinct spicules

1. Toxa-bow-shaped microsclere
    - approx. 21 micrometers long
2. Sigma- microsclere is in a C or S-shape
    - approx. 42 micrometers long
3. Anisochela-a chela with unequal ends
    - approx. 21 micrometers in length
4. Arcuate chela-an isochela with a bow-shaped shaft and free alae
    - approx. 21 micrometers in length
5. Tylostyle-a style with a globular swelling at the base
    - approx. 187.5 micrometers long
6. Same shape as Spicule 2, but much thinner and smaller
    - approx. 16 micrometers

## Species T (see plate 7-figure 19)

**Morphology and General Habitat Description**: Found in black, extremely thin, and encrusting patches growing underneath coral rubble. Texture is glutinous and slimy. Found only at Site 2, occurring twice, in extremely low abundance.
**Spicule Description:**
One distinct shape

1. Fusiform oxea
    - range in size from 187.5-250 micrometers

## Species U (see plate 8-figure 20)

**Morphology and General Habitat Description**: Occurs in a variety of shades of yellow, including beige to a light green. Found in thick clumps on the underside of rubble. Texture is extremely rugose and clathrate, with spicules that are visible to the naked eye. Feels friable to the touch. Found at site locations 2,4,5, and 6 in fairly high abundance. Fifty-four specimens found.

**Spicule Description:**

Two distinct spicule

1. Tignule-gigantic isolated diactin
    - straight spicules
    - range from 300-350 micrometers
2. Tignule-gigantic isolated diactin
    - curved spicules
    - range in size from 500-750 micrometers

## Species V (see plate 8-figure 21)

**Morphology and General Habitat Description**: Occurs in a dark brown and a slimy translucent tan color, both with visible ostia. Found living under coral rubble at sites 3,4,5,and 6 in moderate abundance. Thirty-five specimens found.

**Spicule Description**:

One distinct spicule

1. Somewhere in between the truncaster and spheroxyaster-three-dimensional star with long , blunt rays
    - range in size from 12-16 micrometers

## Species W (see plate 8-figure 22)

**Morphology and General Habitat Description**: Occurs in a pale purple color and found growing in thick, encrusting patches underneath coral rubble. One specimen found at Site 3.

**Spicule Description**:

Two distinct spicules

1. Diactin-two rays and a central swelling (no picture)
    - range in size from 31-50 micrometers
2. Fusiform oxea-a few are slightly curved
    - approx. 30 micrometers long

## Species X (see plate 8-figure 23)

**Morphology and General Habitat Description:** Occurs in a yellow-brown color. Found growing in thin encrusting layers on the underside of coral rubble. Texture is slimy and glutinous. Found at site locations 3 and 5 in very low abundance. Only six specimens found.

**Spicule Description**:

Two distinct spicules

1. Tylostyle-a style with a globular swelling at the base
    - approx. 83 micrometers long
2. Toxa-bow-shaped microsclere
    - approx. 62.5 micrometers in length

## Species Y (see plate 8-figure 24)

**Morphology and General Habitat Description**: Found growing in dark red-orange, thin, encrusting patches. Texture is papillate and smooth. Found at sites 4 and 5 in fairly low abundance. Twenty-two specimens found.
**Spicule Description:**
Four distinct spicules

1. Toxa-bow-shaped microsclere
    - range in size from 21-62.5 micrometers
2. Tylote-diactinal megasclere with a swelling on each end
    - range in size from 125-167 micrometers
3. Cladotylote-monoaxon megasclere; one end with knobs, the other with hooks
    - note the spikes on the shaft
    - approx. 62.5 micrometers in length
4. Tiny cents-sign spicules
    - approx. 8 micrometers in length

## Species Z (see plate 9-figure 25)

**Morphology and General Habitat Description:** Found in various shades of red, including red-orange, a dark red-orange, and a red-orange-peach color. Occurs in thin, encrusting patches on the underside of coral rubble. Found at Site 4 only, occurring in moderate abundance. Forty-six specimens were noted.
**Spicule Description:**
Two distinct spicules

1. Strongyloxea- a fusiform oxea (monoaxon spicule) with one blunt end
    - note some spicules straight, some slightly curved
    - range in size from 83-167 micrometers in length

## Species AA (see plate 9-figure 26)

**Morphology and General Habitat Description**: Occurs in various shades of bright red, including bright red-orange and fluorescent pink-red. Found growing in encrusting patches underneath pieces of rubble. Found only in Site 4 in moderate abundance. Thirty specimens noted.
**Spicule Description:**
Five distinct spicules

1. Tiny cents-sign spicule (no picture)
    - approx. 6 micrometers
2. Style- monoaxon spicule with one end pointed, the other end (base or head) blunt
    - range in size from 167-187.5 micrometers
3. Sigma- microsclere is in a C or S-shape
    - approx. 31 micrometers in length
4. Anisochela-a chela with unequal ends
    - approx. 31 micrometers in length
5. Arcuate chela-an isochela with a bow-shaped shaft and free alae
    - approx. 31 micrometers in length

## Species BB (see plate 9-figure 27)

**Morphology and General Habitat Description:** Occurs in a dark purple color and has a definitive hispid surface texture. Found growing in small, encrusting patches under coral rubble. Found at site locations 4 and 5 in high abundance, occurring 78 times.

**Spicule Description:**

Two distinct spicules

1. Curved oxea
   - approx. 83 micrometers in length
2. Subtylostyle-a tylostyle with one end pointed, the other with a slight swelling or knob
   - note spade shaped head
   - approx. 125 micrometers long

## Species CC (see plate 9-figure 28)

**Morphology and General Habitat Description:** Sponge is globular in form and occurs in a peach color. Texture is smooth and compressible, yet firm. Found growing in a bulbous shape under coral rubble with a similar morphology to Sponge D. Only one specimen found at Site 4.

**Spicule Composition:**

Two distinct spicules

1. Tignule-gigantic isolated diactin
   - may be slightly curved, as well as straight
   - approx. 250 micrometers in length
2. Strongyloxea- a fusiform oxea (monoaxon spicule) with one blunt end
   - range in size from 187.5–250 micrometers

## Species DD (see plate 10-figure 29)

**Morphology and General Habitat Description:** Occurs in bright orange, small, encrusting patches on the underside of coral rubble. Nineteen specimens found in Site 4.

**Spicule Description:**

Two distinct spicules

1. Subtylostyle-a tylostyle with one end pointed, the other with a slight swelling or knob
   - range in size from 83-187.5 micrometers
2. Diactine-a spicule composed of two actines
   - very short in length
   - approx. 8 micrometers long

## Species FF (see plate 10-figure 30)

**Morphology and General Habitat Description:** This translucent brown encrusting sponge has definitive tiny orange spots on its surface. It is glutinous and slimy in texture and found on the underside of coral rubble. Found in Site 5 in low abundance, there were only seven specimens.

**Spicule Description:**

Three distinct spicules

1. Tylostyle-a style with a globular swelling at the base
   - range in size from 125-187.5 micrometers
2. Sigma- microsclere is in a C or S-shape
   - approx. 21 micrometers in length
3. Tiny hook-like spicules-too small to photograph clearly at 40x magnification
   - approx. 8 micrometers long

## Species GG (see plate 10-figure 31)

**Morphology and General Habitat Description:** Occurs in a dull brown color and found in encrusting patches under coral rubble. Found eleven specimens at Site 5 in low abundance.
**Spicule Description:**
Two distinct spicules

1. Subtylostyle-a tylostyle with one end pointed, the other with a slight swelling or knob
   - some slightly curved
   - range in size from 125-187.5 micrometers
2. Tylostyle-a style with a globular swelling at the base
   - approx. 83 micrometers in length

## Species HH (see plate 10-figure 32)

**Morphology and General Habitat Description:** Found in brown-yellow, thin, encrusting patches on the underside of rubble. Texture is glutinous and slimy. Three specimens found at Site 5.
**Spicule Description:**
One distinct spicule

1. Straight, very thin spicule-blunt at each end, but not rounded
   - approx. 83 micrometers in length

## Species JJ (see plate 11-figure 33)

**Morphology and General Habitat Description:** Occurs in thin encrusting patches of yellow-brown underneath coral rubble. One specimen found at Site 5.
**Spicule Description:**
Three distinct spicules found

1. Tignule-gigantic isolated diactin
   - approx. 500 micrometers in length
2. Curved oxea
   - approx. 31 micrometers
3. Strongylaster-aster with free, isodiametric, blunt rays
   - extremely small in comparison to Spicules 1 & 2
   - approx. 8-10 micrometers in size

## Species KK (see plate 11-figure 34)

**Morphology and General Habitat Description:** Occurs in dark blue-green-black encrusting patches on the underside of coral rubble. One specimen found at Site 5.
**Spicule description:**
One distinct spicule

1. Subtylostyle-a tylostyle with one end pointed, the other with a knob
   - note unique shape of knob
   - approx. 125 micrometers in length

## Species LL (see plate 11-figure 35)

**Morphology and General Habitat Description:** Occurs in light yellow brown and texture is soft. Found growing in encrusting patches underneath coral rubble. Ostia are tiny, but visible, thus the surface appears punctuate. Only one specimen found at Site 3.

**Spicule Description:**
Three distinct spicules

1. Tylote-diactinal megasclere with a swelling on each end
   - approx. 125 micrometers in length
2. Sigma-microsclere is in a C or S-shape
   - approx. 21 micrometers long
3. Tiny hook-like spicules- too small to photograph clearly at 40x magnification
   - approx. 13 micrometers in length

## Species MM (see plate 12-figure 36)

**Morphology and General Habitat Description:** Occurs in a distinct shade of yellow. Also found in a peach color. Appearance is fuzzy, due to its villose surface. Ostia are tiny yet visible and texture is soft and velvety. Found growing on the underside of coral rubble. Six specimens found in low abundance at Site 5.
**Spicule Description:**
Two distinct spicules

1. Similar to a Subtylostyle shape, but with a knob end and the other end tapers to a blunt tip
   - range in size from 125-187.5 micrometers
2. Diactine-a spicule composed of two actines
   - extremely thin
   - approx. 47 micrometers in length

## Species NN (see plate 12-figure 37)

**Morphology and General Habitat Description:** Occurs in a pale tan color on the underside of coral rubble. Grows in thin encrusting patches and has a soft compressible texture. Ostia are extremely small and surface appears smooth. One specimen found only in Site 4.
**Spicule Description:**
Four distinct spicules

1. Toxa-bow-shaped microsclere
   - approx. 62.5 micrometers long
2. Strongyloxea- a fusiform oxea (monoaxon spicule) with one blunt end
   - range in size from 125-187.5 micrometers
3. Tiny hook-like spicules
   - approx. 8 micrometers in length
4. Blunt oxea
   - approx. 62.5 micrometers long

## Species OO (see plate 12-figure 38)

**Morphology and General Habitat Description:** Occurs in a grey-green with distinct light spots. Surface is glutinous. Found growing in thick , encrusting layers on the underside of rubble. Texture is soft and compressible. Five specimens found at Site 6 in low abundance.
**Spicule Description:**
Two distinct spicules

1. Spheroxyaster-euaster (astrose microsclere) with a centrum that is more than one-third the total diameter
   - approx. 12.5 micrometers in length
2. Curved oxea-very thin
   - approx. 62.5 micrometers

## Species PP (see plate 12-figure 39)

**Morphology and General Habitat Description:** Occurs under coral rubble and is grey in color. Grows in thick, clump-like patches. Texture is friable with visible ostia on the surface. Two specimens found growing at Site 6.
**Spicule Description:**
Two distinct spicules

1. Fusiform oxea
   - extremely thin
   - approx. 62.5 micrometers
2. Curved oxea
   - extremely thin
   - approx. 62.5 micrometers

## Species QQ (see plate 13-figure 40)

**Morphology and General Habitat Description:** Found in a light-green color, growing in thick, clumpy patches on the underside of coral rubble. Surface is distinctly rugose and clathrate, with a texture that is rough to the touch. Six specimens found growing only at Site 6.
**Spicule Description:**
Seven distinct spicules

1. Sigma- microsclere is in a C or S-shape
   - approx. 47 micrometers in length
2. Anisochela-a chela with unequal ends
   - approx. 16 micrometers long
3. Arcuate chela-an isochela with a bow-shaped shaft and free alae
   - approx. 21 micrometers long
4. Toxa-bow-shaped microsclere
   - approx. 47 micrometers in length
5. Tiny hook-like spicules
   - approx. 6-8 micrometers long
6. Subtylostyle-a tylostyle with one end pointed, the other with a slight swelling or knob
   - range in size from 187.5-250 micrometers
7. Curly, thin microsclere –hooked almost into a loop
   - range in size from 16-21 micrometers

## Species RR (see plate 13-figure 41)

**Morphology and General Habitat Description:** Occurs in an orange color and grows in thin encrusting layers on the underside of coral rubble. Surface noticeably glutinous and texture is smooth and compressible. One specimen found at Site 6.
**Spicule Description:**

Three distinct spicules

1. Toxa-bow-shaped microsclere
   - range in size from 8-31 micrometers
2. Tylostyle-a style with a globular swelling at the base
   - range in size from 125-187.5 micrometers
3. Tiny hook-like spicules
   - approx. 8 micrometers in length

## Species SS (see plate 13-figure 42)

**Morphology and General Description:** Found in a yellow-orange color growing in distinct clumps on the underside of rubble. Surface is clathrate and the texture friable with noticeable ostia. Two specimens found at Site 6.

**Spicule Description:**
Three distinct spicules

1. Tylostyle-a style with a globular swelling at the base
   - range in size from 125-250 micrometers
2. Tylostyle-a style with a globular swelling at the base
   - approx. 62.5 micrometers in length
3. Tiny hook-like spicules
   - approx. 6 micrometers long

# PLATE 1

FIGURE 1: Specimen A

1.1
1.2

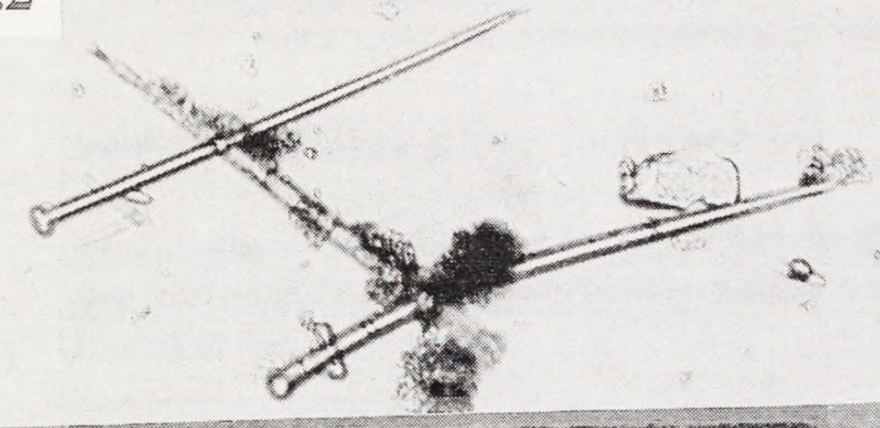


FIGURE 2: Specimen B

2.1
2.2

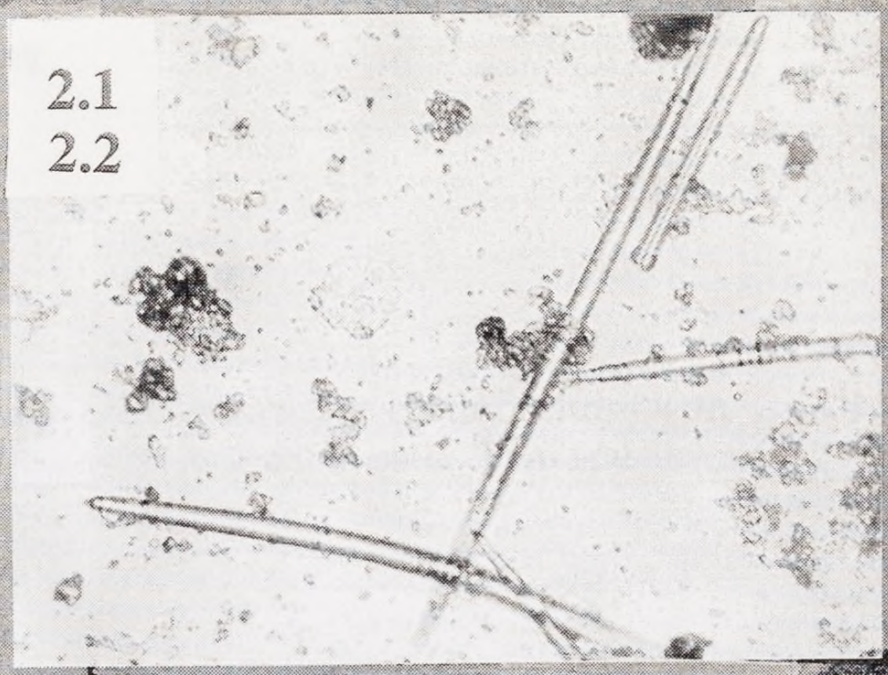
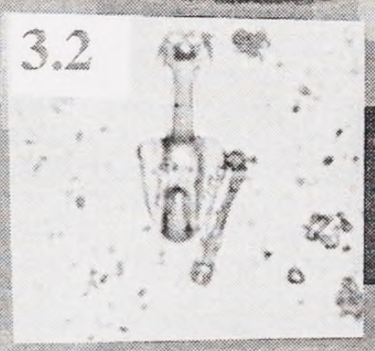


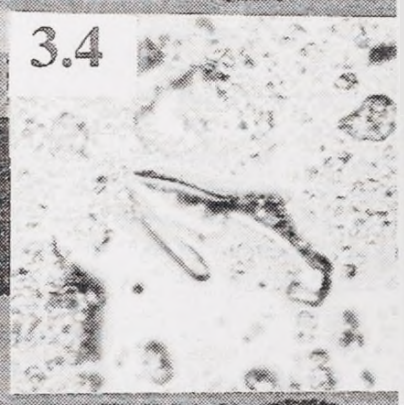
FIGURE 3: Specimen C

3.1

3.2



3.4



3.3

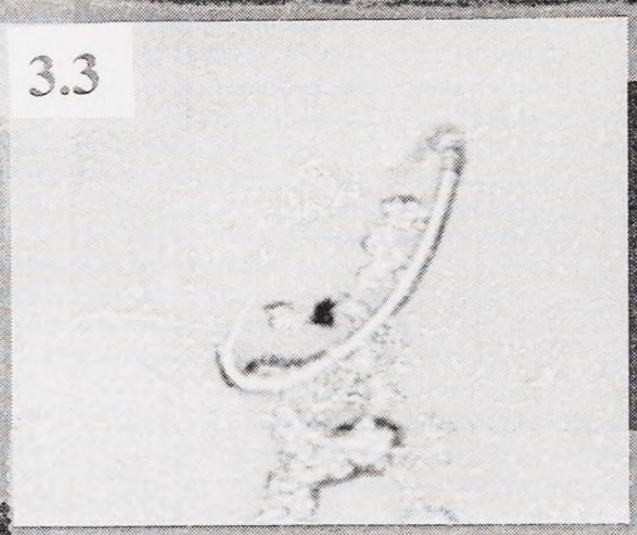
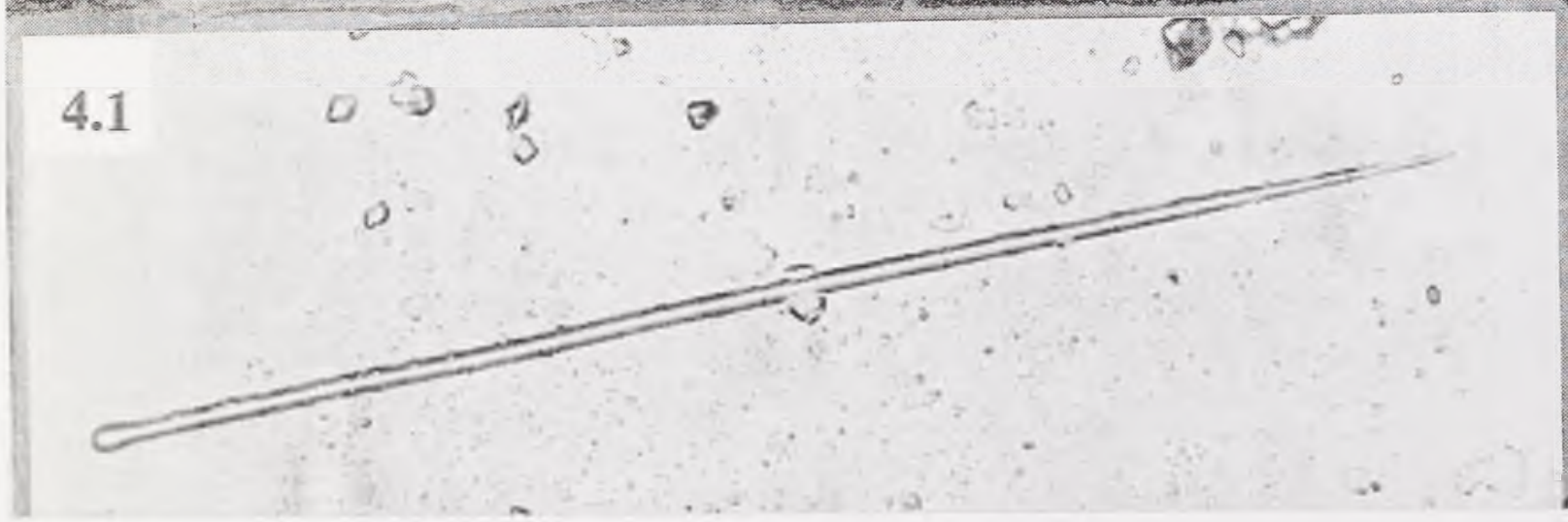
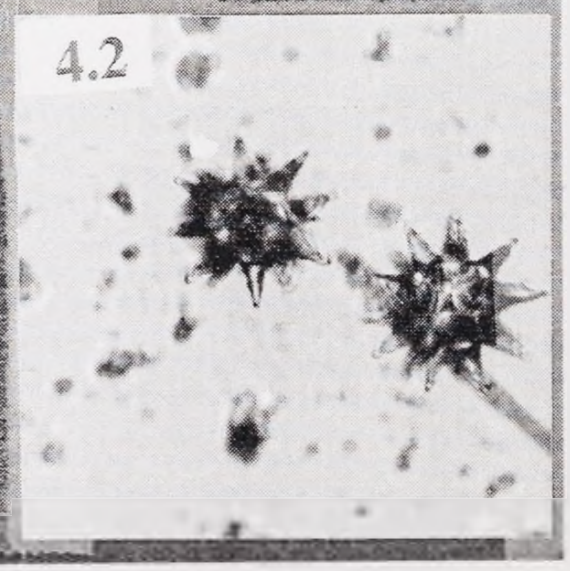


FIGURE 4: Specimen D

4.1



4.2



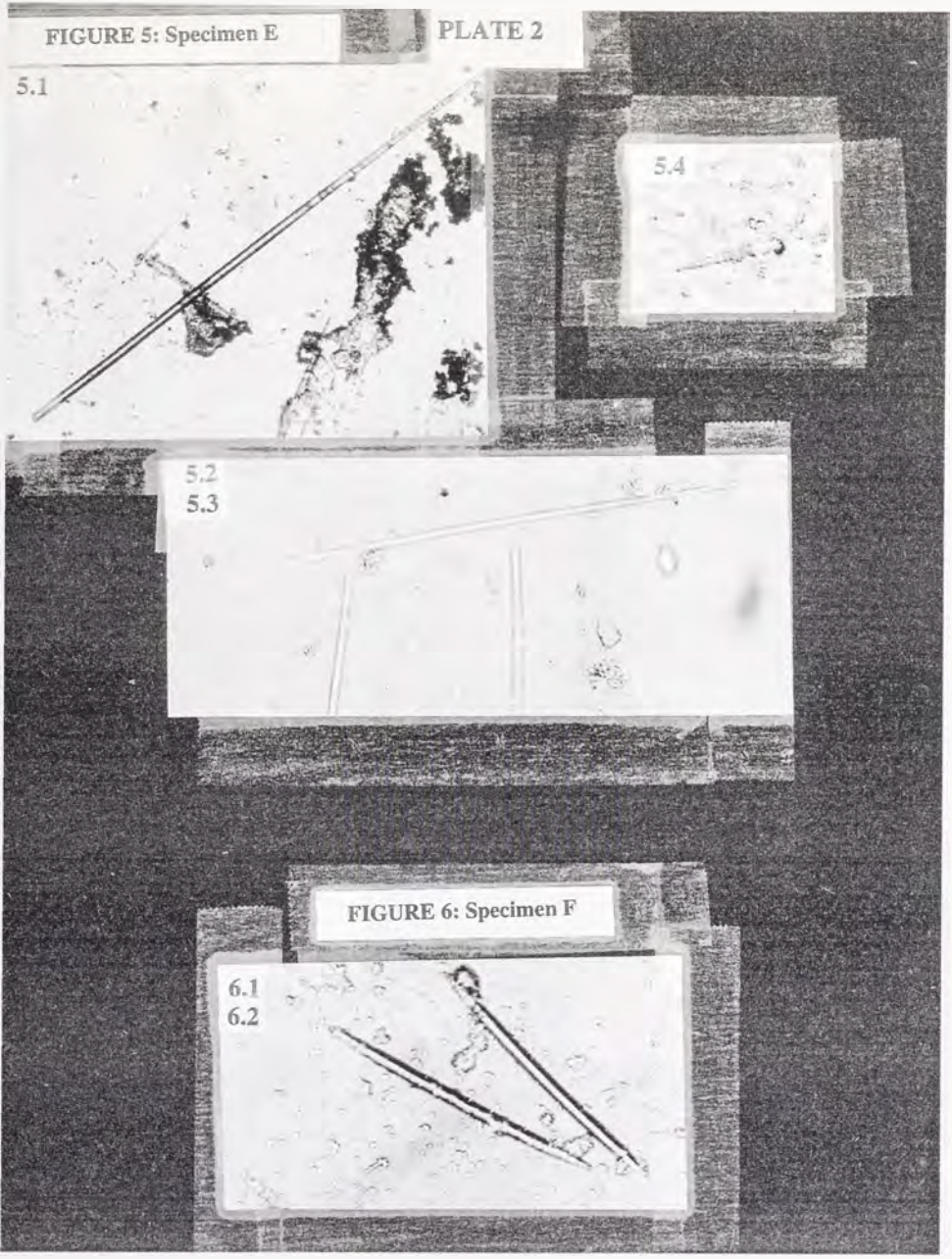


FIGURE 5: Specimen E
PLATE 2
5.1
5.4
5.2
5.3
FIGURE 6: Specimen F
6.1
6.2

# PLATE 3

**FIGURE 7: Specimen G**

7.1

7.2

7.3

7.5

**FIGURE 8: Specimen H**

8.1

8.2

8.3

8.4

PLATE 4

IGURE 9: Specimen I

9.1

2

FIGURE 10: Specimen J

10.2

10.1

FIGURE 11: Specimen K

11.1

11.2

11.3

11.4

PLATE 5

FIGURE 12: Specimen M

12.1

12.2

FIGURE 13: Specimen N

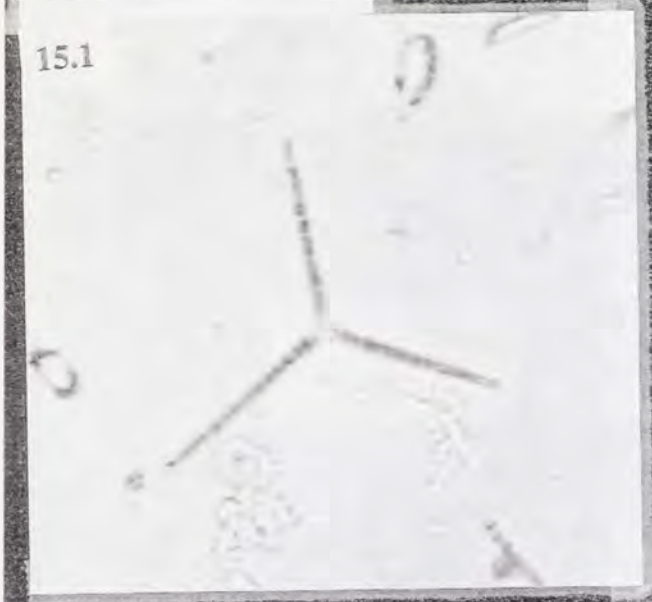
13.1

FIGURE 14: Specimen O

14.1

FIGURE 15: Specimen P

15.1



**GURE 16: Specimen Q**

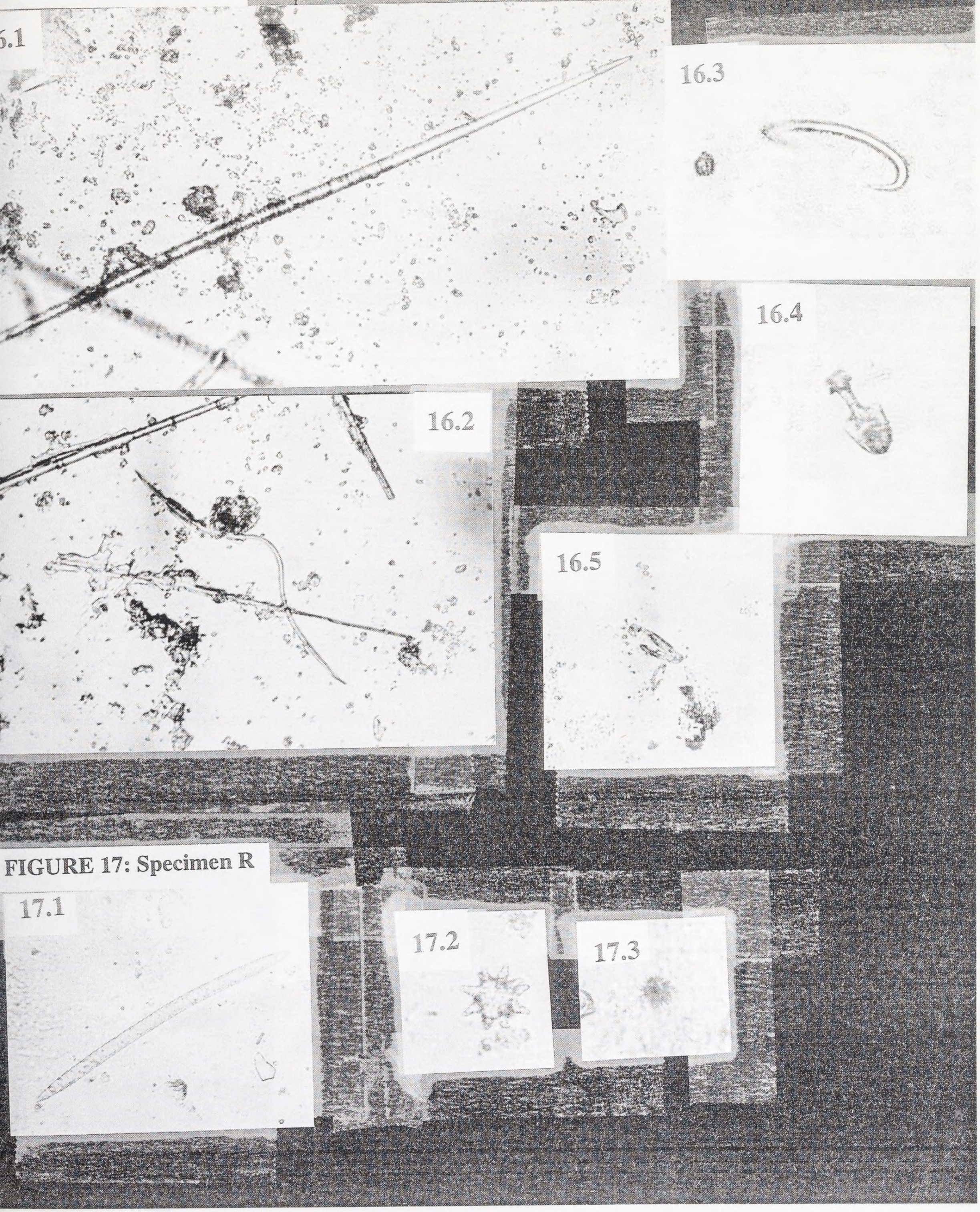



**FIGURE 17: Specimen R**

PLATE 7

18.1

18.2

18.3

18.4

FIGURE 18: Specimen S

18.5

FIGURE 19: Specimen T

19.1

# PLATE 8

FIGURE 20: Specimen U

20.2

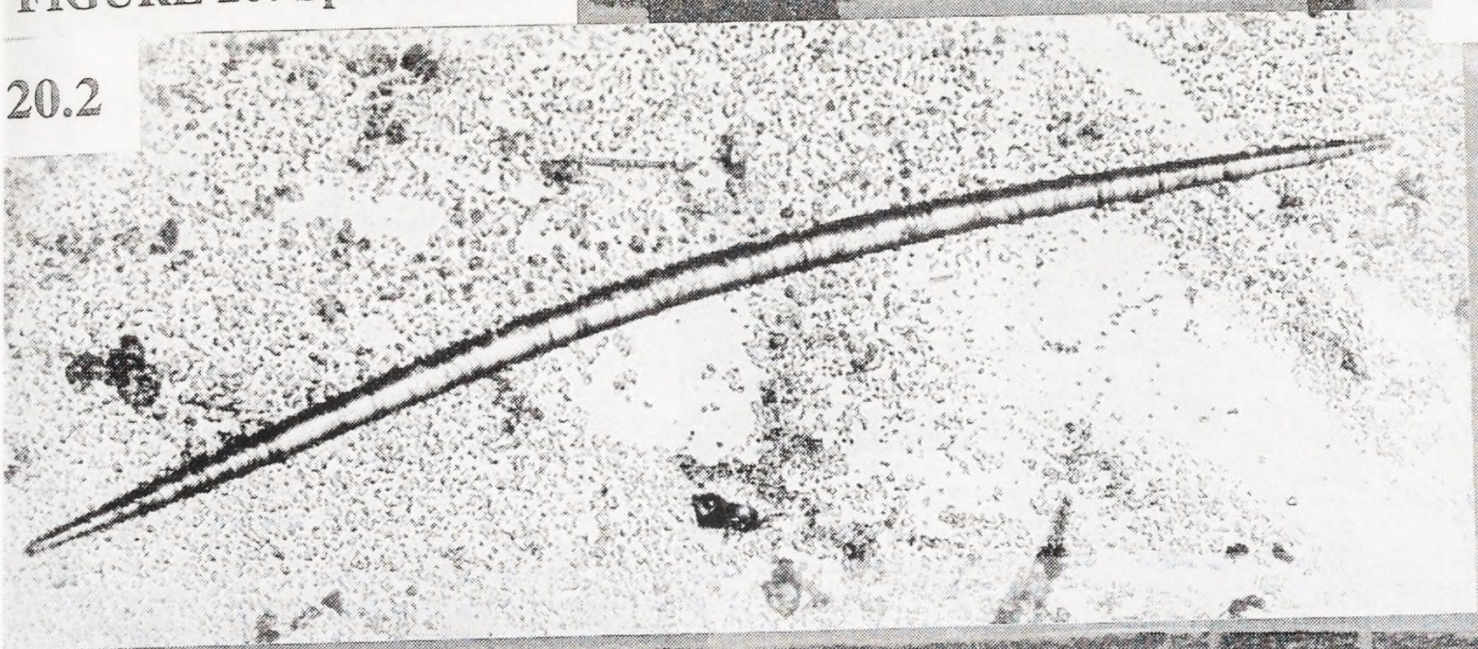


FIGURE 21: Specimen V

21.1

FIGURE 22: Specimen W

22.2

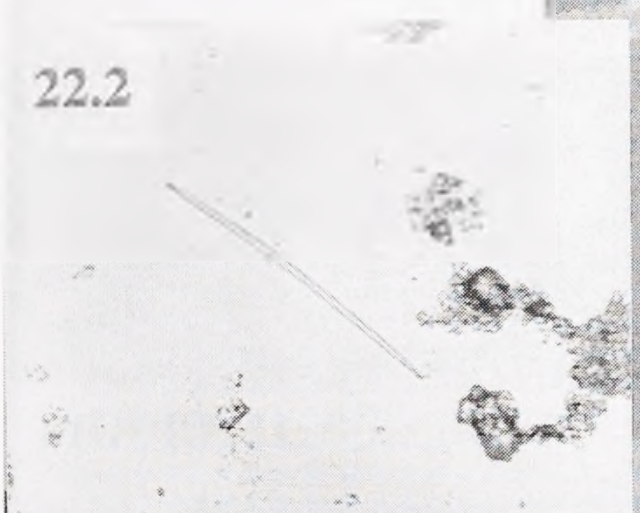


FIGURE 23: Specimen X

23.1

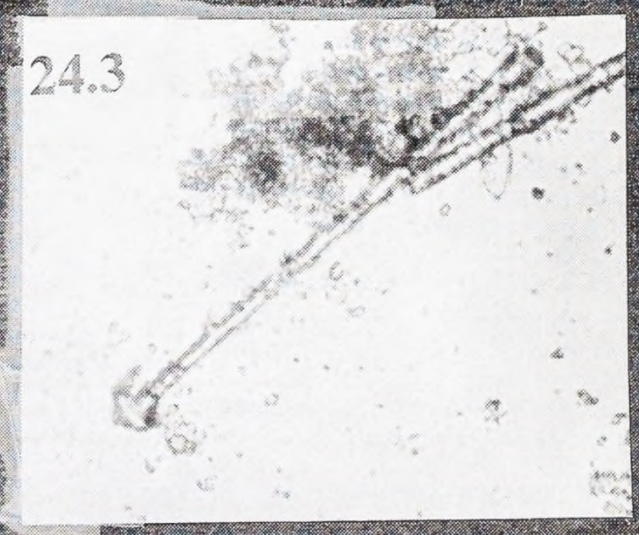
23.2



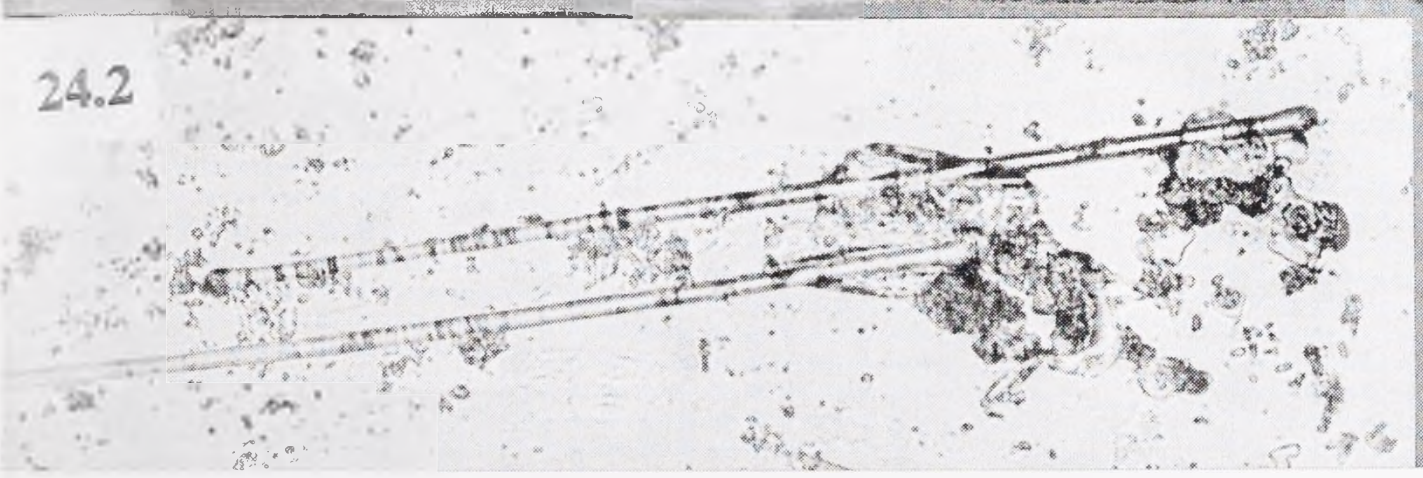
FIGURE 24: Specimen Y

24.1

24.3



24.2



24.4

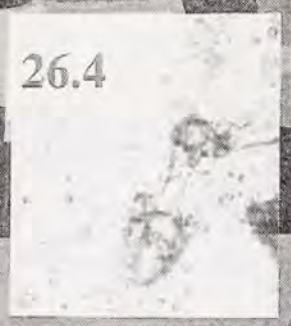
PLATE 9

FIGURE 25: Specimen Z

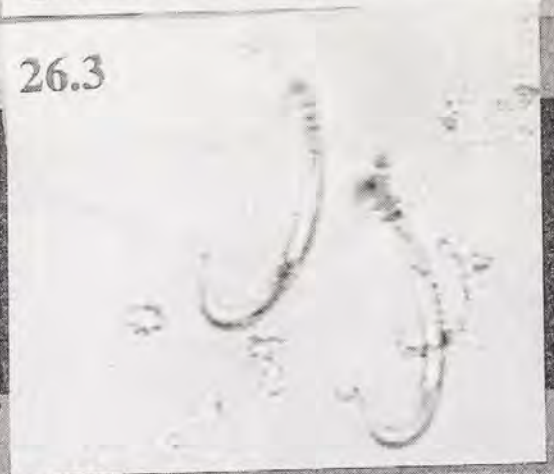
25.1

FIGURE 26: Specimen AA

26.4



26.3



26.5

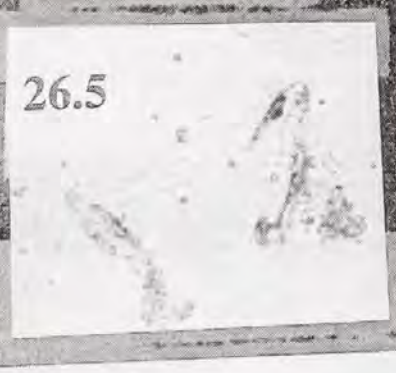
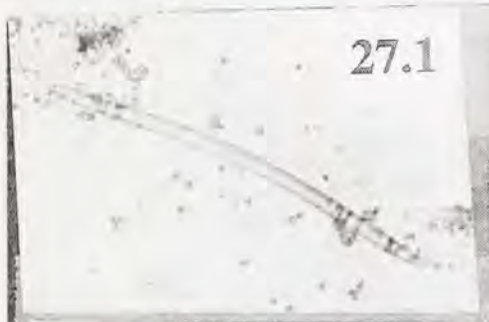
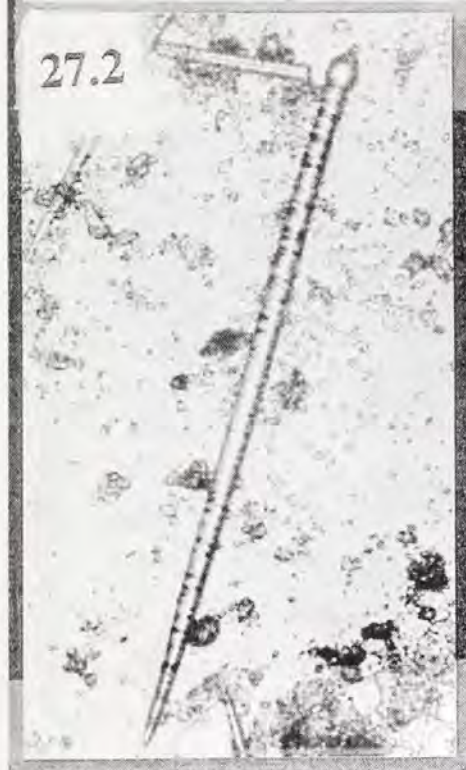


FIGURE 27: Specimen BB

27.1



27.2



26.2

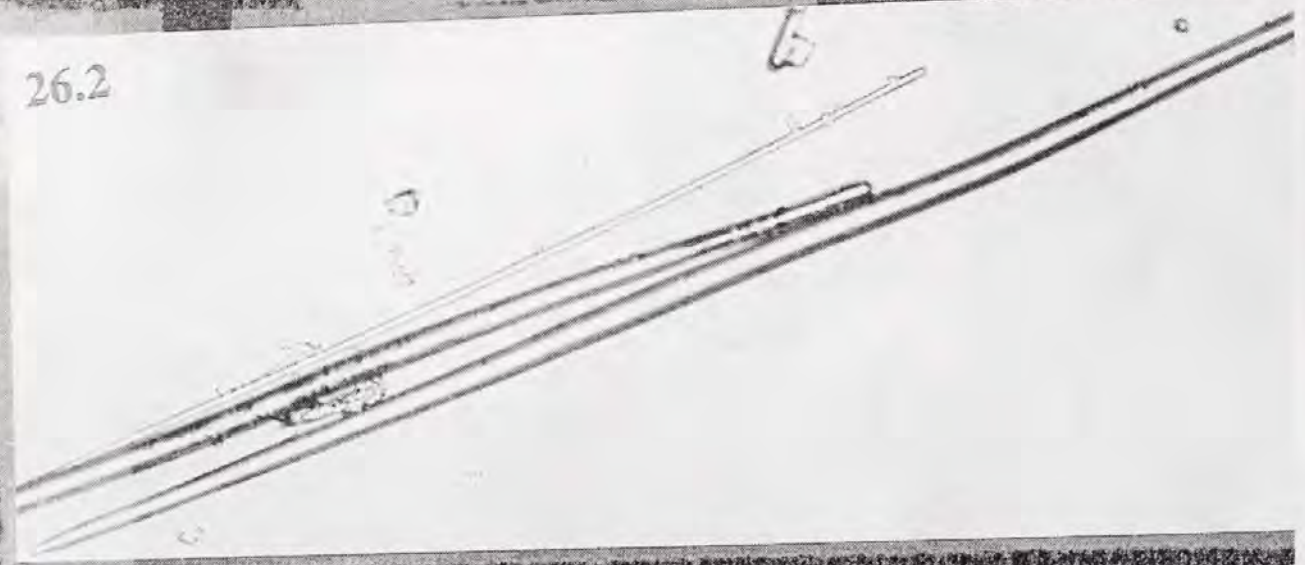


FIGURE 28: Specimen CC

28.1

28.2

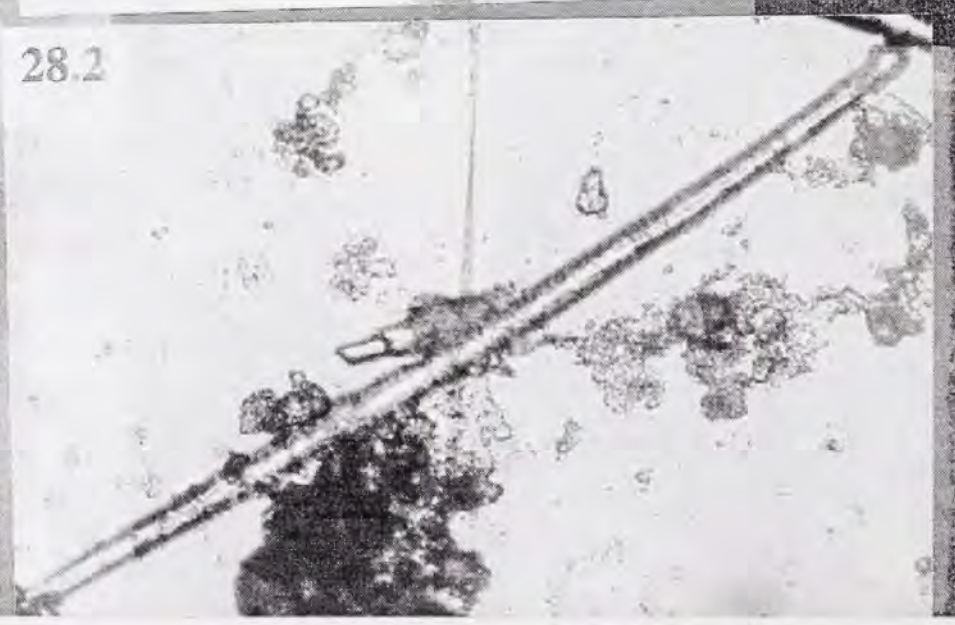


PLATE 10

29.2

FIGURE 29: Specimen DD

29.1

FIGURE 30: Specimen FF

30.1

30.2

FIGURE 31: Specimen GG

31.1

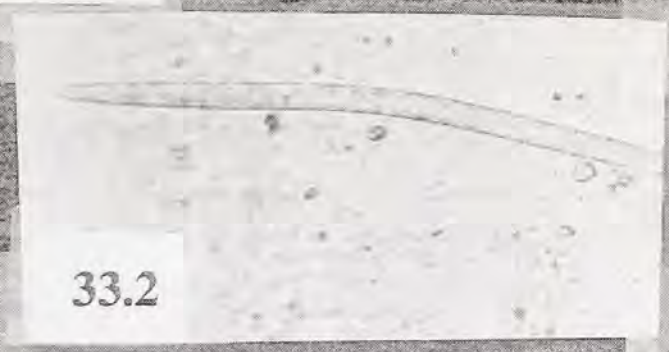
31.2

FIGURE 32: Specimen HH

32.1

FIGURE 33: Specimen JJ

33.1



33.2

33.3

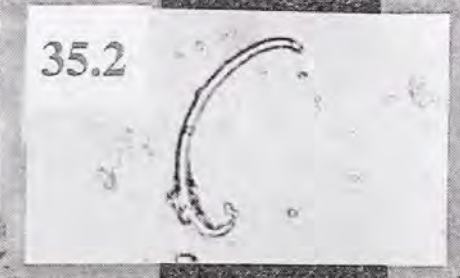
FIGURE 34: Specimen KK

34.1

FIGURE 35: Specimen LL

35.1

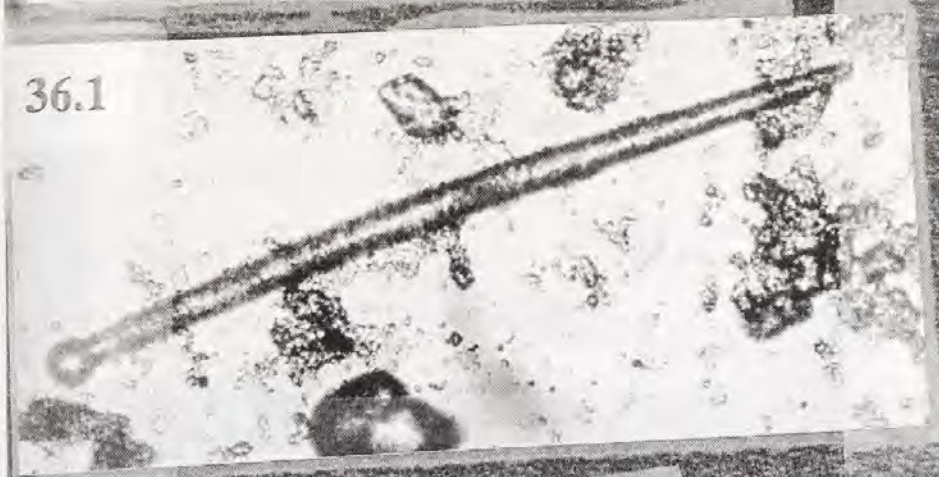
35.2



# PLATE 12

FIGURE 36: Specimen MM

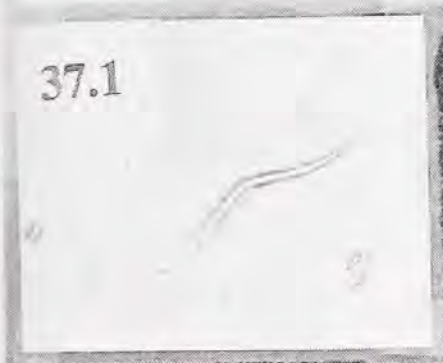
36.1



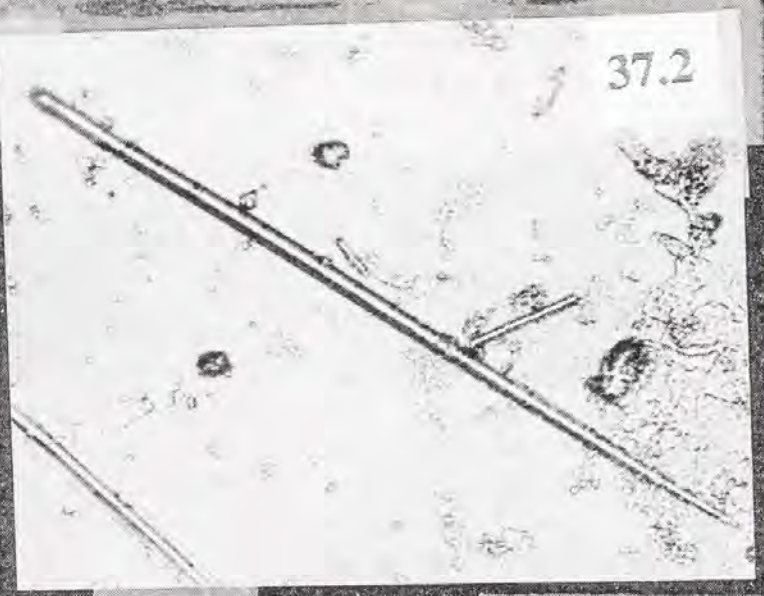
36.2

FIGURE 37: Specimen NN

37.1



37.2



37.3

37.4

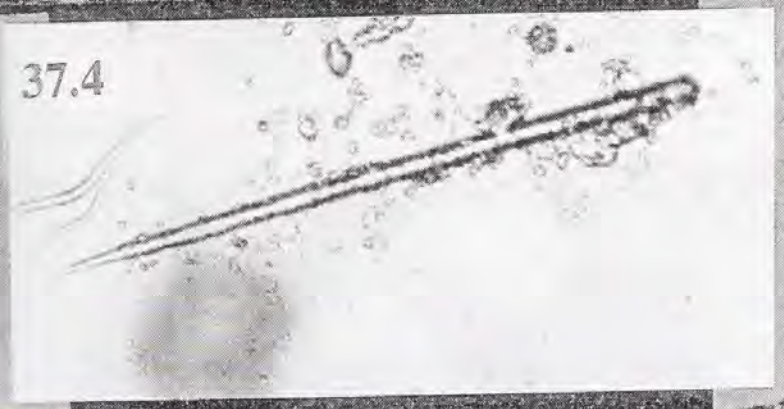


FIGURE 38: Specimen OO

38.1

38.2

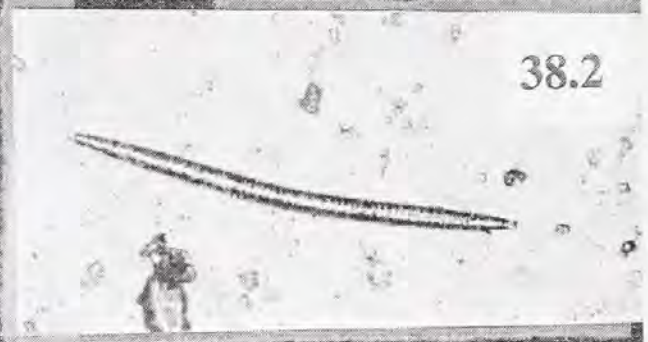
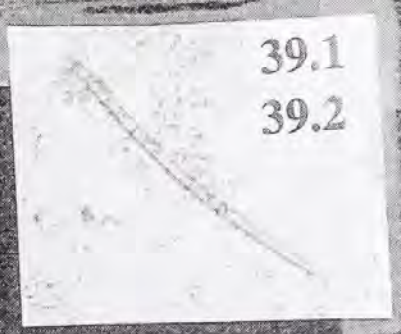


FIGURE 39: Specimen PP

39.1
39.2



# PLATE 13

FIGURE 40: Specimen QQ


FIGURE 41: Specimen RR

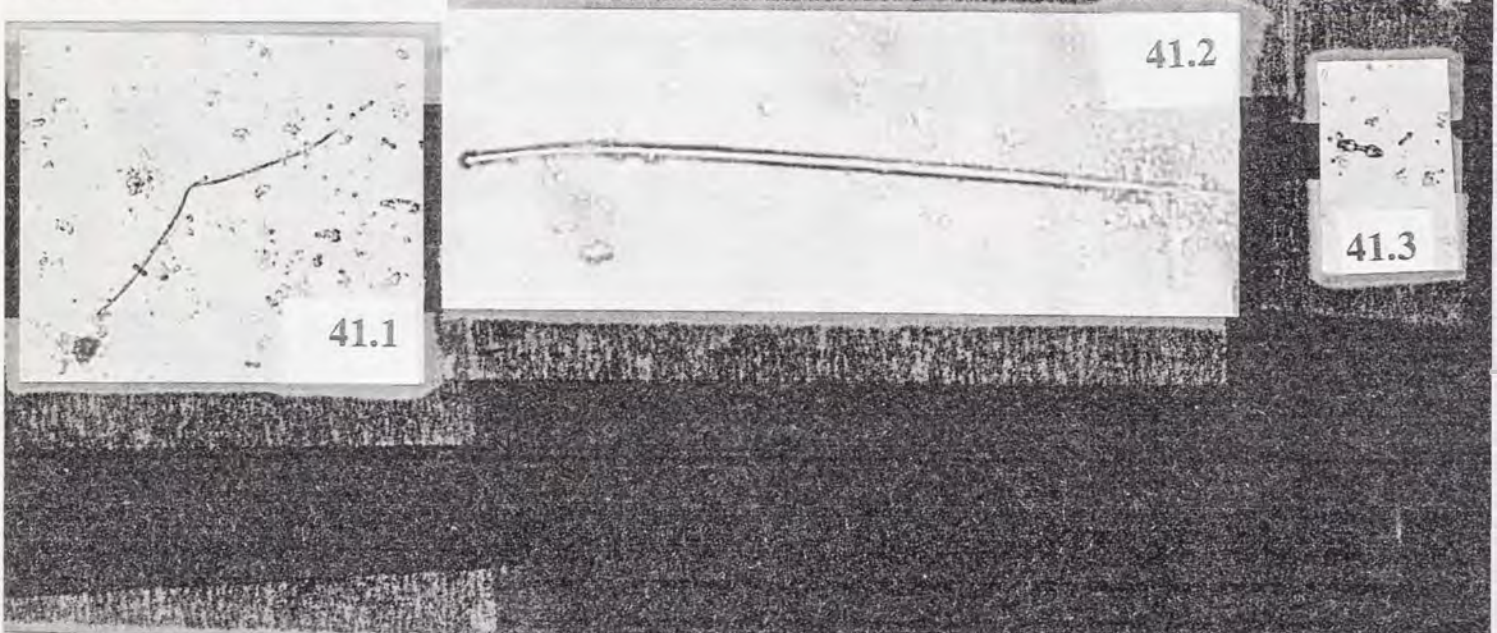
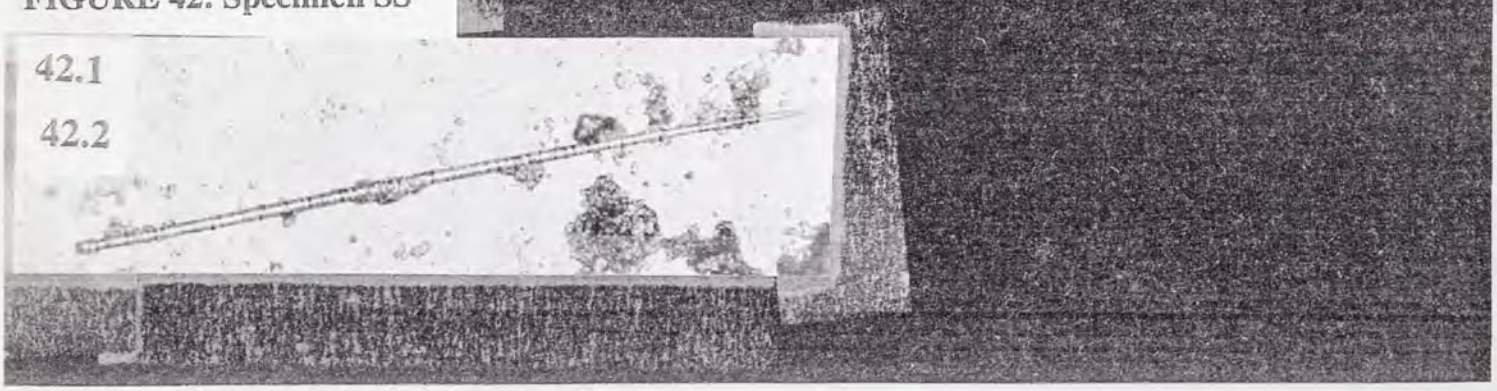



FIGURE 42: Specimen SS



# *Morinda citrifolia* in Moorea: a preliminary macroinvertebrate survey and agronomic status report

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ABSTRACT. *Morinda citrifolia* is a small tree in the Rubiaceae family introduced to the Society Islands by Polynesian settlers who valued it as a source of dyes and medicinal preparations. The first *M. citrifolia* plantations in Moorea, French Polynesia were planted in 1997. This study contains three parts: a review of the literature on *M. citrifloa* including current industry information obtained through interviews conducted in October and November of 1998; an agronomic status survey of the plantations present in Moorea as of November 1998; and a preliminary survey of the macroinvertebrate fauna present on *M. citrifolia* in two natural and one cultivated populations. At the time of this study 84,008 $m^2$ are under *M. citrifolia* cultivation in Moorea, with a total of 7, 818 trees planted. Macroinvertebrate community composition was found to differ among the study sites as sampled through sticky trapping, sweep net samples and leaf collection at each of three growing environments surveyed (a motu plant community, a high island mixed forest, and a monoculture plantation). Whitefly egg masses (family Aleyroididae) were found in highest density at the plantation site (32.94+/- 3.96 egg masses per leaf), while at all three sites the density of whitefly eggs was higher in *M. citrifolia* than in *Hibiscus tiliaceus* (a common neighboring tree species). No significant difference was found between *M. citrifolia* and *H. tiliaceus* at each site or among the *M. citrifolia* samples at the three sites in percent of leaf eaten by herbivores, number of leaf mines per leaf, or density of fungal infections. The dominant macroinvertebrates found in sweep samples in *M. citrifolia* in the plantation and motu sites were members of the family formicidae (69% of macroinvertebrates in motu sweep samples, 68% of those in the plantation site). Sweep samples in the high island mixed forest in both *M. citrifolia* and *H. tiliaceus* demonstrated no single dominant species in the macroinvertebrate community. Sticky trap samples demonstrated flies (families sirphidae, otitdidae, and phoridae) dominating both the motu and plantation site samples, while psyllids dominates the high island mixed forest site sticky trap samples.

## Introduction

The history of Polynesian agriculture is one of differentiation, expansion and intensification. Human colonization of the South Pacific Islands now known as the Society Island archipelago was soon followed by anthropogenic changes in the landscape: forest clearance, alteration of indigenous biotic communities, erosion, siltation, and other forms of physical modifications (Kirch 1982). The development of agricultural systems was closely linked to cultural modifications of island landscapes (Kirch 1991). Post-European modifications of Polynesian agriculture, and the social and economic context of the present day have created a blend of traditional subsistence farming practices and export oriented agronomic policies. Recently, a new export crop has entered the scene in French Polynesia. The plant itself, *Morinda citrifolia*, is one that has been growing on Moorea and Tahiti for at least 2,500 years. It is naturally dispersed throughout the high island of Moorea and its motus, at both low and high elevations; growing in areas of sandy and volcanic soils, and in dry as well as moist environments. Until 1995, however, this small fruit tree grew only in small numbers in cultivation. In 1995, an export market was initiated for the *M. citrifolia* fruit (known as Nono in French Polynesia) and subsequently local farmers in Moorea began to grow the trees in plantations.

*Species description*

*M. citrifolia* is found all over South East Asia, Australia and the South Pacific. Known as Indian Mulberry in some parts of the world, it is a small tree in the Rubiceae family, rarely surpassing five meters in height. It has oval shaped, smooth and luminous leaves in opposite arrangement. The fruit is composite, between 8 and 16 centimeters long and 7 and 12 centimeters wide when mature, shaped like a small potato. The flowers are white, with four or five petals. After fertilization the ovaries swell and weld together forming the fruit. The seeds have a thick seed coat and an air sac, and are thus easily water dispersed.

*Polynesian ethnobotany*

*M. citrifolia* plays an important part in Tahitian botanical culture. In Polynesian mythology, plants originated from human beings. For example, the breadfruit tree, or Uru, was born from a man: the trunk was his body, the branches his extremities, the fruit his head and the heart of the fruit his tongue. Nono is said to have originated from earwax (Petard 1984). A bright yellow dye is made with the bark of the tree. An orange dye can be extracted from the roots. These were used by the Polynesians in the past to dye tapa and more cloths (Smith 1813). In addition to its value as a source of natural dyes, the fruit, leaves, bark and roots of the Nono tree are used in the preparation of many medicinal treatments. It was fed to domesticated animals, and used as a human food in times of famine (Petard 1984). Astringent, antibiotic and antioxidant qualities are attributed to this fruit in traditional Polynesian medicine. It is combined with other plant products and used both internally and externally to treat a variety of ailments. A widely known use of the Nono fruit is as an external poultice for the treatment of stonefish stings (*Synanaceja verrrucosa* Blotch and Schneider). According to Sydney Parkingson's journal of Cook's first voyage (1784), *Morinda citrifolia* was present on Tahiti at the time of the first European contact, and is thus thought to be either a Polynesian introduction to these islands or a naturally dispersed colonial species (Parkingson 1784).

*Scientific literature review*

The biochemical properties of *M. citrifolia* and its release of anthraquinones in cell suspensions have been the subject of recent studies (Van Der Plas, et al. 1998: Bassetti et al. 1996, Bassetti and Tramper 1995, Hagendoorn et al. 1994, Kieran et al. 1995). These workers have shown that it is a model system for the study of the interactions between secondary and primary metabolism in plant cells. Possible anti-cancer activities of *M. citrifolia* extracts have been reported in studies of lung cancer in mice (Hirazumi et al 1994; Hiramatsu 1993; Ganal et al 1993). Several papers have been published regarding the sensitivity of certain drosophilid flies (Jones 1998) and other insects (Legal et al. 1995) to octanoid and other active secondary plant compounds. Subgroups (i.e. *Drosphila sechellia*), in both of the aforementioned studies were found to show resistance to these compounds. Jones used this resistance to analyze the genetic markers forming a basis for resistance in *Drosophila sechellia*. Other areas of *M. citrifolia* plant biochemistry and insect-host plant relations remain to be investigated.

According to the Department of Applied Agronomic Research in French Polynesia, the preliminary stages of research on *M. citrifolia* will include observation and in depth studies of the species in its natural environment, in order to best plan for its agricultural future in French Polynesia. Populations of *M. citrifolia* on the high island as well as on the motus are to be monitored in order to develop a working knowledge of the soil and developmental needs of the plant (Garnier 1997). In view of its up and coming economic importance in Tahiti and its neighboring islands, the Rural Development Services Agency is conducting studies in research plots of *M. citrifolia*. The research objectives of these plots include: 1) improved biological understanding of the plant's physiology and reproduction 2) census of pests in the natural environment and in the presence of other neighboring plants to determine their impact upon the agronomic development of *M. citrifolia* and 3)evaluation of productivity in monoculture under different management regimes (fertilizing, watering, etc.) (Garnier 1997). The results thus far in these agricultural experimentation plots have been published by the agencies involved (Garnier 1997) and include recommendations for management and establishment of a plantation. Research development is also directed in the field of plant interactions and possible intercropping strategies (Garnier, pers. Comm. 1998).

*Industry Profile*

The following information was obtained in an interview conducted October 24, 1998 in Papeete, French Polynesia, with John J. Wadsworth, Vice President of Morinda Inc.

Morinda Inc. was the first company to enter the international market of *M. citrifolia* products; initiated in July of 1996 by eight United States citizens and one Tahitian citizen. Survey and study of the plant by Morinda Inc. researchers began in December of 1994. In August of 1995, they developed a pasteurization technique and became the first to export the fruit puree to the United States, where they are currently processing, bottling and distributing Noni™ juice and hair and skin care products. As of November 1998, Morinda Inc. products are exported to 18 countries around the world. About 96% of the market is currently based in the US, Canada, and Taiwan. While Morinda Inc. obtains most of its Nono fruit from Polynesia, several other private enterprises have since begun to market the fruit and export it from Hawaii, Fiji, Samoa, and Tonga. Morinda Inc. is currently in negotiations with the French Polynesian government to obtain preferential treatment in taxing and exporting duties. Noni™ products are marketed door to door by Morinda Inc. sales representatives in a pyramid sales format. The fruits used to make the puree that is exported to Los Angeles for processing and bottling

come from 247 islands in the South Pacific, adding up to a total of over 900 tons of fruit per month. More than 50% of this fruit comes from the Marquesan Archipelago, where the plant is very abundant. In 1998, at least 70% of the Nono obtained by Morinda Inc. for puree production came from local collectors who gather the fruits from naturally occurring trees. These collectors receive about 60 central pacific francs per kilogram of fruit (Garnier, 1997). About 5% of the *M. citrifolia* fruits exported by Morinda Inc. currently comes form Moorea. Much of this fruit is purchased from collectors because the young plantations have not yet become and important source of the fruit for Morinda Inc. (Waddsworth 1998).

*Industry Future*

At this early stage, the market for products containing *M citrifolia* extract in the US is unpredictable. Critics of Morinda Inc. cite reliance upon testimonials rather than clinical research and speculation about the pharmacological effects of xeronine in the literature published by the corporation (Altmed 1998). In 1998, Morinda Inc. was fined a total of $100,000 in fines for publicizing health benefits without the approval of the US FDA. Nonetheless, *M. citrifolia* farmers in the South Pacific are encouraged by the $65 million annual sales of Morinda Inc. (DuPrel 1998).

*Research objectives*

The onset of *M. citrifolia* agriculture in Moorea raises a host of agronomic and ecological questions. The transformation from natural distribution to large-scale cultivation will certainly affect the plant ecology widely. The functions of genetics, pollination, pathogen transmission, microbial and other organism interactions will have corresponding effects on the agroecosystems and the industry. As a preliminary course of applied research, a descriptive survey of the invertebrate communities present on *M. citrifolia* provides future workers with baseline information.

Bacterial and viral plant infections are often vectored by certain insects (leafhoppers, whiteflies, thrips, beetles, etc.) and arthropods (mites) (University of California 1980). The economic importance of these as vectors of disease, as well as the role of invertebrates in pollination, herbivory, and biological control warrants a close monitoring of their populations and distributions. The following study has two main objectives 1) To document the status of *M. citrifolia* agriculture as of November 1998 in Moorea and 2) to use a descriptive sampling approach to compare and contrast the macroinvertebrate community composition on *M. citrifoila* in natural and agricultural growing environments.

**Materials and Methods**

*Part I. Plantation survey*

In order to evaluate the current status of *M. citrifolia* as an agricultural crop in Moorea, French Polynesia, I mapped each of the nine plantations of more than one hundred trees on the island. I used a hand-held GPS unit to obtain coordinate system waypoints at the boundaries of each plantation. Using the field mapping techniques of pacing and compass bearings, I determined the area in meters squared devoted to *M. citrifolia* cultivation as of November 1998. In addition, I interviewed the plantation managers in person to obtain management information and land use history (Appendix 1).

*Part II. Macroinvertebrate community composition survey*

With the aim of quantifying ecological community differences in the macroinvertebrate fauna, I sampled three different growing environments of *M. citrifolia* on the island of Moorea and its Motu Tiahura during the months of October and November, 1998. I chose three sites to represent two "natural" growing environments (that of the motu plant community and that of the high island mixed forest) and one agricultural setting in a monoculture plantation. At each of these sites I followed the sampling protocol described bellow. I chose three different sampling methods in order to achieve a descriptive picture of the macroinvertebrate community from which to discern patterns within and between the growing environments.

*Site descriptions*

The island of Moorea lies 25km to the North West of Tahiti, at 17°30' South latitude and 149°50' West longitude. This island is part of the Society Archipelago, French Polynesia.

*Site 1: Motu Plant Community*

Motu Tiahura is the representative "motu environment" site. This is a small (approximately 1km squared) coralline islet, 100 meters offshore on the Northwest side of Moorea (Figure 1). This site has a dry environment and sandy soil in comparison with that on the high island. The highest canopy layer is dominated by *Cocos nucifera* and *Casurina equisetifolia*. *M. citrifolia* grows here in patches of about five to thirty individuals, some of which are under partial shade and some of which are in full sun. The spacing between the individuals in a patch is from zero to five meters. The ground cover vegetation

# Moorea, French Polynesia

149°55'W
149°50'W
149°45'W
17°30'S
17°35'S

Site 1
Motu Tiahura
Motu Fareone
Club Med
Papetoai
Opunohu Bay
Site 3
Gump Station
Cook's Bay
Pao Pao
Teaharoa
Maharepa
Temae
Opunohu
Riv. Paopao
Riv. Opunohu
Site 2
Teavaro
Vaiare
Ferry Terminal
Afareaitu
Motu AN
Ha'apiti
Hauml
Ma'atea
PK 0
PK 1
PK 2
PK 3
PK 4
PK 5
PK 6
PK 7
PK 8
PK 9
PK 10
PK 11
PK 12
PK 13
PK 14
PK 15
PK 16
PK 17
PK 18
PK 19
PK 20
PK 21
PK 22
PK 23
PK 24
PK 25
PK 26
PK 27
PK 28
PK 29
PK 30
PK 31
PK 32
PK 33
PK 34
PK 35

Coastline
Primary road
Unpaved road
River
100 m contour
PK 19 Kilometer Post
Town
Study Site

N

1 mile
1 Kilometer
0 500 1000 meters

around many of the patches is dominated by ferns (*Phymatosorous* sp.). Other common members of the motu plant community include *Tacca leontopetaloides*, *Cassytha filiformis*, *Tournefortia argentea*, *Pandanus tectorius* and *Hibiscus tiliaceus*.

*Site 2: High Island Mixed Forest*

A second study site, representative of high island mixed forest areas on Moorea, is located on Richard Gump Biological Research Station property, just West of the laboratories and dormitories (Figure 1). *M. citrifolia* is found here in patches of about one to ten individuals amongst *Hibiscus tiliaceus, Ianocarpus fagifer, Cocos nucifera, Barringtonia speciosa, Terminalia catappa* and other tree species. The ground is mostly covered with leaf litter and debris. The light conditions for *M. citrifolia* at this site are partially to mostly shady.

*Site 3: Agricultural Valley, Monoculture plantation of the Opunohu Agricultural School*

The plantation managed by the Opunohu Agricultural School, a representative monoculutre plantation, is the third sampling site (Figure 1). Located in the center of the Opunohu Valley, this 7, 208 $m^2$ plantation was planted in November of 1997. Herbicides have been applied several times since planting to keep the ground bare of weeds. NPK standard fertilizers have been applied every six months to promote tree growth. The *M. citrifolia* trees in this plot are in full sun. A riparian belt of many tree and vine species, including *H. tiliaceus*, raps around the South and East sides of the plot. The neighboring fields are planted in coffee (*Coffea arabica*), pineapple (*Ananas comosus*), and taro (*Colocasia esculenta*). A frequently traveled earthern road runs along the Northwestern boundary of the orchard.

*Sampling methods*

1. Sticky traps:

I placed eight traps made with white, 4 5/8" by 7" Write-in-the-Rain™ paper and a 2mm layer of Tanglefoot™ insect trapping substance 16cm away form the main trunk of the tree on the highest woody branch. I chose at random four *M. citrifolia* trees (one at each cardinal direction within the patch) and four trees of other species (of approximatley the same height) on the periphery of the *M. citrifolia* patch at each of the four directions. The traps remained on the trees for twelve days at each of the sites. After twelve days, I removed the traps and used a one inch squared grid for analysis of the macroinvertebrates present.

2. Leaf colleciton:

I collected 100 leaves from *M. citrifolia* trees and 100 leaves from surrounding *H. tiliaceus*. I took two leaves from each tree chosen at random from within the patch or plot. On *M. citrifolia* trees, I chose the two oldest leaves (most basal), and on *H. tiliaceus* trees I chose the two leaves at the base of a haphazardly chosen branch. I recorded the number of whitefly egg masses, patches of dead tissue (possible fungus infections), leaf mines, and percent of the leaf eaten by herbivores.

3. Sweep samples:

I used an insect sweep net to take six sets of forty sweeps each in *M. citrifolia* and in the surrounding *H. tiliaceus* at randomly chosen locations within the site. I sorted the samples, placed all insects and small invertebrates in 70% ethanol and recorded the numbers and types of species found.

**Results**

*Part I: Agronomic Status Survey*

At the inception of the *M. citrifolia* export industry, and historically (for local consumption), the fruits were harvested mainly from the natural populations on the motus and along the coastal strand. An expansion of the market for the fruit prompted several local property owners, beginning in May 1997, to plant the crop at a larger scale than ever before in Moorea. The map (Figure 2) below shows the distribution and relative sizes of the *M. citrifolia* plantations surveyed during October and November 1998. Plantations of less than 100 trees are not included.

The land area, planting density and land use history of each of the nine plantations is presented in Table 1. Plantation owners or managers provided the information regarding land use history at each site. The conversion to *M. citrifolia* agriculture from other land uses requires clearing the area of thick underbrush vegetation, but in several cases trees such as *Cocos nucifera* from previous plantations were left in place. Since *M. citrifolia* is able to grow in a wide range of environmental conditions on Moorea, the plantations have been planted from the coastal strand to the high valley slopes. The difficulties most commonly reported by the growers include the control of invasive weeds and damage caused by livestock. None of the plantation managers had experienced insect or pathogen damage at the time of this survey.

Table 2 summarizes the agricultural status of *M. citrifolia* in Moorea. After 17 months of large-scale agricultural history in Moorea, the total land devoted to *M. ctitrifolia* cultivation on the island is 84,000 $m^2$,

# Moorea
## *Morinda citrifolia* Plantations

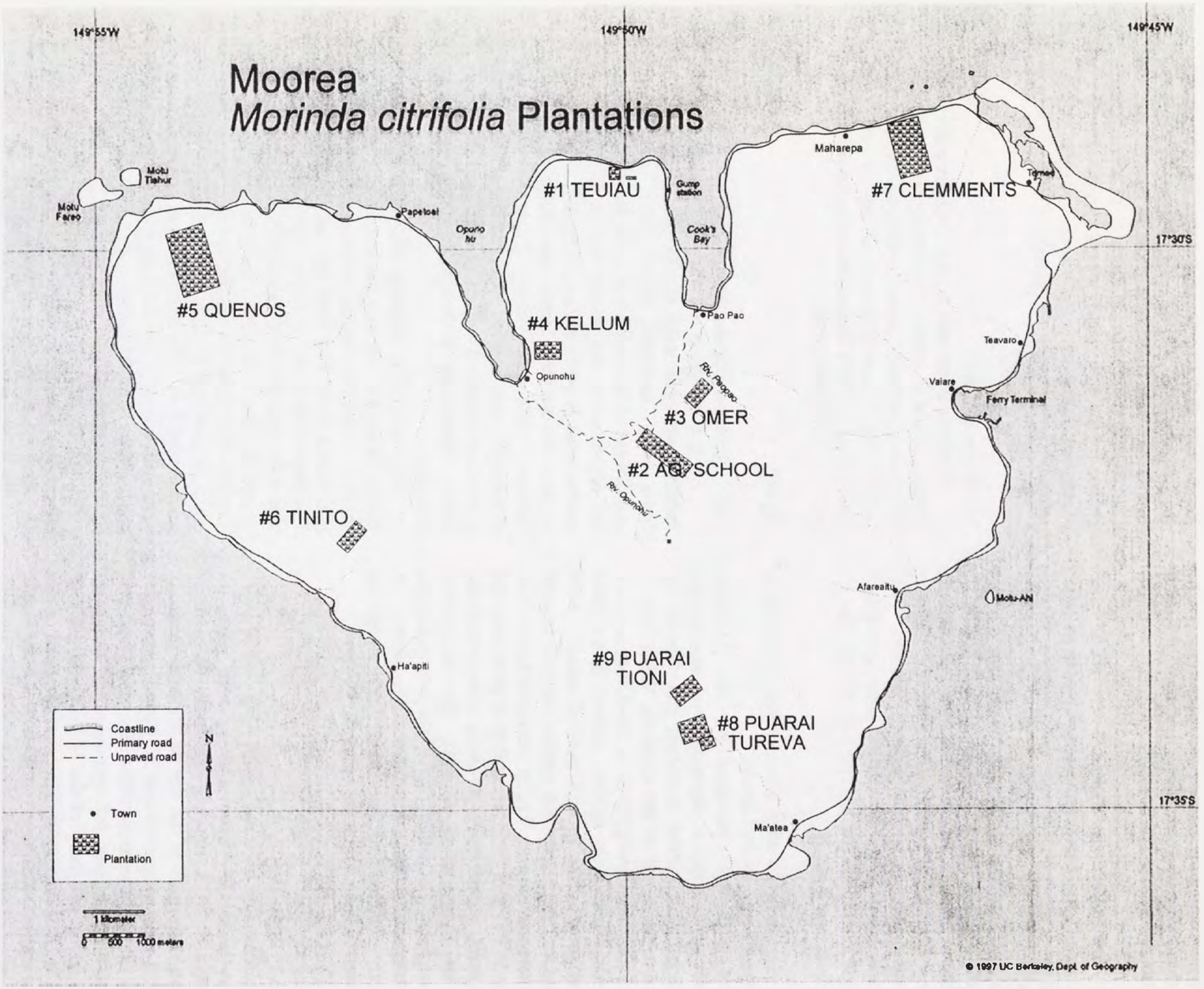


Table 1. Field mapping plantation information summary.

| **Plantation number** | **Land area ($m^2$)** | **Number of trees** | **Density of trees/ 10 $m^2$** | **Previous Land Use History** |
|---|---|---|---|---|
| 1 (A and B) | 12,300 | 700 | 0.56 | Cleared land, residential or agricultural in the past but abandoned for more tan 2 years. |
| 2 | 7,210 | 118 | 0.16 | Pineapple (*Ananas comosus*) plantation. |
| 3 | 3,400 | 600 | 1.8 | Pomelo (*Citrus maxima*) orchard. |
| 4 | 1,000 | Currently re-planting | N.A. | Grazing area, fruit tree orchard. |
| 5 | 19,200 | 3,000 | 1.6 | Copra plantation (*Cocos nucifera*) |
| 6 | 990 | 300 | 3.0 | Mixed forest, home garden area (fruit trees). |
| 7 | 18,600 | 1,500 | 0.80 | Copra plantation(*Cocos nucifera*). |
| 8 | 14,800 | 1,700 | 1.2 | Papaya (*Carica papaya*) and Watermelon (*Citrullus lanatus*) cultivation. |
| 9 | 6,500 | Curently planting | N.A. | Mape (*Inocarpus fagifer*) and other native trees forest |

Table 2. Satus of *M. citrifolia* agriculture in Moorea, French Polynesia as of November, 1998.

| | |
|---|---|
| Total land area devoted to *M. citrifolia* cultivation in Moorea | **84,000 $m^2$** |
| Mean size of a plantation (with 95% confidence interval) | **9,330 $m^2$ +/-4,670** |
| Total number of *M. citrifolia* trees in plantations | **7,818** |
| Mean density of trees in plantations (in trees per 10 m2) | **1.3** |

which is about 5% of the total land area of the island. The average plantation is about ten hectares, but they vary in size from one to 19.2 hectares. Fruit production of a *M. citrifolia* tree once it has reached maturity (about 8-10 months) is contiguous throughout the year (flowering, developing and ripening fruits are found on the same tree simultaneously). Average fruit weight is 150 grams, and one tree may have up to 30 to 40 fruits in different stages of development at one time (Garnier 1997).

Four of the nine plantations surveyed are of more than 12,000 $m^2$ in area. The largest of these (19, 206 $m^2$) is planted at the site of what was formerly the largest copra (*C. nucifera*) plantation in Moorea (Figure 2). A processing plant producing Nono juice and lotions as well as Tiare perfumes (*Gardenia taitensis*) and a visitors center is planned for this site, which is across from one of the main hotel-resorts on the island.

The coordinate system waypoints obtained with a hand-held GPS unit, owner information, location of plantation, and date planted are reported in the appendix (Appendix 1). This preliminary geographic information is intended for future use by the Department of Applied Agronomic Research in French Polynesia, as Global Information Systems records of *M. citrifolia* agricultural development in Moorea.

*Part II: Insect Survey Results*

*Sweep samples*

The sweep net samples in *M. citrifolia* and *H. tiliaceus* at each of the three sampling sites contained a range of macroinvertebrates including insects (formicids, fulgoroidids, psyllids, sirphids, tachinids, otidids, curculionids, melyrids, tettigonids, psocopterans), gastropods (terrestrial molluscs), and arthropods (arachnids). I have assigned each morphologically distinct type a number and listed it under the family (for insects), phyllum (for gastropods), or class (for arthropods) to which it is most likely to belong (since positive identification have not been verified by experts in the groups). Future work on these macroinvertebrate communities should include more rigorous identification of these species. A list of all of the distinguishable individual species found in the sweep samples, their assigned group and number, and a brief description of their appearance is included in Appendix 2. All insect specimens are on file at the Essig Museum of Entomology, University of California.

Tables 3 and 4 summarize the results of the sweep sampling done in *M. citrifolia* and *H. tiliaceus* respectively at the three sites. The taxon and number of each of the specimens collected, with their total numbers in the site samples in parentheses, are listed here.

Tables 5 and 6 provide a profile of the sweep sampling results, listing the total number of species found at each site in *M. citrifolia* sweep samples, and the species found to be most abundant (in highest relative density).

The overall number of species found in sweep samples in *H. tiliaceus* is higher than that in *M. citrifolia*. Ants and plant hoppers are the most common species on *M. citrifolia* while molluscs, psyllids and psocopoterans were found to be the most common in *H. tiliaceus*.

No statistically significant difference was found between the sites in either plant in total number of species found.

*Sticky trap samples*

Four traps from within a *M. citrifolia* patch at each site were analyzed using the sequential comparison index (theory of runs) which is a mathematical equivalent of Simpson's diversity index. Tables 7, 8 and 9 show the total numbers of individuals on each trap, the sequential comparison diversity index value, and the dominant insect type found on the trap. The four traps located in the periphery of the patch are marked with an asterix.

No significant difference was demonstrated between the periphery and the patch traps in either total number of individuals or diversity index at any of the sites. The dominant macroinvertebrates found on the Motu sticky traps were dipterans for all traps, while on the plantation dipterans were dominant within the patch and several groups were equally common (psyllids, fulgoroidids, dipterans) in the periphery. All but one of the traps at the mixed forest site were dominated by psyllids. Table 8 summarizes the mean diversity index values for the three sites.

*Leaf samples*

Tables 11 and 12 provide a summary of the leaf surface data for M. citrifolia and H. tiliaceus leaf samples. The means listed for each category (number of whitefly egg clumps, number of fungus infections, number of leaf mines, percent herbivory) are accompanied by a 95% confidence interval (n= 100). Herbivory (measured by percent of leaf eaten) was not significantly higher at any of the sites over the others. Also, no difference in percent herbivory between the leaf samples of *M. citrifolia* and *H. tiliaceus* was found. This supports my decision to sample in *H. tiliaceus* as well as in *M. citrifolia* to compare the insect communities at different sites. The mean number of leaf mines was highest in the mixed forest

Table 3. M.citrifolia sweep sample results

| Site | Macroinvertebrates found in 6 sets of 40 sweeps each (total number found at this site) | Total number of individuals in samples from this site |
|---|---|---|
| Motu Tiahura | Formicid#1(46), Mollusk#1 (9), Formicid#2 (5), Psyllid#1 (4), Dipteran#1 (1), Coleopteran#1 (1) | 69 |
| Opunohu Agricultural School Plantation | Formicid#3 (20), Dipteran#2 (2), Arachnid#2 (2), Dipteran #5 (1), Fulgoroidid#2 (1), Tettigonid#1(1), Arachnid#5 (1), Arachnid#6 (1), Neuropteran#1(1) | 30 |
| Mixed Forest at Gump Station | Fulgoroidid#1 (7), Psyllid#1 (6), Fulgoroidid#2 (3), Mollusk#1 (2), Formicid#3 (1), Dipteran#6 (1), Coleopteran#2 (1), | 21 |

Table4. H. tiliaceus sweep sample results.

| Site | Macroinvertebrates found in 6 sets of 40 sweeps each (total number found at this site) | Total number of individuals in samples from this site |
|---|---|---|
| Motu Tiahura | Mollusk#1 (20), Psyllid#1 (12), Fulgoroidid#1 (5), Fulgoroidid#2 (5), Arachnid#1 (2), Lepidopteran#1 (2), Lepidopteran#2 (2), Dipteran#1 (1), Dipteran#2 (1), Dipteran#3 (1), Lepidopteran#3 (1), Arachnid#2 (1), Arachnid#3 (1) | 56 |
| Opunohu Agricultural School Plantation | Psyllid#1 (52), Formicid#3 (30), Fulgoroidid#2 (27), Fulgoroidid#1 (8), Tettigonid#1 (7), Formicid#4 (2), Dipteran#3 (2), Dipteran#4 (2), Lepidopteran#1 (1), Neuropteran#1 (1), Culicid#1 (1) | 134 |
| Mixed Forest at Gump Station | Psocopteran#1 (28), Psyllid#1 (27), Fulgoroidid#2 (11), Formicid#3 (6), Fulgoroidid#1 (2), Hemipteran#1 (2), Orthopteran#2 (2), Dipteran#4 (1), Dipteran#5 (1), Ichneumonid#1 (1), Lepidopteran#1 (1), Coleopteran#2 (1) | 84 |

*M. citrifolia* leaf samples. The plantation leaf samples of both *M. citrifolia* and *H. tiliaceus* had significantly lower mean numbers of fungus infections per leaf than the leaf samples from the other two sites (Tables 11 and 12). The mean number of whitefly egg masses per *M. citrifolia* leaf was significantly higher in the monoculture site, as expected. Figure 4 shows the mean number of whitefly egg masses on *M. citrifolia* leaves at each of the three sites. The mean number of whitefly egg clumps per leaf was significantly higher for *M. citrifolia* than for *H. tiliaceus* at all sites, most markedly at the plantation (Figures 5.0 –5.2 show the mean number of whitefly egg masses per leaf in *M. citrifolia* and *H. tiliceus* at each of the three sites).

**Discussion**

*Part I: Agronomic survey*

Currently, *M. citrifolia* agriculture is in the early stages of development in Moorea. There are nine plantations, ranging from just over 100 to more than 3,000 trees (Table 1). The plantations are located throughout the island (Figure 2) and are replacing several types of land use, including abandoned copra (*Cocos nucifera*) plantations, pineapple (*Ananas cosmosus*), pomelo (*Citrus maxima*), and watermelon (*Citrullus lanatus*) cultivates, grazing land and native forest (Table 1).

Currently, agroecosystems that include *M. citrifolia* trees range from monocultures to complex, multi-canopy systems. Intercropping with papaya (*Carica papaya*) and with banana (*Musa sp.*) is taking place at two of the plantations, but further research is pending on the most beneficial combinations of *M. citrifolia* and other crops in French Polynesia. At this time, management strategies are generally non-intensive: no irrigation, some chemical fertilizers, no regular use of pesticides (Garnier 1997). Two of the nine plantations (numbers 1 and 8, Table 1) have reached reproductive maturity. *M. citrifolia* fruits are locally processed and consumed or sold to Morinda Inc, for export (Wadsworth, pers. comm. 1998). Presently, the industry is at a critical time of growth, and the direction of development of the export market will determine the future of *M. citrifloia* agriculture in Moorea.

*Part II: Macroinvertebrate survey*

*Site 1: Motu Tihuara*

The macroinvertebrate community at this site was shown to have the most different (among the sites sampled) composition. Six different species were found in sweep samples in the *M. citrifolia* patch at the motu, and thirteen species in the sweep samples in *H. tiliaceus* at the same site (Table 3,4). The dominant species in the *M. citrifolia* sweep samples at the motu was formicid #1, an ant about 4mm in length, with large, five pointed mandibles and reddish brown coloration (Appendix 2). This ant was observed in the field entering and exiting the *M. citrifolia* flowers, indicating that it may play a role in pollination. Formicid #1, as well as formicid #2, syrphid #1 and melyrid #1 were found exclusively in the weep samples from the motu site (Table 6.1). The sticky trap sampling analysis showed that the motu has the highest diversity of the three sites (Simpson's index .44 versus .35 for both of the other sites (Table 10). The leaf surface analysis of *M. citrifolia* leaves at Motu Tihura demonstrates the lowest mean number of whitefly egg masses per leaf out of the three sites (Table 11). The same is true for the *H. tiliaceus* leaf surface analysis (Table 12). Notably, the mean number of fungus infections per leaf was high on the motu in both plants, as it was in the mixed forest. Natural enemy interactions, environmental conditions, and colonization patterns may account for this observed trend at Motu Tiahura. This isolated site may well have a unique set of environmental conditions and colonization requirements that influence the macroinvertebrate presence. *M. citrifolia* is one of the dominant plant species on Motu Tiahura, and thus this environment should be closely monitored if information about the plant's ecology in nature is sought.

*Site 2: Richard Gump Biological Station Mixed Forest*

Samples of macroinvertebrates in the high island mixed forest plant community on Gump Station property did not demonstrate the diversity predicted for the study site with the highest apparent plant diversity. In sweep samples, a total of seven species were found in *M. citrifolia* and 12 species in *H. tiliaceus* (Tables 5 and 6). The dominant species in the *M. citrifolia* sweeps was Fulgoroidid #1 (Appendix 2). No group was found exclusively a this site (Table 6.1). The sticky trap results showed the same diversity index value as that found for the plantation site (.35, Table 10). The traps here were dominated by psyllids, and the total number of individuals per trap was generally lower than at either of the other two sites (Table 9). In view of the leaf surface data for this site, the mean number of whitefly egg masses per leaf was slightly higher than that at the motu site (5+/-7.12 in the mixed forest, 1.59+/-0.51 at the motu, Table 11), yet lower than the mean density at the plantation by a large margin (32.94+/-3.96 whitefly egg masses per leaf at the plantation, Table 11). The mean number of fungus infections per *M. citrifolia* leaf was significantly higher

Table 5. Sweep sample in *M. citrifolia*; profile.

| Site | Total number of groups found | Group found in highest number |
|---|---|---|
| Motu Tiahura | 6 | Formicid#1 |
| Opunuhu Plantation | 9 | Formicid#3 |
| Mixed Forest at Gump Station | 7 | Fulgoroidid#1 |

Table 6. Sweep samples in *H. tiliaceus*; profile.

| Site | Total number of groups found | Group found in highest abundance |
|---|---|---|
| Motu Tiahura | 13 | Mollusk#1 |
| Opunuhu Plantation | 11 | Psyllid#1 |
| Mixed Forest at Gump Station | 12 | Psocopteran#1 |

Table 6.1 Sweep sample groups found exclusively at each of the three sampling sites.

| Site | Groups of invertebrates found exclusively at the site |
|---|---|
| Motu Tiahura | Formicid#1, Formicid#2, Dipteran#1, Coleopteran#1 |
| Opunohu Plantation | None |
| Mixed forest (Gump Station) | None |

Table 7. Motu Tiahura sticky trap results.

| Trap number | Total number of individuals | Sequential comparison index | Dominant invertebrate taxon |
|---|---|---|---|
| 1 | 21 | 0.62 | Diptera |
| 2 | 41 | 0.40 | Diptera |
| 3 | 18 | 0.61 | Diptera |
| 4 | 54 | 0.28 | Diptera |
| 5* | 23 | 0.52 | Diptera |
| 6* | 23 | 0.35 | Diptera |
| 7* | 27 | 0.52 | Diptera |
| 8* | 36 | 0.25 | Diptera |

Table 8. Opunuhu plantation sticky trap results.

| Trap number | Total number of individuals | Sequential comparison index | Dominant invertebrate taxon |
|---|---|---|---|
| 1 | 130 | 0.31 | Diptera |
| 2 | 198 | 0.24 | Diptera |
| 3 | 40 | 0.45 | Diptera |
| 4 | 105 | 0.41 | Diptera |
| 5 | 32 | 0.39 | Psyllidae |
| 6* | 35 | 0.58 | Fulgoroididae |
| 7* | 97 | 0.17 | Fulgoroididae |
| 8* | 37 | 0.26 | Diptera |

Table 9. Gump Station sticky trap results.

| Trap number | Total number of individuals | Sequential comparison index | Dominant invertebrate taxon |
|---|---|---|---|
| 1 | 13 | 0.31 | Psyllidae |
| 2 | 29 | 0.24 | Psyllidae |
| 3 | 31 | 0.45 | Psyllidae |
| 4 | 34 | 0.41 | Psyllidae |
| 5 | 51 | 0.39 | Psyllidae |
| 6* | 33 | 0.58 | Psyllidae |
| 7* | 30 | 0.17 | Aphididae |
| 8* | 27 | 0.26 | Psyllidae |

Table 10. Mean diversity index comparison for sticky trap samples.

| Site | Mean diversity index value |
|---|---|
| Motu Tiahura | .44 |
| Opunohu Plantation | .35 |
| Mixed forest at Gump Station | .35 |

Table 11. *M. citrifolia* leaf surface data summary

| Site | Mean # of whitefly egg clumps per leaf | Mean number of fungus infections per leaf | Mean number of leaf mines per leaf | Mean percent herbivory of each leaf |
|---|---|---|---|---|
| Motu | 1.59 +/- 0.51 | 6.51 +/-1.19 | 0.2 +/-0.17 | 6.83 +/-1.53 |
| Plantation | 32.94+/- 3.96 | 2.02 +/-0.37 | 1.05 +/-0.29 | 8.17 +/-1.71 |
| Mixed forest | 5 +/- 7.12 | 7.94+/- 1.27 | 1.36 +/-0.43 | 6.12 +/-1.28 |

Table 12. *H. tiliaceus* leaf surface data summary.

| Site | Mean # of whitefly egg clumps per leaf | Mean number of fungus infections per leaf | Mean number of leaf mines per leaf | Mean percent herbivory of each leaf |
|---|---|---|---|---|
| Motu | 0.32 +/- 0.16 | 4.69 +/-.89 | 0.04 +/-.06 | 6.7 +/-1.52 |
| Plantation | 0.65 +/-0.25 | 3.17+/-0.75 | 0.01 +/-.02 | 9.5 +/-1.46 |
| Mixed Forest | 2.32+/- 0.99 | 4.94+/-0.79 | 0.13 +/-0.15 | 7.7 +/-1.45 |

**Figure 4. White Fly Egg Masses On *Morinda citrifolia* leaves**

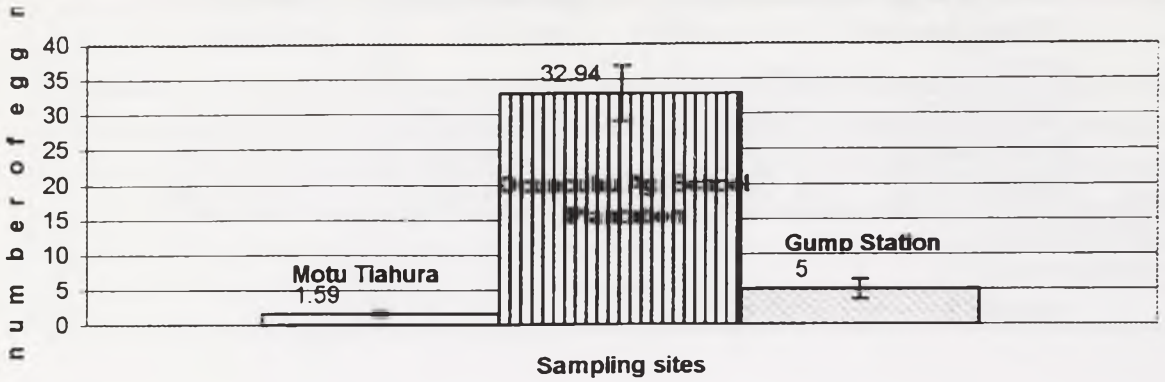



Figure 5.0.Motu Tiahura White fly Egg Mass Counts

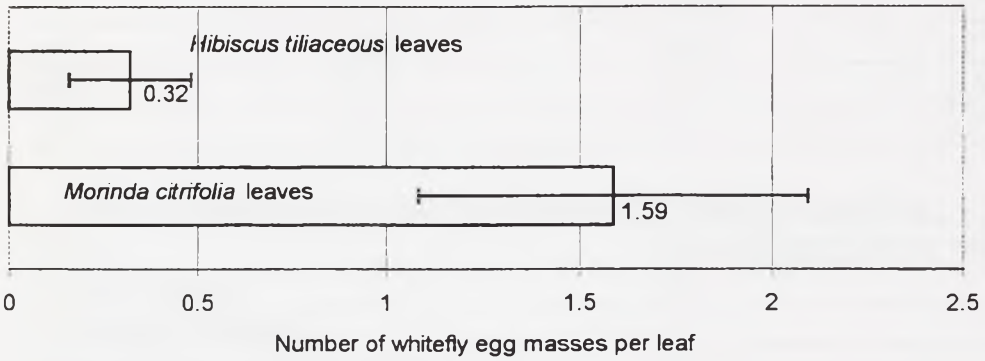



Figure 5.1. Opunouhu Plantation White Fly Egg Mass Counts

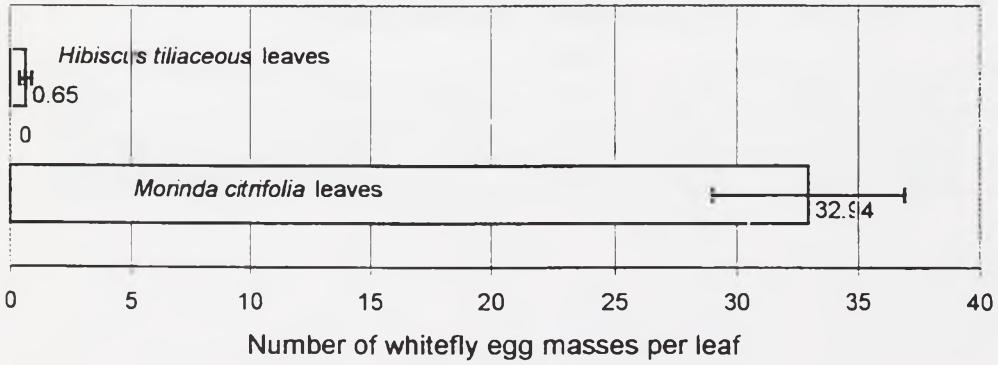
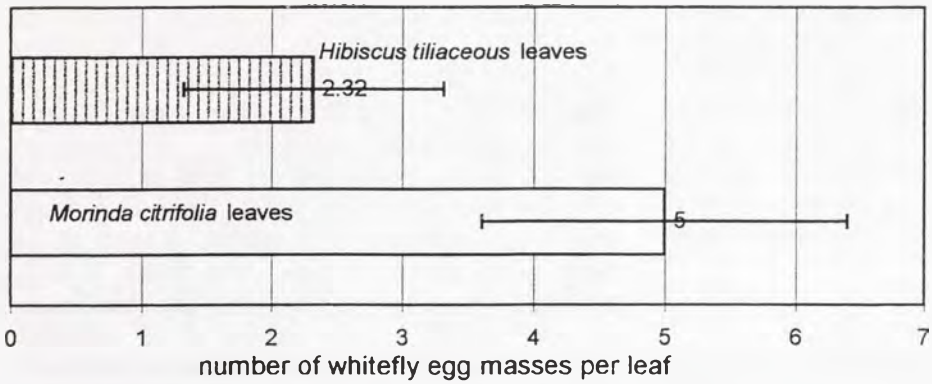


Figure 5.2. Mixed Forest (at Gump Station) White fly Egg Mass Counts



than that in the plantation samples, but the same as that in the motu samples (Table 11). No significant differences in leaf mine density or percent herbivory in either plant sampled occurred. Factors that should be considered in further study of the trends observed within the mixed forest *M. citrifolia* population are the effects of sunlight and moisture ad well as the other plant species in the community and how these affect the macroinvertebrate populations. The expectation that this mixed forest site would be the most diverse in macroinvertebrate fauna was not supported by the data I collected. In particular the fungal infections could be correlated to sunlight and moisture regimes (but I have no data to prove this by).

*Site 3: Opunohu Agricultural School Plantation*

The presence of other crop species, as well as natural stream and plant community nearby is likely to affect insects and other invertebrate life cycles and host plant preference at the monoculture plantation study site. The total number of species (in sweep samples) in *M. citrifloia* at the plantation site was only two less than that found in *H. tiliaceus* sweeps in the periphery of the plantation (Tables 7, 8), yet five of the nine species found in *M. citrifolia* were not found in the *H. tiliaceus* sweeps (Tables 3, 4). This indicates the highest relative choice by macroinvertebrates of *M. citrifolia* over *H. tiliaceus* of the three sites studied. The dominant species found in sweeps within the plantation was formicid#3 (Table 3, Appendix 2), a 3mmm reddish brown ant with a very bristly appearance. Field observations are inconclusive on this species; it may be pollinating, or it may be may be involved in a symbiotic relationship with one of the homopteran species found on the *M. citrifolia* that produce a honeydew. Further investigation is needed to determine the role of this ant in the plantation environment.

The riparian belt that raps around the plantation is likely to have an effect on the macroinvertebrate communities present there, due to the available moisture, nutrients and a variety of host plants. The highest number of species found in sweep samples of *M. citrifolia* at any site occurs at the plantation (Table 5). Sticky trap data shows a diversity index value equal to that of the mixed forest samples (Table 10). This is surprising considering the higher diversity of plant species in the mixed forest. The proximal riparian area and nearby agricultural crops could account for this high diversity in the monoculture. Phorid flies, psyllids, and fulgoroiids were dominant in sticky traps at the plantation while in the mixed forest psyllids dominated the traps (Tables 8 and 9). A correlation between the groups found and the ecosystem function should be worked out in future research. The role of population density must also be investigated through long-term studies.

The most significant difference of the plantation site in relationship to the other two study sites was that of the leaf surface data on whitefly egg mass density. Whitefly egg masses are in highest density in *M. citrifolia* at the plantation (32.94+/-3.96, Figures 5.0-5.2). Whitefly population explosions are a common agricultural occurrence. Whiteflies are abundant in the tropics and are pests of citrus and other fruit trees around the world. Field observations verify that a sooty fungus is present on some of the leaves on the plantation trees. This fungus is likely growing on the honeydew excreted by the whiteflies on the leaf surface. This fungus is of economic importance because it can greatly reduce the yields of a plant due to decreasing the photosynthetic ability of the leaves.

The last significant trend in the plantation data was that of the lowest mean number of fungal infections per leaf in the *M. citrifolia* at this site. This may be explained by the environmental conditions (relatively drier, full sun), or it may indicate that this fungus has not yet been introduced into this population. The potential for spread is present, because the trees are in an orchard system where transmission is greatly facilitated. Genetic selectivity and root-stalk resistance programs have not been developed for this crop, and thus the presence of fungal, viral and bacterial infections should be closely monitored.

**Conclusions**

Further studies including a long term, seasonal database of the macroinvertebrate populations (specifically those of economic importance and ecological significance) on *M. citrifolia* in French Polynesia are needed. The data from sweep, sticky trap and leaf samples in this preliminary study supports the hypothesis that the three growing environments (coralline islet, monoculture plantation and high island mixed forest) vary in the community composition of macroinvertebrates present. The unexpected result of a higher diversity in the plantation macroinvertebrate community may be explained by the choice of sites (this particular plantation being very close to a riparian community), thus several replicates of each type of site should be included in future studies of this nature. Overall, a higher diversity of macroinvertebrates was found in sweep samples of *H. tiliaceus* than in *M. citrifolia*. Explanations for this reduced host-specific community could be along phytochemical, population

dynamics, or environmental lines. According to this study, the most evident agronomic concern in terms of macroinvertebrates are currently whiteflies (family Aleyroididae), due to their implications as fungal infection catalysts and as vectors of other plant pathogens.

The young agricultural industry of *M. citrifolia* in Moorea is unfolding rapidly. The importance of research and applied agroecological experimentation at his early stage of the transition from natural dispersal to cultivation should be emphasized. The concerns of local farmers in Moorea in terms of how to best benefit from the developing market for this crop internationally, as well as how to best insure the long term agroecosystem health of this traditional Polynesian plant must be immediately addressed.

**Acknowledgements**

I wish to thank: Virginia Matzec, for the idea for this research project, continued support and inspiration; Tegan Churcher for encouragement and insight, a policy and socioeconomic perspective and photography; Amy Lesen for wisdom, enthusiasm for invertebrates, and Arnotts galore; Dr. Vince Resh, for support, data analysis suggestions and entomological viewpoints; Dr. Jere Lipps for holding together this fantastic academic experience; Dr. David Stoddart for botanical wisdom, support and research assistance as well as the use of a fantastic library; Dr. Cherie Norton for field assistance, photographs, GPS advising, and mapping-guru-work. Dr's. Debbie and John Woodward and Michael and Kellie Woodward for their hospitality and magnificent running of the research station; Dr. Steve Welter for great suggestions and direction with experimental design; Dr. Alexander Purcell for assistance with insect identification; Joel Hahe of the Applied Agronomic Research Center in Moorea for transportation to and assistance in surveying all of the plantations; Dr. Charles Garnier, Director of Research at the Agronomic Development Agency in Tahiti for providing information and research sugestions; Edouard Tuairau, Director of Polynesian Operations and John J. Wadsworth, V.P. International Markets/Manufacturing for Morinda Inc.for taking the time to speak with me about their business; Jean Claude Peri, Director of the Agricultural School in Opunohu for information and permission to work on the school's site, and of course the entire Moorea'98 class for research help, friendship, laughs and insight.

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Appendix 1: Plantation site geographic information.
Plantation site #1 (Aand B)
Owner: Lou and Olga Pahua
Location: North Shore, between Cooks and Opunouhu Bay (PK13)
Date planted: May, July and October of 1998 (in three sections)
GPS Waypoints:
A.

| |
|---|
| A1 (S17*29.233', W 148*50.195') |
| A2 (S17*29.252' W 149*50.195') |
| A3 (S17*29.223' W 149*50.198') |
| A4 (S17*29.241' W 149*50.222') |
| A5 (S17*29.241' W 149*50.218') |
| A6 (S17*29.211' W 149*50.195') |

B.

| |
|---|
| A7 (S17*29.186' W149*50.365') |
| A8 (S17*29.235' W149*50.370') |
| A9 (S17*29.214' W149*50.332') |
| A10 (S17*29.159' W149*50.307') |
| A11 (S17*29.151' W149*50.340') |
| A12 (S17*29.151' W149*50.407') |

Plantation site #2
Owner: Opunouhu Agricultural School, Moorea
Location: Opunouhu Valley Road (PK18, south on dirt road for 1.75 km)
Date planted: September, 1997
GPS Waypoints:

| |
|---|
| B1 (S17*31.535' W 149*50.183') |
| B2 (S17*31.571' W 149*50.131') |
| B3 (S17*31.524' W 149*50.165) |
| B 4 (S17*31.524' W 149*50.165') |

Plantation site #3
Owner: Omer
Location: PaoPao Valley, PK 9.5 .7km south on dirt road.
Date planted: May, 1997
GPS Waypoints:

| |
|---|
| C1 (S 17*31.137' W 149*49.513') |
| C2 (S 17*31.161' W 149*49.571') |
| C3 (S 17*31.166' W 149*49.566') |
| C4 (S 17*31.168' W 149*49.539') |

Plantation site #4
Owner: Maremare Kellum
Location: PK 17.5, just East of main road
Date planted: first attempt (1997) failed due to cattle damage, in the process of clearing the plot for replanting in November, 1998.
GPS Waypoints:
D1 (S17*30.890' W 149*50.870') (weeds and vegetation obscured the boundaries, only one point taken at this site)

Plantation Site #5
Owner: Quenos
Location: PK 26, North West coast, South site of main road in valley.
Date planted: June 1998, continued planting in sections in progress as of November 1998.
GPS Waypoints:

| |
|---|
| E1 (S17*29.739' W149*53.503') |

E2 (S 17°29.770' W149°53.636')
E3 (S17°29.875' W149°53.542')
E4 (S17°29.918' W149°53.642')

Plantation Site #6
Owner: Tinito (family name)
Location: PK34.5 Northeast on dirt road 2km in valley
Date planted: June 1998 and in progress
GPS Waypoints:

F1 (S17°32.423' W149°53.313')
F2 (S17°32.433' W149°53.293')

Plantation Site #7
Owner: Edmound Clemments
Location: PK4 Near Maharepa, just South of main road.
Date planted: Starting in June, 1997 and in progrees as of November, 1998.
GPS Waypoints:

K1 (S17°28.752' W149°46.998')
K2 (S17°28.743' W149°47.036')
K3 (S17°28.667' W149°47.010')
K4 (S17°28.665' W149°46.987')
15.2m 12.0m 10.4m 10.6m

Plantation Site #8
Owner: Puarai Tureva
Location: PK13.7, West on Maatea dirt road, up the Mahaerua river valley 1,800m, on high valley slope.
Date planted: January 1998
GPS Waypoints:

L1 (S17°34.371' W 149°49.136')
L2 (S17°34.355' W 149°49.149')
L3 S17°34.328' W 149°49.185')
12.8, 12.6, 14.7

Plantation Site #9
Owner: Puarai Tioni
Location: PK13.7, West on Maatea dirt road up the Mahaerua river valley, 2km at end of dirt road next to forest.
Date planted: in planting as of November, 1998.
GPS Waypoints:

M 1 (S17°34.053' W149°49.449')
M2 (S17°34.012' W149°49.449')
M3 (S17°34.034' W149°49.535')

Appendix 2. List of Insects and other Macroinvertebrates found in sweep samples and sticky traps.

I identified the following insects to their probable families based upon external morphological characteristics. Dr. Alexander A. Purcell of the department of Environmental Science, Policy and Management at UC Berkeley kindly aided with these identifications. Insect specimens are deposited in the Essig Museum of Entomology, UC Berkeley.
Phyllum Arthropoda
Class Insecta
Order Psocoptera

Family Lachesillidae: lachesillid#1: members of this large family are inhabitants of persistent dead leaves of a great variety of plants; some inhabit the foliage of conifers.

Order Homoptera

Family Psyllidae: psyllid#1: jumping plant lice; feeders on plant juices, specific food-plant relationships. One western species, the Potato Psyllid, Paratrioza cockerelli, transmits a virus that causes psyllid yellows in potatoes, tomatoes, peppers, and eggplants. This disease causes a reduction in yield resulting from dwarfing and discoloration of the plant.

Family Cicadellidae: cicadellid#1: leaf hoppers; feed principally on leaves of host plants; food-plant specific; many economically important pests species in this family.

Family Aleyroididae: alevroidid#1: whiteflies: most abundant in the tropics and subtropics; in the US the most important pest secies of this family attack citrus trees and greenhouse plants; they suck sap from plants. One of the most serious pests in this family is Aleurocanthus woglumni (Ashby), attacking citrus trees and established in the West Indies and Mexico. Sooty fungus oftern grows on the honeydew excreted by whiteflies and interferes with photosynthesis. This fungus is more prevalent in the South and in the tropics.

Superfamily fulgoroidea: Plant hoppers; feed on plant juices; produce honeydew, very few cause economic damage to plants.

Family Delphacidae: delphacidae#1: This is the same family as the Sugar Cane Leafhopper *Perkinsiella saccharicida* (Kirkaldy), once a serious economic pest in Hawaii.

Family Cixiidae: cixiid#1: Some species in this family are subterranean feeders on the roots of plants in nymphal stages.

Order Coleoptera

Family Melyridae: melyrid#1: Soft winged flower beetles

Superfamily curculionidae: curculionid#1: weevils.

Order Diptera

Family Syrphidae: syrphid#1:

syrphid#2: flower flies (pollinators).

Family Tachinidae: tachinid#1: valuable group because larval stage is parasitic of other insects (ie. pests such as lepidopterans, sawflies, beetles, hemipterans, orthopterans, etc.)

Family Otididae: otidid#1: some of these feed on plans and occasionally damage cultivated plants or crops.

Family Phoridae: phorid#1 (on sticky traps at Opunohu plantation): humpbacked flies; adults common in many habitats, most abundant among decaying vegetation; larae sometimes feed on decaying matter, sometimeson fungi, sometimes are external parasites of other insects. Some members of this family act as parasites or commensals in the nests of ants or termites.

Order Hymenoptera

Family Formicidae: formicid#1: (ants) 4mm in length, 11 segmented anennae, 5 pointed mandibl, abdomen with two different colors (brown and gold) in ringed pattern.

formicid#2: 3mm in lenth, black head and abdoment, 3 light brown thoracic segments

formicid#3: 3mm, reddish brown ant, much more bristly than #1 or #2.

Other Macroinvertebrates found:

Gastropoda: mollusc#1: 2-3mm, conical shell, light brown in color.

Arthropoda: arachnidae: arachnid#1: 2mm black body, 1mm white legs

arachnid#2: 5mm brownish red cephalothorax and abdomen, large black eyes.

arachnid#3: 3mm light brown (tetragnathid?)

arachnid#4: 5mm white and brown patterns on abdomen.

# Nearshore aquatic effects of anthropogenically modified shorelines in Cook's Bay, Moorea, French Polynesia

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**ABSTRACT.** The island of Moorea (17°30'S, 149°50'W) consists of mountainous terrain and two bays, Opunohu Bay and Paopao Bay. Paopao Bay, also known as Cook's Bay, exhibits shoreline modification throughout the majority of its perimeter. An ecological comparison study was conducted at the Richard Gump Biological Research Station on the Northwest side of Cook's Bay, which contains examples of both modified and unmodified shorelines. This study compares and contrasts the aquatic plants and animals residing along these modified and unmodified shorelines. The stretch of unmodified shoreline sampled, approximately 150m in length, is the only pristine shoreline remaining in Cook's Bay. Using a 30m transect tape and a 0.5m x 0.5m quadrat, diversity and richness of nearshore aquatic plants and animals were measured via random sampling. Species diversity was found to be consistent between the modified and unmodified shorelines, with a higher number along the modified shoreline. However, higher species richness was observed along the unmodified shoreline. This richness may be the natural ecosystem of Cook's Bay shoreline, but further studies are needed to make a more precise analysis.

**Introduction**

Moorea (17°30'S, 149°50'W; Illustration 1), a triangular shaped island, has a circumference of 61km and an area of 134km². Moorea consists of two large bays on its northern coast, Opunohu Bay and Paopao Bay. Paopao Bay, also known as Cook's Bay, is Moorea's northeastern-most bay. Shoreline modification is primarily exhibited throughout the perimeter of Cook's Bay. On the northwest side of Cook's Bay, at the Richard Gump Biological Research Station (Illustration 2), an ecological comparison study was conducted. This study was designed to test the effects of anthropogenically modified shorelines on nearshore aquatic biota. To do this, an experiment via random sampling was performed comparing aquatic populations along both modified and unmodified shorelines. For each study site, species richness and species diversity were tested.

The shoreline of UC Berkeley's Gump Research Station is composed of both modified and unmodified shorelines. The stretch of unmodified shoreline identified, approximately 150m in length, is the only original shoreline remaining along the coast of Cook's Bay. Human modifications to island coastlines have produced significant changes to island environments (Nunn 1994), including nearshore aquatic biota. Such changes range from the crude embankments and seawalls to wholesale reconstruction (Nunn 1994) for waterfront protection, containment, and enhancement. These man-made structures can have many negative impacts, markedly altering patterns of sediment and nutrient transport (Norse 1993). In Moorea, huge boulders are stacked on one another to line the edge of the shore as a source of protection. An example of such modification is the Gump Research Station.

In examining the nearshore biota (mostly benthic), a comparison was made between modified and unmodified shorelines to ascertain the effects of human modification. Both aquatic plant and animal species were sampled along modified and unmodified shorelines to observe diversity and richness. Using the Gump Research Station's modified shoreline as the 'standard,' a contrast was made to three nearby sites of unmodified

**Illustration 1.** Moorea, French Polynesia

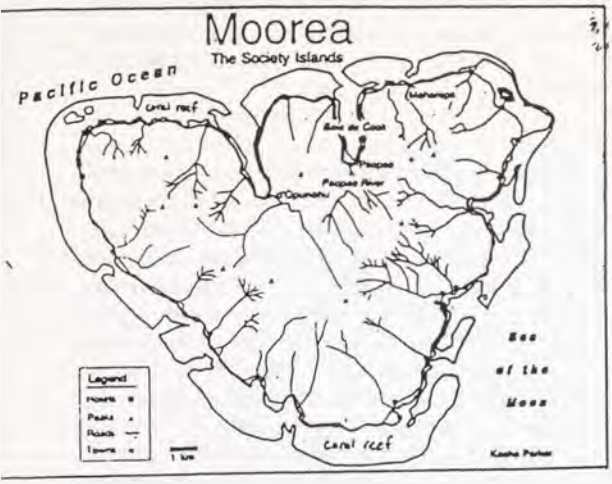
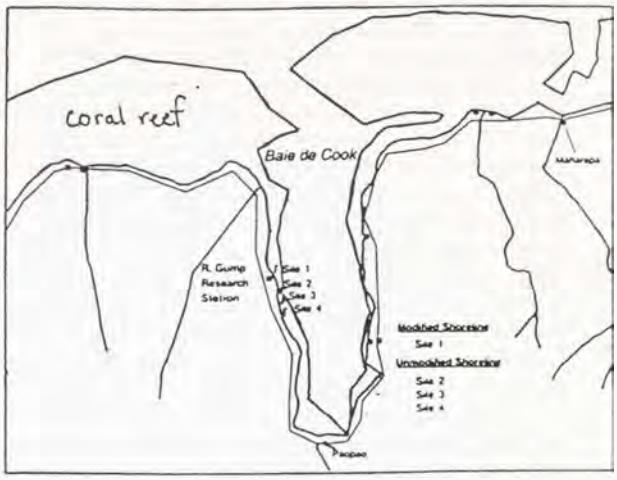
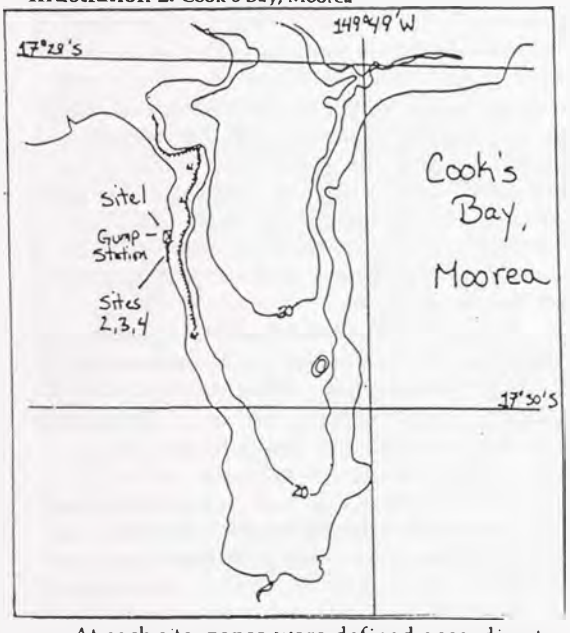



**Illustration 3.** Site Locations




shorelines, in which the most abundant growth of benthic marine life occurs on hard substrates (Lobban 1997). There were a total of four sites along the contours of the Gump Research Station, three of which were from the unmodified shoreline (Illustration 3).

**Illustration 2.** Cook's Bay, Moorea




At each site, zones were defined according to substrate composition. Along the modified shoreline, Site 1, where construction necessitated a landfill extending some fifty meters, there were five zones: beachrock shelf, sand, beachrock, beachrock and sand, and coral rubble and sand. Site 2 consisted entirely of beachrock; Site 3, beachrock and sand; and Site 4 was comprised of coral rubble and sand. For the unmodified shoreline (Sites 2-4), there was only one substrate zone for each site. Thus, the latter three of Site 1's five zones were used for comparison. An analysis on species diversity was done using Jaccard's Coefficient, and a series of student T-tests. Species richness was analyzed through observational data collection.

**Materials and Methods**

A 30m transect tape and a 0.5m x 0.5m quadrat were the primary materials used to sample the population at random. In addition, a refractometer and thermometer were also used. Transects were aligned perpendicular to the shoreline until the reef shelf dropped into the depths of the bay. At each of the four sites, five transects were positioned 10m apart for a width of 40m. A total of twenty transects were placed. In each defined zone, five quadrats were sampled using random number tables. Zones shorter than 5m had only two quadrats sampled. At each of these sites along the central transect, the temperature, salinity, and average depth were measured.

The modified shoreline (Illustration 4) was used as the 'standard' for comparison

to unmodified shorelines. Site 1 was the only tested example of a modified shoreline. Although Cook's Bay consists mainly of modified shorelines, the Gump Research Station has only a small stretch of modification, excluding the landfill area. The five substrate zones in Site 1 (Illustration 5) showed a unique characteristic to the contours of Cook's Bay. The zones were linear and parallel to the shore, unlike the remainder of the bay's shorelines where there only existed one or two zones at a time. The five transects at Site 1 (Transects 1-5) had the longest distance between the shoreline and the shelf drop. These transect lengths varied from 73m and 93m, where at least four of the five zones were represented (Table 1).

Along the unmodified shoreline (Illustration 6), Sites 2-4, only one zone was represented for each site. Site 2 (Transects 6-10) is the closest to the Gump Research Station's center of development. It is located directly south of Gump's boating channel, and showed an average distance of 24m between the shoreline and the shelf. Site 3 was located farther south from Site 2, in which an effluent was omitted. Here, the average transect length was only 18m, the shortest of all site locations. Site 3 contained a beachrock and sand substrate composition, and averaged a distance of 26m. In the aspect of length, the sites along the unmodified shoreline greatly differed from the modified shoreline.

The Quantitative Jaccard's coefficient, Q-mode, was used to count species diversity in each quadrat for analysis. Species richness was averaged in each zone. This comparison consisted of the following formula: $C = (2W)\div(A+B)$; in which W is the total number of species in the fauna, A is the sum of quantitative measures of species in sample one (Site 1), and B is the sum of quantitative measures of species in sample two (Site 2, 3, or 4). Using this formula, Site 2, Site3, and Site 4, were separately compared against the corresponding substrate zone in Site 1.

The student t distribution, or student t-test, was also used as a method of analysis for species diversity. The formula for this analysis is as follows: $T = (X-\mu)\div S/(\text{sq. rt.})n$. In this formula, X is the sample mean, $\mu$ is the population mean, S is the sample standard deviation, and n is the number of species within the sample. Species richness was observed and analyzed through data collection, but was not statistically calculated.

**Results**

Similar and comparable species were found along both modified and unmodified shorelines. However, certain species were more abundant, while other species showed higher diversity along the modified shoreline. These results were also found existing along the unmodified shoreline. Some species were absent from one shoreline and present along the other. This is possibly due to the different natural contours of the areas themselves. Only Site 1 showed multiple substrate zones, which extended almost 100m (Table 1). Sediment and an expanse of habitat were common features to this area. In contrast, all along the unmodified shoreline, there was only one substrate zone present in a defined area. Here, the areas were compact and short. Beachrock, sand, and rubble were common substrate features along this shoreline.

Some unique characteristics of Site 1 were: large coral heads (mostly *Porites lobata* and *Porites lutea*), *Culcita novaeguineae* (cushion stars), large *Bohadschia argus* (sea cucumbers), abundant *Padina gymnospora* (funnelweed), and rare *Hexabranchus sanguineus* (Spanish dancers), and their egg masses (Tables 2 and 3). The large size of such species is due to the vast expanse of the surrounding site. Along the modified shoreline there was an abundance of fine, man-made sediment. Beachrock does not exist near this area, and is not present until some 20m away from this modification.

Despite the transect length limitations (Table 4), the sites along the unmodified shorelines showed a large abundance of *Caulerpa serrulata, Echinometra mathaei, Halimeda micronesica, Lithothamnion prolifer,* crabs, hermit crabs, snails, tunicates, as well as elusive organisms; including eels (not counted). Algae was the most abundant, commonly attached to rocks and loose beachrock. In these sites of unmodified shorelines, all coral heads

(mostly *Porites solida*) were very small as opposed to Site 1. However, *Fungia costulata* and *Herpolitha limax* (two types of coral fungi), were absent from this region.

Sites 2, 3, and 4 each consisted of different substrate zones, as well as a variation in species diversity and abundance. Site 2, beachrock, had numerous *Echinometra mathaei*, and *Ophiocoma erinaceus* found throughout the zone (Table 5). Site 3's beachrock and sand zone showed an abundance of *Padina gymnospora*, and unknown red encrusting algae M (Table 6). Despite the richness in Sites 2 and 3, Site 4 (coral rubble and sand) did not have high species richness aside from *Halimeda micronesica* and *Lithothamnion prolifer* (Table 7). This site is near local development and showed the closest correlation to Site 1 and the modified shoreline. Thus Jaccard's Quantitative coefficient showed that the modification of shorelines have affected nearshore communities that are close to development.

**Table 8.** Jaccard's Quantitative coefficient Results

| | Site 1 |
|---|---|
| Site 2 | C=3.6875 |
| Site 3 | C=4.1027 |
| Site 4 | C=7.4470 |

This also shows that the sites closer to the Gump Research Station have both species diversity and abundance for many plant and animal species.

The student t-distribution test was calculated to compare species diversity and showed the following in Table 9.

**Table 9.** Student t-distribution Results

| Student t- distribution | | T = |
|---|---|---|
| beachrock | Site 1 | 3.8648 |
| | Site 2 | 2.7223 |
| bchrk/sand | Site 1 | 4.859 |
| | Site 3 | 2.5929 |
| rubble/sand | Site 1 | 5.1742 |
| | Site 4 | 3.6853 |

These results indicate higher species diversity along the modified shoreline at the Gump Research Station.

Table 10 gives results to temperature and salinity measurements. Depth and temperature were measured on Sunday, November 15, 1998 at 3-4pm, and the salinity was measured on Tuesday November 17, 1998 at 10am.

**Table 10.** Temperature and Salinity Results

| Temperature and Salinity Test | | | | | |
|---|---|---|---|---|---|
| | Trans. No. | Temp. 1min | Depth | Refraction | Salinity ppt |
| **Site 1** | mid zones | deg. Celcius | | | |
| zone 1 | 3 | 28.5 | 1.3m | 1.3396 | 36 |
| zone 2 | | 28.5 | 1m | 1.3396 | 36 |
| zone 3 | | 31 | 0.7m | 1.3396 | 36 |
| zone 4 | | 31 | 0.4m | 1.3396 | 36 |
| **Site 2** | 8 | 28.5 | 1.5m | 1.3396 | 36 |
| **Site 3** | 13 | 29 | 0.7m | 1.3396 | 36 |
| **Site 4** | 18 | 30 | 0.5m | 1.3399 | 39 |

**Discussion**

In some areas, species found along the shorelines of the Richard Gump Research Station were abundant. Data obtained in both collection and statistical analysis reveals some impact on the nearshore biota along modified shorelines. For example, certain species are absent from such modified shorelines. There is also an impact along unmodified shorelines near development and other modified shorelines (Site 4), such that many species are absent from this region. In addition, the data indicates a decrease in species richness along this area.

In general, there have been four types of observations: 1. some species share similar habitats along both shorelines, 2. some species are absent along one shoreline and present along the other, 3. some species are scarce along one shoreline and very abundant along the other, and 4. species diversity and abundance play opposing roles. Statistically, there is an impact

on nearshore aquatic species richness and diversity. The evidence presented above shows that there is need for concern, and that human development on land is affecting those plants and animals in the sea.

Species richness is displayed along the unmodified shoreline at the Gump Station, as presented in Tables 3-7. This shoreline contains a greater amount of species richness than diversity. In contrast, there is evidence of higher species diversity along the modified shoreline. This difference is possibly due to distributional and spatial patterns. When species are highly diverse, richness decreases. In the presence of species richness, diversity decreases. There seems to be an opposite effect on species diversity and abundance.

Along the modified shoreline, sedimentation makes it difficult for species to survive and thrive, such as *Echinometra mathaei* (purple sea urchins) and other rock inhabitants. Sediments carried into coastal waters diminish light penetration, hence productivity, and discourage species that visually locate prey or filter-feed, thus altering the community composition, structure, and function (Norse 1993). Closer to the landfilled area, there was a decrease in both species richness and diversity. It seems that the extension of the land along the Gump Station has significantly affected the presence of certain aquatic biota. Such that increased supplies of sediment have resulted in island shoreline progradation (Nunn 1994). The dormitory (1985), and two bungalows (1998) are along Site 1. Here, there showed a correlation between impact and age. There was more species abundance along the shores of the newly built structures. Also, greater abundance and diversity appeared farther from shore. Such that with newly developed structures and distance, the greater species diversity and abundance are. Nonetheless, in observing the entire contours of Cook's Bay, the Gump Station's property is well maintained in comparison. The modified shoreline at the Gump Station shows little effect on nearshore biota. On the other hand, shoreline restoration is needed for the remainder of Cook's Bay.

Further research is needed on comparisons between modified and unmodified shorelines. Research on this subject-matter appears to be fairly new. Studies are needed to obtain more accurate results. It is hard to predict whether the nearshore biota will eventually become absent, or if an alternate community will inhabit this nearshore area. Studies are needed to be conducted over a longer period of time in order to view such long term changes. Analysis on each species and their habitat preferences may provide clues as to whether the modification of shorelines have large effects on them. Only then can it be told whether the modification of shorelines has a greater impact on key species.

Temperature and salinity measurements indicated normal characteristics as given by Galzin and Pointier (1985).

**Conclusion**

The experimental objective was to discover if anthropogenically modified shorelines affect the nearshore biota of a tropical bay environment. This was done using two shorelines, modified and unmodified, along Cook's Bay for comparison. The population was randomly sampled along a 40m length for each site selected. In the experiment, transects, placed perpendicular to the shore, and quadrats, were used for this comparison. Quadrat selection was random, plotted with a random numbers table.

Jaccard's Quantitative coefficient and the student t-distribution tests showed two subtle differences. (1) Species diversity and richness are slightly impacted closer to the shore and near developments. (2) Species diversity is higher along the modified shoreline, while the richness of species is the dominating factor along the unmodified shoreline.

Although the impact of shoreline modification along Richard Gump Biological Research Station on nearshore biota exists, the data is not significant. Depending on the species, some were either commonly found throughout both shorelines; found along one shoreline and absent from the other; or abundant at one shoreline, while rare at the other. Species diversity and richness were also opposing factors. For example, high diversity at the modified site showed low species richness. On the other hand, the unmodified shoreline exhibited high species richness and low species diversity.

In conclusion, the data gathered indicates that there is a significant, but minor effect. Further ecological comparison studies are needed in such tropical environments to truly observe major human disturbance implications on nearshore aquatic biota.

**Acknowledgments**

I would like to thank all instructors and teaching assistants who participated with this class; especially Vince Resh for such enthusiasm and motivation. All involved professors have aided in giving me an experience to build on, and never forget. I would also like to recognize my fellow classmates for the joy of such wonderful times. Hafeezah Dalji, thank you for all of your comments and assistance.

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Illustration 4. Map of Site 1 – Modified Shoreline

Substrate Zones - Site 1, Modified Shoreline

Transect 1

Transect 2

Transect 3

Transect 4

Transect 5

SAND

SAND

CORAL RUBBLE AND SAND

BEACHROCK

BEACHROCK AND SAND

BEACHROCK AND SAND

SHELF

73m

75m

CORAL RUBBLE AND SAND

SHELF

86m

80m

Illustration 5. Map of Substrate Zones - Site 1

Illustration 6. Map of Sites 2, 3, and 4 - Unmodified Shoreline

## Modified Shoreline: Zonation
## Richard Gump Biological Reasearch Station

Transect 1 (0m)

| Zone | Substrate | Length | Sample No. |
|---|---|---|---|
| 1 | beachrock shelf | 0m-5.3m | 2 |
| 2 | beachrock and sand | 5.3m-32.3m | 5 |
| 3 | sand and coral rubble | 32.3m-45m | 5 |
| 4 | sand | 45m-73m | 5 |

Total length: 73m

Transect 2 (10m)

| Zone | Substrate | Length | Sample No. |
|---|---|---|---|
| 1 | beachrock shelf | --- | --- |
| 2 | beachrock and sand | 0m-27.5m | 5 |
| 3 | sand and rubble | 27.5m-58m | 5 |
| 4 | beachrock | 58m-69.4m | 5 |
| 5 | sand | 69.4m-75m | 2 |

Total length: 75m

Transect 3 (20m)

| Zone | Substrate | Length | Sample No. |
|---|---|---|---|
| 1 | beachrock shelf | 0m-4m | 2 |
| 2 | sand and beachrock | 4m-70.5m | 5 |
| 3 | beachrock | 70.5m-89.5m | 5 |
| 4 | sand | 89.5m-92.9m | 2 |

Total length: 92.9m

Transect 4 (30m)

| Zone | Substrate | Length | Sample No. |
|---|---|---|---|
| 1 | beachrock shelf | 0m-1.3m | 2 |
| 2 | sand and coral rubble | 1.3m-12m | 5 |
| 3 | beachrock and sand | 12m-63.5m | 5 |
| 4 | beachrock | 63.5m-81.5m | 5 |
| 5 | sand | 81.5m-86.4m | 2 |

Total length: 86.4m

Transect 5 (40m)

| Zone | Substrate | Length | Sample No. |
|---|---|---|---|
| 1 | beachrock shelf | 0m-3.5m | 2 |
| 2 | sand and coral rubble | 3.5m-11.5m | 5 |
| 3 | sand and beachrock | 11.5m-57.2m | 5 |
| 4 | beachrock | 57.2m-76m | 5 |
| 5 | sand | 76m-80m | 2 |

Total length: 80m

# Table 2. Species Per Quadrat - Site 1



Transect 1 (0m)

I. Zone 1 (shelf) 0m-5.3m
  A. quadrat 1 (2.2m-2.7m)
    100% beachrock
    3 anemone fish, lt. blue spots
    1 *Corythoichthys flavofasciatus*
    1 *Fungia costulata*
    1 *Herpolitha limax*
    1 *Porites solida*
    1 *Stichodactyla gigantea*
    1 *Synanceja verrucosa*
  B. quadrat 2 (4.8m-5.3m)
    100% beachrock
    1 sm. *Diadema savignyi*
    50% *Porites lobata/lutea*

II. Zone 2 (beachrock/sand) 5.3m-32.3m
  A. quadrat 1 (8.9m-9.4m)
    1 sm. *Echinometra mathaei*
    1 *Porites lobata/lutea*
  B. quadrat 2 (10.5m-11m)
    10% *Dictyota sp.*
    4 *Porites lobata/lutea*
    (2 yellow, 1 cream, 1 purple)
  C. quadrat 3 (11.2m-11.7m)
    95% beachrock
    5% sand
    90% *Dictyota sp.*
    3 *Porites lobata/lutea*
    (2 yellow, 1 purple)
  D. quadrat 4 (26.8m-27.3m)
    2% *Halimeda micronesica*
    40% *Padina gymnospora*
    1 sm. black *Parapercis millepunctata*
    25% *Sargassum sp.*
    2% *Turbinaria sp.*
  E. quadrat 5 (28.9m-29.4m)
    2% *Halimeda micronesica*
    20% *Padina gymnospora*
    1 sm. black *Parapercis millepunctata*

III. Zone 3 (sand/coral rubble) 32.3m-45m
  A. quadrat 1 (32.5m-33m)
    90% rubble
    10% sand
    15% *Caulerpa serrulata*
    5% *Dictyota sp.*
    4% *Halimeda micronesica*
    10% *Padina gymnospora*
  B. quadrat 2 (35.1m-35.6m)
    10% E
    4% *Halimeda micronesica*
    30% Padina gymnospora
  C. quadrat 3 (38.6m-39.1m)
    2% *Caulerpa serrulata*
    1% *Dictyota sp.*
    2% *Halimeda micronesica*
    2 wht. *Parapercis millepunctata*
    1 unknown wht. worm
  D. quadrat 4 (40.9m-41.4m)
    20 % rubble
    80% sand
    1% *Dictyota sp.*
    2% *Halimeda micronesica*
    5% *Padina gymnospora*
  E. quadrat 5 (42.1m-42.6m)
    7% rubble
    93% sand
    5% *Caulerpa serrulata*
    1 crab (approx. 1cm)
    2% *Dictyota sp.*
    3% *Padina gymnospora*
    1 wht. Parapercis millepunctata
    1 snail (approx. .25cm)
    1 *Valonia ventricosa*

IV. Zone 4 (sand) 45m-73m
  A. quadrat 1 (48.4m-48.6m)
    15% *Padina gymnospora*
    45% *Porites lobata/lutea* (yellow)
  B. quadrat 2 (55.3m-55.8m)
    5% *Halimeda micronesica*
    2% *Padina gymnospora*
    1% *Sargassum sp.*
    1% *Turbinaria sp.*
  C. quadrat 3 (62.9m-63.4m)
    2% *Dictyota sp.*
    5% *Padina gymnospora*
  D. quadrat 4 (70.3m-70.8m)
    100% sand
    10% D
  E. quadrat 5 (71.7m-72.2m)
    100% sand

**Transect 2 (10m)**

I. Zone 1 (shelf) absent

II. Zone 2 (beachrock/sand) 0m-27.5m

A. quadrat 1 (5m-5.5m)
- 45% beachrock
- 1 *Echinometra mathaei*
- 1% *Padina gymnospora*

B. quadrat 2 (13m-13.5m)
- 45% beachrock
- 5% *Caulerpa serrulata*
- 5% *Dictyota sp.*
- 5% E
- 1% *Halimeda micronesica*
- 1 *Nennalpheus sp.*
- 5% Padina gymnospora
- 1 sm. *Porites lobata/lutea*

C. quadrat 3 (19m-19.5m)
- 20% beachrock
- 15% E
- 40% *Padina gymnospora*

D. quadrat 4 (25m-25.5m)
- 25% beachrock
- 2% *Dictyota sp.*
- 10% E
- 1 sm. hermit crab
- 20% *Padina gymnospora*
- 5% *Sargassum sp.*

E. quadrat 5 (27m-27.5m)
- 75% beachrock
- 20% *Caulerpa serrulata*
- 1 sm. crab
- 5% *Dictyota sp.*
- 40% E
- 2% *Halimeda micronesica*
- 10% *Padina gymnospora*
- 1 *Valonia ventricosa*

III. Zone 3 (sand/coral rubble) 27.5m-58m

A. quadrat 1 (33m-33.5m)
- 5% *Dictyota sp.*
- 1 *Echinometra mathaei*
- 1% F
- 25% *Padina gymnospora*
- 7% *Sargassum sp.*

B. quadrat 2 (35m-25.5m)
- 10% beachrock
- 90% sand
- 1 sm. crab
- 10% *Dictyota sp.*
- 15% E
- 4% *Halimeda micronesica*
- 1% *Padina gymnospora*

C. quadrat 3 (43m-45.5m)
- 25% beachrock
- 5% *Dictyota sp.*
- 10% E
- 2% *Halimeda micronesica*
- 10% *Padina gymnospora*

D. quadrat 4 (45m-45.5m)
- 30% beachrock
- 2% *Caulerpa serrulata*
- 10% *Halimeda micronesica*
- 1 *Nennalpheus sp.*
- 25% *Padina gymnospora*
- 25% *Porites lobata/lutea* (purple)
- 2 blk. *Parapercis millepunctata*

E. quadrat 5 (49m-49.5m)
- 1 sm. crab
- 30% *Dictyota sp.*
- 30% E
- 1 *Gastrolepidia clavigera*
- 20% *Halimeda micronesica*
- 25% *Padina gymnospora*
- 1 *Porites lobata/lutea* (purple)
- 1 unknown wht. Worm

IV. Zone 4 (beachrock) 58m-69.4m)

A. quadrat 1 (58m-58.5m)
- {trash abundant}
- 90% leaf cover
- 50% beachrock
- 2% *Dictyota sp.*
- 15% G
- 1% *Halimeda micronesica*
- 1 *Neomeris annulata*
- 45% *Padina gymnospora*

B. quadrat 2 (59m-59.5m)
- 100% leaf cover
- 3% Caulerpa serrulata
- 2% *Dictyota sp.*
- 2% *Halimeda micronesica*
- 10% G
- 30% *Padina gymnospora*
- 5% *Sargassum sp.*

C. quadrat 3 (61m-61.5m)
- 100% leaf cover
- 40% beachrock
- 10% G
- 10% *Halimeda micronesica*
- 2% I
- 1 *Neomeris annulata*
- 40% *Padina gymnospora*
- 1% *Turbinaria sp.*

D. quadrat 4 (62m-62.5m)
- 50% beachrock
- 2% *Dictyota sp.*
- 5% *Halimeda micronesica*
- 7 *Neomeris annulata*
- 30% *Padina gymnospora*
- 2% *Turbinaria sp.*

E. quadrat 5 (66m-66.5m)
- 100% leaf cover
- 100% beachrock
- 0.25% *Halimeda micronesica*
- 2% I
- approx. 50 *Neomeris annulata*
- 5% *Padina gymnospora*

V. Zone 5 (sand) 69.4m-75m

A. quadrat 1 (71m-71.5m)
- 100% sand
- 100% rock/pebbles
- (size approx. 1cm)

B. quadrat 2 (72m-72.5m)
- 100% sand
- 100% rocks/pebbles
- (size approx. 2cm)

**Transect 3 (20m)**

I. Zone 1 (shelf) 0m-4m

A. quadrat 1 (0m-0.5m)
- 1 blk. Damsel fish
- 20% *Dictyota sp.*
- 1 *Fungia costulata*
- 40% *Halimeda micronesica*
- 1 Herpolitha limax
- 95% J
- 1 *Montipora undata*
- 2 *Porites lobata/lutea*
  (1 yellow, 1 purple)
- 2 *Porites solida*
  (1 brown)
- 1 *Valonia ventricosa*

B. quadrat 2 (3m-3.5m)
- 1% D
- 20% *Dictyota sp.*
- 20% *Halimeda micronesica*
- 3 *Porites solida*
- 1% *Turbinaria sp.*
- 4 *Valonia ventricosa*

II. Zone 2 (sand/beachrock) 4m-70.5m

A. quadrat 1 (4m-4.5m)
- 90% sand
- 1 *Culcita novaeguineae*
- 2% D
- 10% *Dictyota sp.*
- 2% *Halimeda micronesica*

B. quadrat 2 (17m-17.5m)
- {*Porites/Mont.* competition}
- 35% *Dictyota sp.*
- 5% *Halimeda micronesica*
- 45% K
- 1 *Montipora undata*
- 1 *Neomeris annulata*
- 25% *Padina gymnospora*
- 1 *Porites lobata/lutea*
- 1% *Turbinaria sp.*

C. quadrat 3 (29m-29.5m)
- 10% *Caulerpa serrulata*
- 2% D
- 20% E
- 30% *Turbinaria sp.*
- 2 *Valonia ventricosa*

D. quadrat 4 (48m-48.5m)
- 20% beachrock
- 15% *Caulerpa serrulata*
- 10% *Dictyota sp.*
- 20% E
- 1 *Echinometra mathaei* (1cm)
- 2% *Halimeda micronesica*
- 1 sm. hermit crab
- 20% *Lithothamnion prolifer*

1 *Neomeris annulata*
30% *Turbinaria sp.*

E. quadrat 5 (58m-58.5m)
20% *Caulerpa serrulata*
40% *Dictyota sp.*
5% *Halimeda micronesica*
10% *Turbinaria sp.*

III. Zone 3 (beachrock) 70.5m-89.5m
NOTE: burrowing shrimp are abundant!

A. quadrat 1 (76m-76.5m)
100% beachrock
10% *Caulerpa serrulata*
5% *Dictyota sp.*
10% *Halimeda micronesica*
1% *Lithothamnion prolifer*
2 *Neomeris annulata*
20% *Padina gymnospora*
3 *Parapercis millepunctata*
(1 black, 1 gray, 1 white)

B. quadrat 2 (80m-80.5m)
100% beachrock
1 (lg.) *Echinometra mathaei*
3% *Halimeda micronesica*
1% *Lithothamnion prolifer*
2 *Porites solida* (polyps .5cm)
1 *Valonia ventricosa*

C. quadrat 3 (84m-84.5m)
90% beachrock
10% sand
10% broken bivalve shells
25% *Dictyota sp.*

D. quadrat 4 (86m-86.5m)
70% beachrock
30% sand
5% broken bivalve shells
2 *Neomeris annulata*
10% *Turbinaria sp.*

E. quadrat 5 (89m-89.5m)
100% beachrock
90% sand (over beachrock)
30% broken bivalve shells
1 *Neomeris annulata*
5% *Turbinaria sp.*

IV. Zone 4 (sand) 89.5m-92.9m

A. quadrat 1 (90m-90.5m)
100% lg. rocks/rubble
(size approx. 2cm-5cm)
5% *Padina gymnospora*

B. quadrat 2 (92m-92.5m)
100% lg. rocks/rubble
(size approx. 3cm-10cm)

**Transect 4 (30m)**

I. Zone 1 (shelf) 0m-1.3m

A. quadrat 1 (0.2m-0.7m)
1 *Acropora sp.*
1% *Dictyota*
2% *Halimeda micronesica*
3 *Porites lobata/lutea*
(1 yellow, 2 purple)

B. quadrat 2 (0.7m-1.3m)
2% D
5% *Dictyota sp.*
5% *Halimeda micronesica*
1% *Lithothamnion prolifer*
1% M (red)
1 *Montipora efflorescens*
1 *Porites lobata/lutea*

II. Zone 2 (sand/coral rubble) 1.3m-12m

A. quadrat 1 (5m-5.5m)
100% sand
5% rock
1 *Halichoeres trimaculatus*
1% *Lithothamnion prolifer*
1 *Parupeneus barberinus*

B. quadrat 2 (6m-6.5m)
100% sand
15% rock
2 *Neomeris annulata*
1 wht. *Parapercis millepunctata*
1 sm. *Porites lobata/lutea* (purple)

C. quadrat 3 (8m-8.5m)
90% sand
15% beachrock (10% remvble)
1 sm. crab (approx. 1cm)
4% *Dictyota sp.*
2% *Halimeda micronesica*
1 *Hexabranchus sanguineus: orange* egg mass, approx. 5cm
10% K
2% M (red)
4 *Neomeris annulata*
1% *Padina gymnospora*
1 (lg.) *Porites lobata/lutea* (yellow)

D. quadrat 4 (9m-9.5m)
50% sand
15% beachrock
35% rubble
4% D
5% *Dictyota sp.*
1% *Halimeda micronesica*
2 *Neomeris annulata*
5% *Padina gymnospora*

E. quadrat 5 (11m-11.5m)
95% sand
2% D
1% *Dictyota sp.*
1% *Halimeda micronesica*
2% M (red)
1 *Neomeris annulata*
10% *Padina gymnospora*
1 (lg.) *Porites lobata lutea* (yellow, approx. 1mX1.5m)
2 *Tridacna maximus*
1 *Valonia ventricosa*
3% unknown white egg mass

III. Zone 3 (beachrock/sand) 12m-63.5m
A. quadrat 1 (27m-27.5m)
60% beachrock (25% remvble)
30% sand
2% *Dictyota sp.*
1% *Halimeda micronesica*
25% K
25% *Lithothamnion prolifer*
2 *Neomeris annulata*
40% *Padina gymnospora*

B. quadrat 2 (30m-30.5m)
80% beachrock
1% D
1% *Dictyota sp.*
30% F
1% *Halimeda micronesica*
10% *Lithothamnion prolifer*
25% *Padina gymnospora*
1 blk. *Parapercis millepunctata*
10% unknown Tunicate
3 *Valonia ventricosa*

C. quadrat 3 (31m-31.5m)
50% beachrock
50% sand
5% D
5% *Halimeda micronesica*
10% K
20% *Lithothamnion prolifer*
5% M (red/pink)
7 *Neomeris annulata*
15% *Padina gymnospora*
1 sm. *Porites solida* (wht.)

D. quadrat 4 (41m-41.5m)
15% beachrock
85% sand
5% F
15% *Halimeda micronesica*
10% K
2% *Lithothamnion prolifer*
10% *Padina gymnospora*
2% *Sargassum sp.*

E. quadrat 5 (53m-53.5m)
70% beachrock (50% remvble)
30% sand
20% *Caulerpa serrulata*
1% D
15% *Halimeda micronesica*
30% K
10% *Lithothamnion prolifer*
6 *Neomeris annulata*
7% *Padina gymnospora*
5% unknown Tunicate

IV. Zone 4 (beachrock) 63.5m-81.5m
A. quadrat 1 (66m-66.5m)
90% beachrock
2% *Caulerpa serrulata*
5% *Dictyota sp.*
10% *Halimeda micronesica*
2% M (red)
30 *Neomeris annulata*
2% *Padina gymnospora*
5 *Parapercis millepunctata* (4 black, 1 white)
2 unknown snail

B. quadrat 2 (71m-71.5m)
90% beachrock
5% *Halimeda micronesica*
10% M (red)

C. quadrat 3 (77m-77.5m)
50% beachrock
40% rubble
3% *Lithothamnion prolifer*

D. quadrat 4 (80m-80.5m)
60% beachrock
40% rubble
5% *Padina gymnospora*

E. quadrat 5 (81m-81.5m)
45% beachrock
55% rubble
2% *Dictyota sp.*
10% *Padina gymnospora*

V. Zone 5 (sand) 81.5m-86.4m
A. quadrat 1 (83m-83.5m)
100% sand
50% rubble
5% *Padina gymnospora*

B. quadrat 2 (84m-84.5m)
100% sand
95% rubble
5% *Padina gymnospora*

**Transect 5 (40m)**

I. Zone 1 (shelf) 0m-3.5m
   A. quadrat 1 (0m-0.5m)
      8 anemone fish, lt. blue spots
      2 black Damsel fish
      1 *Herpolitha limax*
      1 *Montipora sp.*
      3 *Porites solida*
      1 *Stichodactyla gigantea*
   B. quadrat 2 (2m-2.5m)
      2% D
      10% *Dictyota sp.*
      1 *Echinometra mathaei*
      2 *Fungia costulata*
      15% *Halimeda micronesica*
      1% *Padina gymnospora*
      1 blk. *Parapercis millepunctata*
      2% unknown Tunicate
II. Zone 2 (sand/coral rubble) 3.5m-11.5m
   A. quadrat 1 (4m-4.5m)
      98% sand
      3% rubble
      2% non-removable rock
      1 burrowing shrimp (gray)
      1% M (red)
      1 wht. *Parapercis millepunctata*
   B. quadrat 2 (5m-5.5m)
      95% sand
      10% rubble
      5% non-removable rock
      1% D
      1% *Dictyota sp.*
      3% *Halimeda micronesica*
   C. quadrat 3 (8m-8.5m)
      100% sand
      30% rubble
      1% *Caulerpa serrulata*
      3% D
      1% *Halimeda micronesica*
      2% M (red)
      1 *Neomeris annulata*
      1 snail (tan calry shell)
   D. quadrat 4 (9m-9.5m)
      60% sand
      1 wht. *Parapercis millepunctata*
      40% *Porites lobata/lutea* (yellow/purple)
      4 *Valonia aegagropila*
   E. quadrat 5 (11m-11.5m)
      90% sand
      20% rubble
      2 'baby' *Canthigaster bennetti*
      4% D
      1% *Dictyota sp.*
      1% E
      1% *Halimeda micronesica*
      1 *Halichoeres trimaculatus*
      9 *Neomeris annulata*
      1 wht *Parapercis millepunctata*
      3 *Porites lobata/lutea* (2 yellow, 1 yellow/purple)
III Zone 3 (sand/beachrock) 11.5m-57.2m
   A. quadrat 1 (15m-15.5m)
      60% beachrock
      30% sand
      20% rubble
      4% D
      1 black striped Damsel fish
      20% *Dictyota sp.*
      1% E
      10% *Halimeda micronesica*
      1% *Lithothamnion prolifer*
      1 *Neomeris annulata*
      20% *Padina gymnospora*
      10% *Porites lobata/lutea* (yellow)
   B. quadrat 2 (19m-19.5m)
      55% beachrock
      5% sand
      2% D
      1 black striped Damsel fish
      10% *Dictyota sp.*
      15% *Halimeda micronesica*
      2 *Neomeris annulata*
      5% *Padina gymnospora*
      40% *Porites lobata/lutea*
      10% *Turbinaria*
   C. quadrat 3 (24m-24.5m)
      40% beachrock
      60% sand
      20% rubble
      10% E
      1% *Halimeda micronesica*
      1 *Hexabranchus sanguineus: white* egg mass, approx. 5cm
      4% *Lithothamnion prolifer*
      1 *Neomeris annulata*
      1 wht. *Ophiocoma erinaceus*
      3% *Padina gymnospora*
      1 wht. *Parapercis millepunctata*

4 *Porites lobata/lutea*
(purple, approx. 1cm ea.)

D. quadrat 4 (47m-47.5m)
50% beachrock
20% sand
10% *Caulerpa serrulata*
2 crabs (approx. 1.5cm)
1% *Dictyota sp.*
1 *Echinometra mathaei*
5% *Halimeda micronesica*
20% *Lithothamnion prolifer*
1 *Neomeris annulata*
5% M (orange)
10% M (pink)
2% M (red)
30% *Padina gymnospora*
1 wht. *Parapercis millepunctata*
1 *Valonia aegagropila*

E. quadrat 5 (49m-49.5m)
20% beachrock
70% sand
10% rubble
1 crab (approx. 2cm)
1% E
1 *Echinometra mathaei*
2% *Halimeda micronesica*
5% K
5% *Lithothamnion prolifer*
1% M (red)
1 *Neomeris annulata*
4% *Padina gymnospora*

IV. Zone 4 (beachrock) 57.2m-76m

A. quadrat 1 (58m-58.5m)
100% beachrock
15% sand
30% *Caulerpa serrulata*
25% *Dictyota sp.*
5% *Halimeda micronesica*
1 *Nennalpheus sp.*
1 *Neomeris annulata*
2% *Padina gymnospora*
30 small snails (cone shape)
Trash: 1 metal can covered in algae

B. quadrat 2 (59m-59.5m)
100% beachrock
1% D
25% *Dictyota sp.*
2 *Echinometra mathaei*
30% *Halimeda micronesica*
1 *Nennalpheus sp.*
3 *Neomeris annulata*
5% *Padina gymnospora*
2 blk. *Parapercis millepunctata*
1 *Porites lobata/lutea* (cream)
1 *Porites solida*

C. quadrat 3 (61m-61.5m)
100% beachrock
25% sand
30% *Caulerpa serrulata*
30% *Dictyota sp.*
10% *Halimeda micronesica*
1 *Nennalpheus sp.*
3 *Neomeris annulata*
1 blk. *Parapercis millepunctata*
3 *Porites solida* (brown)

D. quadrat 4 (71m-71.5m)
NOTE: very murky waters
100% beachrock
30% sand
1 crab (approx. 2cm)
10% *Halimeda micronesica*
2% *Lithothamnion prolifer*

E. quadrat 5 (72m-72.5m)
100% beachrock
30% sand
2% rock
5% *Caulerpa serrulata*
5% *Halimeda micronesica*
3 *Neomeris annulata*
5% *Padina gymnospora*

V. Zone 5 (sand) 76m-80m

A. quadrat 1 (78m-78.5m)
100% sand
70% rock
(size approx. 10cm-15cm)

B. quadrat 2 (79m-79.5m)
100% sand
80% rock
(size approx. 10cm-15cm)

Tables 3, 5, 6, and 7 are on file with the University of California, Berkeley, BioSciences Library's, copy of this report.

Table 4. Transect Lengths For All Sites

## Transect Lengths

| Transect Number | Length |
|---|---|
| **Modified Shoreline:** | |
| **[Site 1]** | |
| 1 | 73m |
| 2 | 75m |
| 3 | 92.9m |
| 4 | 86.4m |
| 5 | 80m |
| **Unmodified Shoreline:** | |
| **[Site 2 - beachrock]** | |
| 6 | 30m |
| 7 | 29m |
| 8 | 23m |
| 9 | 20.2m |
| 10 | 17m |
| **[Site 3 - beachrock and sand]** | |
| 11 | 16.3m |
| 12 | 17.6m |
| 13 | 16.5m |
| 14 | 20m |
| 15 | 21m |
| **[Site 4 - coral rubble and sand]** | |
| 16 | 25.2m |
| 17 | 27.2m |
| 18 | 26.5m |
| 19 | 25.2m |
| 20 | 25.2m |

Table 3. Species Index - Site 1

| Transect 1 (0m) | | Zone 1 | | Zone 2 | | | | | Zone 3 | | | | | Zone 4 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 |
| species name | description | | | | | | | | | | | | | | | | | |
| **Animalia** | | | | | | | | | | | | | | | | | | |
| **P: Arthropoda; F: Alpheidae** | | | | | | | | | | | | | | | | | | |
| | gray burrowing shrimp | | | | | | | | | | | | | | | | | |
| *Nennalpheus sp.* | red burrowing shrimp | | | | | | | | | | | | | | | | | |
| **P: Chordata; F: Labridae** | | | | | | | | | | | | | | | | | | |
| *Halichoeres trimaculatus* | Three spot wrasse | | | | | | | | | | | | | | | | | |
| **P: Chordata; F: Mullidae** | | | | | | | | | | | | | | | | | | |
| *Parupeneus barberinus* | Dot & dash goatfish | | | | | | | | | | | | | | | | | |
| **P: Chordata; F: Pinguiedidae** | | | | | | | | | | | | | | | | | | |
| *Parapercis millepunctata* | Spotted sandperch-white | | | | | | | | | | 2 | | | | | | | |
| " | Spotted sandperch-gray | | | | | | | | | | | | | | | | | |
| " | Spotted sandperch-black | | | | | | 1 | 1 | | | | | | | | | | |
| **P: Chordata; F: Pomacentridae** | | | | | | | | | | | | | | | | | | |
| unknown | black striped damsel | | | | | | | | | | | | | | | | | |
| unknown | black damsel | | | | | | | | | | | | | | | | | |
| unknown | black anemone fish, blue spots | 3 | | | | | | | | | | | | | | | | |
| **P: Chordata; F: Scorpaenidae** | | | | | | | | | | | | | | | | | | |
| *Synanceja verrucosa* | Stonefish | 1 | | | | | | | | | | | | | | | | |
| **P: Chordata; F: Syngnathides** | | | | | | | | | | | | | | | | | | |
| *Corythoichthys flavofasciatus* | Pipe fish | 1 | | | | | | | | | | | | | | | | |
| **P: Chordata; F: Tetraodontidae** | | | | | | | | | | | | | | | | | | |
| *Canthigaster bennetti* | Bennett's sharpnose puffer | | | | | | | | | | | | | | | | | |
| **P: Chordata; SubP: Urochorda** | | | | | | | | | | | | | | | | | | |
| unknown | brown tunicate | | | | | | | | | | | | | | | | | |
| **P: Cnidaria; O: Scleractinia** | | | | | | | | | | | | | | | | | | |
| *Acropora sp.* | branching; bush-like form | | | | | | | | | | | | | | | | | |
| *Fungia (cycloseris) costulata* | circular fungia | 1 | | | | | | | | | | | | | | | | |
| *Herpolitha limax* | elongated, mountain-like fungia | 1 | | | | | | | | | | | | | | | | |
| *Montipora undata* | plate-like; brown and/or purple | | | | | | | | | | | | | | | | | |
| *Porites lobata and/or P. lutea* | massive; cream, yellow, brown | | 1 | 1 | 4 | 3 | | | | | | | | 1 | | | | |
| *Porites solida* | brown or greenish yellow | 1 | | | | | | | | | | | | | | | | |

| Transect 1 (0m) | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 |
| species name | description | | | | | | | | | | | | | | | | | | | |
| unknown A. | pale cream, massive; 'swirly' | | | | | | | | | | | | | | | | | | | |
| unknown B. | lt. yellow, branching; bush-like | | | | | | | | | | | | | | | | | | | |
| **P: Cnidaria; O: Stichodactylidae** | | | | | | | | | | | | | | | | | | | | |
| *Stichodactyla gigantea* | sea anemone | 1 | | | | | | | | | | | | | | | | | | |
| **P: Echinodermata** | | | | | | | | | | | | | | | | | | | | |
| *Bohadschia argus* | sea cucumber | | | | | | | | | | | | | | | | | | | |
| *Culcita novaeguineae* | Cushion star | | | | | | | | | | | | | | | | | | | |
| *Diadema savignyi* | black diadema | | 1 | | | | | | | | | | | | | | | | | |
| *Echinometra mathaei* | purple sea urchin | | | 1 | | | | | | | | | | | | | | | | |
| *Ophiocoma erinaceus* | black brittle star (also white) | | | | | | | | | | | | | | | | | | | |
| **P: Mollusca** | | | | | | | | | | | | | | | | | | | | |
| *Tridacna maximus* | giant clam | | | | | | | | | | | | | | | | | | | |
| unknown | bivalve-clam (all species) | | | | | | | | | | | | | | | | | | | |
| **P: Mollusca; C: Gastropoda** | | | | | | | | | | | | | | | | | | | | |
| *Hexabranchus sanguineus (eggs)* | Spanish dancer egg mass | | | | | | | | | | | | | | | | | | | |
| | snail (all species) | | | | | | | | | | | | 1 | | | | | | | |
| | small crab (all species) 1-2cm | | | | | | | | | | | | 1 | | | | | | | |
| | hermit crab (all species) | | | | | | | | | | | | | | | | | | | |
| **P: Porifera** | | | | | | | | | | | | | | | | | | | | |
| *Haliclona sp. (Haplosclerida Chalinidae)* | purple sponge | | | | | | | | | | | | | | | | | | | |
| **P: Unknown** | | | | | | | | | | | | | | | | | | | | |
| *Gastrolepidia clavigera* | scale worm | | | | | | | | | | | | | | | | | | | |
| | unknown white worm | | | | | | | | | | 1 | | | | | | | | | |
| P: Unknown- egg mass | unknown white egg mass | | | | | | | | | | | | | | | | | | | |
| **Planta** (in % coverage, except H) | | | | | | | | | | | | | | | | | | | | |
| **Green Algae** | | | | | | | | | | | | | | | | | | | | |
| *Caulerpa serrulata* | light green; unknown C | | | | | | | | 15 | | 2 | | 5 | | | | | | | |
| *Halimeda micronesica* | coralline alga; unknown B | | | | | | 2 | 2 | 4 | 4 | 2 | 2 | | | 5 | | | | | |
| *Neomeris annulata* | Caterpillar weed; unknown H | | | | | | | | | | | | | | | | | | | |
| Valonia aegagropila | cluster of small green balls | | | | | | | | | | | | | | | | | | | |
| Valonia ventricosa | Sailor's eyeball | | | | | | | | | | | | 1 | | | | | | | |

| Transect 1 (0m) | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 |
| species name | description | | | | | | | | | | | | | | | | | |
| **Red Algae** | | | | | | | | | | | | | | | | | | |
| *Dictyota sp.* | clumpy, brown: unknown A | | | | 10 | 90 | | | 5 | | 1 | 1 | 2 | | | 2 | | |
| (possibly) *Lithothamnion prolifer* | coralline red alga; unknown L | | | | | | | | | | | | | | | | | |
| **Red and Brown Algae** | | | | | | | | | | | | | | | | | | |
| *Padina gymnospora* | Funnelweed | | | | | | 40 | 20 | 10 | 30 | | 5 | 3 | 15 | 2 | 5 | | |
| *Sargassum sp.* | seaweed | | | | | | 25 | | | | | | | | 1 | | | |
| *Turbinaria sp.* | Turbinweed | | | | | | 2 | | | | | | | | 1 | | | |
| unknown red algae | red/brown thick cluster | | | | | | | | | | | | | | | | | |
| **Unknown Algae** | | | | | | | | | | | | | | | | | | |
| | brown clumpy; unknown D | | | | | | | | | | | | | | | | 10 | |
| | green/brown, smooth; E | | | | | | | | | 10 | | | | | | | | |
| | green, short, clustery; F | | | | | | | | | | | | | | | | | |
| | brown, fuzzy, thin leaf; G | | | | | | | | | | | | | | | | | |
| | dark green, 'mossy'; I | | | | | | | | | | | | | | | | | |
| | brown/tan, 'mossy'; J | | | | | | | | | | | | | | | | | |
| | brown/tan, thick, hairy; K | | | | | | | | | | | | | | | | | |
| | orange encrusting algae; M | | | | | | | | | | | | | | | | | |
| | pink encrusting algae; M | | | | | | | | | | | | | | | | | |
| | red encrusting algae; M | | | | | | | | | | | | | | | | | |

| Transect 2 (10m) | | Zone 2 | | | | | Zone 3 | | | | | Zone 4 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 |
| species name | description | | | | | | | | | | | | | | | |
| **Animalia** | | | | | | | | | | | | | | | | |
| **P: Arthropoda; F: Alpheidae** | | | | | | | | | | | | | | | | |
| | gray burrowing shrimp | | | | | | | | | | | | | | | |
| *Nennalpheus sp.* | red burrowing shrimp | | 1 | | | | | | | 1 | | | | | | |
| **P: Chordata; F: Labridae** | | | | | | | | | | | | | | | | |
| *Halichoeres trimaculatus* | Three spot wrasse | | | | | | | | | | | | | | | |
| **P: Chordata; F: Mullidae** | | | | | | | | | | | | | | | | |
| *Parupeneus barberinus* | Dot & dash goatfish | | | | | | | | | | | | | | | |
| **P: Chordata; F: Pinguiedidae** | | | | | | | | | | | | | | | | |
| *Parapercis millepunctata* | Spotted sandperch-white | | | | | | | | | | | | | | | |
| " | Spotted sandperch-gray | | | | | | | | | | | | | | | |
| " | Spotted sandperch-black | | | | | | | | | 2 | | | | | | |
| **P: Chordata; F: Pomacentridae** | | | | | | | | | | | | | | | | |
| unknown | black striped damsel | | | | | | | | | | | | | | | |
| unknown | black damsel | | | | | | | | | | | | | | | |
| unknown | black anemone fish, blue spots | | | | | | | | | | | | | | | |
| **P: Chordata; F: Scorpaenidae** | | | | | | | | | | | | | | | | |
| *Synanceja verrucosa* | Stonefish | | | | | | | | | | | | | | | |
| **P: Chordata; F: Syngnathides** | | | | | | | | | | | | | | | | |
| *Corythoichthys flavofasciatus* | Pipe fish | | | | | | | | | | | | | | | |
| **P: Chordata; F: Tetraodontidae** | | | | | | | | | | | | | | | | |
| *Canthigaster bennetti* | Bennett's sharpnose puffer | | | | | | | | | | | | | | | |
| **P: Chordata; SubP: Urochorda** | | | | | | | | | | | | | | | | |
| unknown | brown tunicate | | | | | | | | | | | | | | | |
| **P: Cnidaria; O: Scleractinia** | | | | | | | | | | | | | | | | |
| *Acropora sp.* | branching; bush-like form | | | | | | | | | | | | | | | |
| *Fungia (cycloseris) costulata* | circular fungia | | | | | | | | | | | | | | | |
| *Herpolitha limax* | elongated, mountain-like fungia | | | | | | | | | | | | | | | |
| *Montipora undata* | plate-like; brown and/or purple | | | | | | | | | | | | | | | |
| *Porites lobata and/or P. lutea* | massive; cream, yellow, brown | | 1 | | | | | | | 1 | 1 | | | | | |
| *Porites solida* | brown or greenish yellow | | | | | | | | | | | | | | | |

| Transect 2 (10m) | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 |
| species name | description | | | | | | | | | | | | | | | |
| unknown A. | pale cream, massive; 'swirly' | | | | | | | | | | | | | | | |
| unknown B. | lt. yellow, branching; bush-like | | | | | | | | | | | | | | | |
| **P: Cnidaria; O: Stichodactylidae** | | | | | | | | | | | | | | | | |
| *Stichodactyla gigantea* | sea anemone | | | | | | | | | | | | | | | |
| **P: Echinodermata** | | | | | | | | | | | | | | | | |
| *Bohadschia argus* | sea cucumber | | | | | | | | | | | | | | | |
| *Culcita novaeguineae* | Cushion star | | | | | | | | | | | | | | | |
| *Diadema savignyi* | black diadema | | | | | | | | | | | | | | | |
| *Echinometra mathaei* | purple sea urchin | 1 | | | | | 1 | | | | | | | | | |
| *Ophiocoma erinaceus* | black brittle star (also white) | | | | | | | | | | | | | | | |
| **P: Mollusca** | | | | | | | | | | | | | | | | |
| *Tridacna maximus* | giant clam | | | | | | | | | | | | | | | |
| unknown | bivalve-clam (all species) | | | | | | | | | | | | | | | |
| **P: Mollusca; C: Gastropoda** | | | | | | | | | | | | | | | | |
| *Hexabranchus sanguineus (eggs)* | Spanish dancer egg mass | | | | | | | | | | | | | | | |
| | snail (all species) | | | | | | | | | | | | | | | |
| | small crab (all species) 1-2cm | | | | | 1 | | 1 | | | 1 | | | | | |
| | hermit crab (all species) | | | | 1 | | | | | | | | | | | |
| **P: Porifera** | | | | | | | | | | | | | | | | |
| *Haliclona sp. (Haplosclerida Chalinidae)* | purple sponge | | | | | | | | | | | | | | | |
| **P: Unknown** | | | | | | | | | | | | | | | | |
| *Gastrolepidia clavigera* | scale worm | | | | | | | | | | 1 | | | | | |
| | unknown white worm | | | | | | | | | | 1 | | | | | |
| P: Unknown- egg mass | unknown white egg mass | | | | | | | | | | | | | | | |
| **Planta** (in % coverage, except H) | | | | | | | | | | | | | | | | |
| **Green Algae** | | | | | | | | | | | | | | | | |
| *Caulerpa serrulata* | light green; unknown C | | 5 | | | 20 | | | | 2 | | | 3 | | | |
| *Halimeda micronesica* | coralline alga; unknown B | | 1 | | | 2 | | 4 | 2 | 10 | 20 | 1 | 2 | 10 | 5 | 0.25 |
| *Neomeris annulata* | Caterpillar weed; unknown H | | | | | | | | | | | 1 | | 1 | 7 | 50 |
| Valonia aegagropila | cluster of small green balls | | | | | | | | | | | | | | | |
| Valonia ventricosa | Sailor's eyeball | | | | | 1 | | | | | | | | | | |

| **Transect 2 (10m)** | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 |
| species name | description | | | | | | | | | | | | | | | |
| **Red Algae** | | | | | | | | | | | | | | | | |
| *Dictyota sp.* | clumpy, brown: unknown A | | 5 | | 2 | 5 | 5 | 10 | 5 | | 30 | 2 | 2 | | 2 | |
| (possibly) *Lithothamnion prolifer* | coralline red alga; unknown L | | | | | | | | | | | | | | | |
| **Red and Brown Algae** | | | | | | | | | | | | | | | | |
| *Padina gymnospora* | Funnelweed | 1 | 5 | 40 | 20 | 10 | 25 | 1 | 10 | 25 | 25 | 45 | 30 | 40 | 30 | 5 |
| *Sargassum sp.* | seaweed | | | | 5 | | 7 | | | | | | 5 | | | |
| *Turbinaria sp.* | Turbinweed | | | | | | | | | | | | | 1 | 2 | |
| unknown red algae | red/brown thick cluster | | | | | | | | | | | | | | | |
| **Unknown Algae** | | | | | | | | | | | | | | | | |
| | brown clumpy; unknown D | | | | | | | | | | | | | | | |
| | green/brown, smooth; E | | 5 | 15 | 10 | 40 | | 15 | 10 | | 30 | | | | | |
| | green, short, clustery; F | | | | | | 1 | | | | | | | | | |
| | brown, fuzzy, thin leaf; G | | | | | | | | | | | 15 | 10 | 10 | | |
| | dark green, 'mossy'; I | | | | | | | | | | | | | 2 | | 2 |
| | brown/tan, 'mossy'; J | | | | | | | | | | | | | | | |
| | brown/tan, thick, hairy; K | | | | | | | | | | | | | | | |
| | orange encrusting algae; M | | | | | | | | | | | | | | | |
| | pink encrusting algae; M | | | | | | | | | | | | | | | |
| | red encrusting algae; M | | | | | | | | | | | | | | | |

| Transect 3 (20m) | | Zone 1 | | Zone 2 | | | | | Zone 3 | | | | | Zone 4 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 | 1 | 2 |
| species name | description | | | | | | | | | | | | | | |
| **Animalia** | | | | | | | | | | | | | | | |
| **P: Arthropoda; F: Alpheidae** | | | | | | | | | | | | | | | |
| | gray burrowing shrimp | | | | | | | | | | | | | | |
| *Nennalpheus sp.* | red burrowing shrimp | | | | | | | | | | | | | | |
| **P: Chordata; F: Labridae** | | | | | | | | | | | | | | | |
| *Halichoeres trimaculatus* | Three spot wrasse | | | | | | | | | | | | | | |
| **P: Chordata; F: Mullidae** | | | | | | | | | | | | | | | |
| *Parupeneus barberinus* | Dot & dash goatfish | | | | | | | | | | | | | | |
| **P: Chordata; F: Pinguiedidae** | | | | | | | | | | | | | | | |
| *Parapercis millepunctata* | Spotted sandperch-white | | | | | | | | 1 | | | | | | |
| " | Spotted sandperch-gray | | | | | | | | 1 | | | | | | |
| " | Spotted sandperch-black | | | | | | | | 1 | | | | | | |
| **P: Chordata; F: Pomacentridae** | | | | | | | | | | | | | | | |
| unknown | black striped damsel | | | | | | | | | | | | | | |
| unknown | black damsel | 1 | | | | | | | | | | | | | |
| unknown | black anemone fish, blue spots | | | | | | | | | | | | | | |
| **P: Chordata; F: Scorpaenidae** | | | | | | | | | | | | | | | |
| *Synanceja verrucosa* | Stonefish | | | | | | | | | | | | | | |
| **P: Chordata; F: Syngnathides** | | | | | | | | | | | | | | | |
| *Corythoichthys flavofasciatus* | Pipe fish | | | | | | | | | | | | | | |
| **P: Chordata; F: Tetraodontidae** | | | | | | | | | | | | | | | |
| *Canthigaster bennetti* | Bennett's sharpnose puffer | | | | | | | | | | | | | | |
| **P: Chordata; SubP: Urochorda** | | | | | | | | | | | | | | | |
| unknown | brown tunicate | | | | | | | | | | | | | | |
| **P: Cnidaria; O: Scleractinia** | | | | | | | | | | | | | | | |
| *Acropora sp.* | branching; bush-like form | | | | | | | | | | | | | | |
| *Fungia (cycloseris) costulata* | circular fungia | 1 | | | | | | | | | | | | | |
| *Herpolitha limax* | elongated, mountain-like fungia | 1 | | | | | | | | | | | | | |
| *Montipora undata* | plate-like; brown and/or purple | 1 | | | 1 | | | | | | | | | | |
| *Porites lobata and/or P. lutea* | massive; cream, yellow, brown | 2 | | | 1 | | | | | | | | | | |
| *Porites solida* | brown or greenish yellow | 2 | 3 | | | | | | | 2 | | | | | |

| Transect 3 (20m) | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 | 1 | 2 |
| species name | description | | | | | | | | | | | | | | |
| unknown A. | pale cream, massive; 'swirly' | | | | | | | | | | | | | | |
| unknown B. | lt. yellow, branching; bush-like | | | | | | | | | | | | | | |
| **P: Cnidaria; O: Stichodactylidae** | | | | | | | | | | | | | | | |
| *Stichodactyla gigantea* | sea anemone | | | | | | | | | | | | | | |
| **P: Echinodermata** | | | | | | | | | | | | | | | |
| *Bohadschia argus* | sea cucumber | | | | | | | | | | | | | | |
| *Culcita novaeguineae* | Cushion star | | | 1 | | | | | | | | | | | |
| *Diadema savignyi* | black diadema | | | | | | | | | | | | | | |
| *Echinometra mathaei* | purple sea urchin | | | | | | 1 | | | 1 | | | | | |
| *Ophiocoma erinaceus* | black brittle star (also white) | | | | | | | | | | | | | | |
| **P: Mollusca** | | | | | | | | | | | | | | | |
| *Tridacna maximus* | giant clam | | | | | | | | | | | | | | |
| unknown | bivalve-clam (all species) | | | | | | | | | | | | | | |
| **P: Mollusca; C: Gastropoda** | | | | | | | | | | | | | | | |
| *Hexabranchus sanguineus (eggs)* | Spanish dancer egg mass | | | | | | | | | | | | | | |
| | snail (all species) | | | | | | | | | | | | | | |
| | small crab (all species) 1-2cm | | | | | | | | | | | | | | |
| | hermit crab (all species) | | | | | | 1 | | | | | | | | |
| **P: Porifera** | | | | | | | | | | | | | | | |
| *Haliclona sp. (Haplosclerida Chalinidae)* | purple sponge | | | | | | | | | | | | | | |
| **P: Unknown** | | | | | | | | | | | | | | | |
| *Gastrolepidia clavigera* | scale worm | | | | | | | | | | | | | | |
| | unknown white worm | | | | | | | | | | | | | | |
| P: Unknown- egg mass | unknown white egg mass | | | | | | | | | | | | | | |
| **Planta** (in % coverage, except H) | | | | | | | | | | | | | | | |
| **Green Algae** | | | | | | | | | | | | | | | |
| *Caulerpa serrulata* | light green; unknown C | | | | | 10 | 15 | 20 | 10 | | | | | | |
| *Halimeda micronesica* | coralline alga; unknown B | 40 | 20 | 2 | 5 | | 2 | 5 | 10 | 3 | | | | | |
| *Neomeris annulata* | Caterpillar weed; unknown H | | | | 1 | | 1 | | 2 | | | 2 | 1 | | |
| Valonia aegagropila | cluster of small green balls | | | | | | | | | | | | | | |
| Valonia ventricosa | Sailor's eyeball | 1 | 4 | | | 2 | | | | 1 | | | | | |

| Transect 3 (20m) | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 | 1 | 2 |
| species name | description | | | | | | | | | | | | | | | |
| **Red Algae** | | | | | | | | | | | | | | | | |
| *Dictyota sp.* | clumpy, brown: unknown A | 20 | 20 | 10 | 35 | | 10 | 40 | 5 | | 25 | | | | |
| (possibly) *Lithothamnion prolifer* | coralline red alga; unknown L | | | | | | 1 | | 1 | 1 | | | | | |
| **Red and Brown Algae** | | | | | | | | | | | | | | | | |
| *Padina gymnospora* | Funnelweed | | | | 25 | | | | 20 | | | | | 5 | |
| *Sargassum sp.* | seaweed | | | | | | | | | | | | | | |
| *Turbinaria sp.* | Turbinweed | | 1 | | 1 | 30 | 30 | 10 | | | | 10 | 5 | | |
| unknown red algae | red/brown thick cluster | | | | | | | | | | | | | | | |
| **Unknown Algae** | | | | | | | | | | | | | | | | |
| | brown clumpy; unknown D | | 1 | 2 | | 2 | | | | | | | | | | |
| | green/brown, smooth; E | | | | | 20 | 20 | | | | | | | | | |
| | green, short, clustery; F | | | | | | | | | | | | | | | |
| | brown, fuzzy, thin leaf; G | | | | | | | | | | | | | | | |
| | dark green, 'mossy'; I | | | | | | | | | | | | | | | |
| | brown/tan, 'mossy'; J | 95 | | | | | | | | | | | | | | |
| | brown/tan, thick, hairy; K | | | | 45 | | | | | | | | | | | |
| | orange encrusting algae; M | | | | | | | | | | | | | | | |
| | pink encrusting algae; M | | | | | | | | | | | | | | | |
| | red encrusting algae; M | | | | | | | | | | | | | | | |

Table 3. page 9

| Transect 4 (30m) | | Zone 1 | | Zone 2 | | | | | Zone 3 | | | | | Zone 4 | | | | | Zone 5 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 | 1 | 2 |
| species name | description | | | | | | | | | | | | | | | | | | | |
| **Animalia** | | | | | | | | | | | | | | | | | | | | |
| **P: Arthropoda; F: Alpheidae** | | | | | | | | | | | | | | | | | | | | |
| | gray burrowing shrimp | | | | | | | | | | | | | | | | | | | |
| *Nennalpheus sp.* | red burrowing shrimp | | | | | | | | | | | | | | | | | | | |
| **P: Chordata; F: Labridae** | | | | | | | | | | | | | | | | | | | | |
| *Halichoeres trimaculatus* | Three spot wrasse | | | 1 | | | | | | | | | | | | | | | | |
| **P: Chordata; F: Mullidae** | | | | | | | | | | | | | | | | | | | | |
| *Parupeneus barberinus* | Dot & dash goatfish | | | 1 | | | | | | | | | | | | | | | | |
| **P: Chordata; F: Pinguiedidae** | | | | | | | | | | | | | | | | | | | | |
| *Parapercis millepunctata* | Spotted sandperch-white | | | | 1 | | | | | | | | | 1 | | | | | | |
| " | Spotted sandperch-gray | | | | | | | | | | | | | | | | | | | |
| " | Spotted sandperch-black | | | | | | | | | 1 | | | | 4 | | | | | | |
| **P: Chordata; F: Pomacentridae** | | | | | | | | | | | | | | | | | | | | |
| unknown | black striped damsel | | | | | | | | | | | | | | | | | | | |
| unknown | black damsel | | | | | | | | | | | | | | | | | | | |
| unknown | black anemone fish, blue spots | | | | | | | | | | | | | | | | | | | |
| **P: Chordata; F: Scorpaenidae** | | | | | | | | | | | | | | | | | | | | |
| *Synanceja verrucosa* | Stonefish | | | | | | | | | | | | | | | | | | | |
| **P: Chordata; F: Syngnathides** | | | | | | | | | | | | | | | | | | | | |
| *Corythoichthys flavofasciatus* | Pipe fish | | | | | | | | | | | | | | | | | | | |
| **P: Chordata; F: Tetraodontidae** | | | | | | | | | | | | | | | | | | | | |
| *Canthigaster bennetti* | Bennett's sharpnose puffer | | | | | | | | | | | | | | | | | | | |
| **P: Chordata; SubP: Urochorda** | | | | | | | | | | | | | | | | | | | | |
| unknown | brown tunicate | | | | | | | | | 10% | | | 5% | | | | | | | |
| **P: Cnidaria; O: Scleractinia** | | | | | | | | | | | | | | | | | | | | |
| *Acropora sp.* | branching; bush-like form | 1 | | | | | | | | | | | | | | | | | | |
| *Fungia (cycloseris) costulata* | circular fungia | | | | | | | | | | | | | | | | | | | |
| *Herpolitha limax* | elongated, mountain-like fungia | | | | | | | | | | | | | | | | | | | |
| Montipora efflorescens | | | 1 | | | | | | | | | | | | | | | | | |
| *Montipora undata* | plate-like; brown and/or purple | | | | | | | | | | | | | | | | | | | |
| *Porites lobata and/or P. lutea* | massive; cream, yellow, brown | 3 | 1 | | 1 | 1 | | 1 | | | | | | | | | | | | |

| Transect 4 (30m) | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 | 1 | 2 |
| species name | description | | | | | | | | | | | | | | | | | | | |
| *Pontes solida* | brown or greenish yellow | | | | | | | | | | 1 | | | | | | | | | |
| unknown A. | pale cream, massive; 'swirly' | | | | | | | | | | | | | | | | | | | |
| unknown B. | lt. yellow, branching; bush-like | | | | | | | | | | | | | | | | | | | |
| **P: Cnidaria; O: Stichodactylidae** | | | | | | | | | | | | | | | | | | | | |
| *Stichodactyla gigantea* | sea anemone | | | | | | | | | | | | | | | | | | | |
| **P: Echinodermata** | | | | | | | | | | | | | | | | | | | | |
| *Bohadschia argus* | sea cucumber | | | | | | | | | | | | | | | | | | | |
| *Culcita novaeguineae* | Cushion star | | | | | | | | | | | | | | | | | | | |
| *Diadema savignyi* | black diadema | | | | | | | | | | | | | | | | | | | |
| *Echinometra mathaei* | purple sea urchin | | | | | | | | | | | | | | | | | | | |
| *Ophiocoma erinaceus* | black brittle star (also white) | | | | | | | | | | | | | | | | | | | |
| **P: Mollusca** | | | | | | | | | | | | | | | | | | | | |
| *Tridacna maximus* | giant clam | | | | | | | 2 | | | | | | | | | | | | |
| unknown | bivalve-clam (all species) | | | | | | | | | | | | | | | | | | | |
| **P: Mollusca; C: Gastropoda** | | | | | | | | | | | | | | | | | | | | |
| *Hexabranchus sanguineus (eggs)* | Spanish dancer egg mass | | | | | 1 | | | | | | | | | | | | | | |
| | snail (all species) | | | | | | | | | | | | | 2 | | | | | | |
| | small crab (all species) 1-2cm | | | | | 1 | | | | | | | | | | | | | | |
| | hermit crab (all species) | | | | | | | | | | | | | | | | | | | |
| **P: Porifera** | | | | | | | | | | | | | | | | | | | | |
| *Haliclona sp. (Haplosclerida Chalinidae)* | purple sponge | | | | | | | | | | | | | | | | | | | |
| **P: Unknown** | | | | | | | | | | | | | | | | | | | | |
| *Gastrolepidia clavigera* | scale worm | | | | | | | | | | | | | | | | | | | |
| | unknown white worm | | | | | | | | | | | | | | | | | | | |
| P: Unknown- egg mass | unknown white egg mass | | | | | | | 3% | | | | | | | | | | | | |
| **Planta** (in % coverage, except H) | | | | | | | | | | | | | | | | | | | | |
| **Green Algae** | | | | | | | | | | | | | | | | | | | | |
| *Caulerpa serrulata* | light green; unknown C | | | | | | | | | | | | 20 | 2 | | | | | | |
| *Halimeda micronesica* | coralline alga; unknown B | 2 | 5 | | | 2 | 1 | 1 | 1 | 1 | 5 | 15 | 15 | 10 | 5 | | | | | |
| *Neomeris annulata* | Caterpillar weed; unknown H | | | | 2 | 4 | 2 | 1 | 2 | | 7 | | 6 | 30 | | | | | | |
| Valonia aegagropila | cluster of small green balls | | | | | | | | | | | | | | | | | | | |

| **Transect 4 (30m)** | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 | 1 | 2 |
| species name | description | | | | | | | | | | | | | | | | | | | |
| Valonia ventricosa | Sailor's eyeball | | | | | | | 1 | | 3 | | | | | | | | | | |
| **Red Algae** | | | | | | | | | | | | | | | | | | | | |
| *Dictyota sp.* | clumpy, brown: unknown A | 1 | 5 | | | 4 | 5 | 1 | 2 | 1 | | | | 5 | | | | 2 | | |
| (possibly) *Lithothamnion prolifer* | coralline red alga; unknown L | | 1 | 1 | | | | | 25 | 10 | 20 | 2 | 10 | | | 3 | | | | |
| **Red and Brown Algae** | | | | | | | | | | | | | | | | | | | | |
| *Padina gymnospora* | Funnelweed | | | | | 1 | 5 | 10 | 40 | 25 | 15 | 10 | 7 | 2 | | | 5 | 10 | 5 | 5 |
| *Sargassum sp.* | seaweed | | | | | | | | | | | 2 | | | | | | | | |
| *Turbinaria sp.* | Turbinweed | | | | | | | | | | | | | | | | | | | |
| unknown red algae | red/brown thick cluster | | | | | | | | | | | | | | | | | | | |
| **Unknown Algae** | | | | | | | | | | | | | | | | | | | | |
| | brown clumpy; unknown D | | 2 | | | | 4 | 2 | | 1 | 5 | | 1 | | | | | | | |
| | green/brown, smooth; E | | | | | | | | | | | | | | | | | | | |
| | green, short, clustery; F | | | | | | | | | 30 | | 5 | | | | | | | | |
| | brown, fuzzy, thin leaf; G | | | | | | | | | | | | | | | | | | | |
| | dark green, 'mossy'; I | | | | | | | | | | | | | | | | | | | |
| | brown/tan, 'mossy'; J | | | | | | | | | | | | | | | | | | | |
| | brown/tan, thick, hairy; K | | | | | 10 | | | 25 | | 10 | 10 | 30 | | | | | | | |
| | orange encrusting algae; M | | | | | | | | | | | | | | | | | | | |
| | pink encrusting algae; M | | | | | | | | | | 5 | | | | | | | | | |
| | red encrusting algae; M | | 1 | | | 2 | | 2 | | | | | | 2 | 10 | | | | | |

Table 3. page 12

| Transect 5 (40m) | | Zone 1 | | Zone 2 | | | | | Zone 3 | | | | | Zone 4 | | | | | Zone 5 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 | 1 | 2 |
| species name | description | | | | | | | | | | | | | | | | | | | |
| **Animalia** | | | | | | | | | | | | | | | | | | | | |
| **P: Arthropoda; F: Alpheidae** | | | | | | | | | | | | | | | | | | | | |
| | gray burrowing shrimp | | | 1 | | | | | | | | | | | | | | | | |
| *Nennalpheus sp.* | red burrowing shrimp | | | | | | | | | | | | | 1 | 1 | 1 | | | | |
| **P: Chordata; F: Labridae** | | | | | | | | | | | | | | | | | | | | |
| *Halichoeres trimaculatus* | Three spot wrasse | | | | | | | 1 | | | | | | | | | | | | |
| **P: Chordata; F: Mullidae** | | | | | | | | | | | | | | | | | | | | |
| *Parupeneus barberinus* | Dot & dash goatfish | | | | | | | | | | | | | | | | | | | |
| **P: Chordata; F: Pinguiedidae** | | | | | | | | | | | | | | | | | | | | |
| *Parapercis millepunctata* | Spotted sandperch-white | | | 1 | | | 1 | 1 | | | 1 | 1 | | | | | | | | |
| " | Spotted sandperch-gray | | | | | | | | | | | | | | | | | | | |
| " | Spotted sandperch-black | | 1 | | | | | | | | | | | | 2 | 1 | | | | |
| **P: Chordata; F: Pomacentridae** | | | | | | | | | | | | | | | | | | | | |
| unknown | black striped damsel | | | | | | | | 1 | 1 | | | | | | | | | | |
| unknown | black damsel | 2 | | | | | | | | | | | | | | | | | | |
| unknown | black anemone fish, blue spots | 8 | | | | | | | | | | | | | | | | | | |
| **P: Chordata; F: Scorpaenidae** | | | | | | | | | | | | | | | | | | | | |
| *Synanceja verrucosa* | Stonefish | | | | | | | | | | | | | | | | | | | |
| **P: Chordata; F: Syngnathides** | | | | | | | | | | | | | | | | | | | | |
| *Corythoichthys flavofasciatus* | Pipe fish | | | | | | | | | | | | | | | | | | | |
| **P: Chordata; F: Tetraodontidae** | | | | | | | | | | | | | | | | | | | | |
| *Canthigaster bennetti* | Bennett's sharpnose puffer | | | | | | | 2 | | | | | | | | | | | | |
| **P: Chordata; SubP: Urochorda** | | | | | | | | | | | | | | | | | | | | |
| unknown | brown tunicate | | 2% | | | | | | | | | | | | | | | | | |
| **P: Cnidaria; O: Scleractinia** | | | | | | | | | | | | | | | | | | | | |
| *Acropora sp.* | branching; bush-like form | | | | | | | | | | | | | | | | | | | |
| *Fungia (cycloseris) costulata* | circular fungia | | 2 | | | | | | | | | | | | | | | | | |
| *Herpolitha limax* | elongated, mountain-like fungia | 1 | | | | | | | | | | | | | | | | | | |
| *Montipora undata* | plate-like; brown and/or purple | 1 | | | | | | | | | | | | | | | | | | |
| *Porites lobata and/or P. lutea* | massive; cream, yellow, brown | | | | | | 1 | 3 | 1 | 1 | 4 | | | | 1 | | | | | |
| *Porites solida* | brown or greenish yellow | 3 | | | | | | | | | | | | | 1 | 3 | | | | |

| Transect 5 (40m) | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 | 1 | 2 |
| species name | description | | | | | | | | | | | | | | | | | | | |
| unknown A. | pale cream, massive; 'swirly' | | | | | | | | | | | | | | | | | | | |
| unknown B. | lt. yellow, branching; bush-like | | | | | | | | | | | | | | | | | | | |
| **P: Cnidaria; O: Stichodactylidae** | | | | | | | | | | | | | | | | | | | | |
| *Stichodactyla gigantea* | sea anemone | 1 | | | | | | | | | | | | | | | | | | |
| **P: Echinodermata** | | | | | | | | | | | | | | | | | | | | |
| *Bohadschia argus* | sea cucumber | | | | | | | | | | | | | | | | | | | |
| *Culcita novaeguineae* | Cushion star | | | | | | | | | | | | | | | | | | | |
| *Diadema savignyi* | black diadema | | | | | | | | | | | | | | | | | | | |
| *Echinometra mathaei* | purple sea urchin | | 1 | | | | | | | | | 1 | 1 | | 1 | | | | | |
| *Ophiocoma erinaceus* | black brittle star (also white) | | | | | | | | | | 1 | | | | | | | | | |
| **P: Mollusca** | | | | | | | | | | | | | | | | | | | | |
| *Tridacna maximus* | giant clam | | | | | | | | | | | | | | | | | | | |
| unknown | bivalve-clam (all species) | | | | | | | | | | | | | | | | | | | |
| **P: Mollusca; C: Gastropoda** | | | | | | | | | | | | | | | | | | | | |
| *Hexabranchus sanguineus (eggs)* | Spanish dancer egg mass | | | | | | | | | | 1 | | | | | | | | | |
| | snail (all species) | | | | | 1 | | | | | | | | 30 | | | | | | |
| | small crab (all species) 1-2cm | | | | | | | | | | | 2 | 1 | | | | 1 | | | |
| | hermit crab (all species) | | | | | | | | | | | | | | | | | | | |
| **P: Porifera** | | | | | | | | | | | | | | | | | | | | |
| *Haliclona sp. (Haplosclerida Chalinidae)* | purple sponge | | | | | | | | | | | | | | | | | | | |
| **P: Unknown** | | | | | | | | | | | | | | | | | | | | |
| *Gastrolepidia clavigera* | scale worm | | | | | | | | | | | | | | | | | | | |
| | unknown white worm | | | | | | | | | | | | | | | | | | | |
| P: Unknown- egg mass | unknown white egg mass | | | | | | | | | | | | | | | | | | | |
| **Planta** (in % coverage, except H) | | | | | | | | | | | | | | | | | | | | |
| **Green Algae** | | | | | | | | | | | | | | | | | | | | |
| *Caulerpa serrulata* | light green; unknown C | | | | | 1 | | | | | | 10 | | 30 | | 30 | | 5 | | |
| *Halimeda micronesica* | coralline alga; unknown B | | 15 | | 3 | 1 | | 1 | 10 | 15 | 1 | 5 | 2 | 5 | 30 | 10 | 10 | 5 | | |
| *Neomeris annulata* | Caterpillar weed; unknown H | | | | | 1 | | 9 | 1 | 2 | 1 | 1 | 1 | 1 | 3 | 3 | | 3 | | |
| Valonia aegagropila | cluster of small green balls | | | | | | 4 | | | | | 1 | | | | | | | | |
| Valonia ventricosa | Sailor's eyeball | | | | | | | | | | | | | | | | | | | |

| Transect 5 (40m) | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 6 | 1 | 2 |
| species name | description | | | | | | | | | | | | | | | | | | | |
| **Red Algae** | | | | | | | | | | | | | | | | | | | | |
| *Dictyota sp.* | clumpy, brown: unknown A | | 10 | | 1 | | | 1 | 20 | 10 | | 1 | | 25 | 25 | 30 | | | | |
| (possibly) *Lithothamnion prolifer* | coralline red alga; unknown L | | | | | | | | 1 | | 4 | 20 | 5 | | | | 2 | | | |
| **Red and Brown Algae** | | | | | | | | | | | | | | | | | | | | |
| *Padina gymnospora* | Funnelweed | | 1 | | | | | | 20 | 5 | 3 | 30 | 4 | 2 | 5 | | | 5 | | |
| *Sargassum sp.* | seaweed | | | | | | | | | | | | | | | | | | | |
| *Turbinaria sp.* | Turbinweed | | | | | | | | | 10 | | | | | | | | | | |
| unknown red algae | red/brown thick cluster | | | | | | | | | | | | | | | | | | | |
| **Unknown Algae** | | | | | | | | | | | | | | | | | | | | |
| | brown clumpy; unknown D | | 2 | | 1 | 3 | | 4 | 4 | 2 | | | | | 1 | | | | | |
| | green/brown, smooth; E | | | | | | | 1 | 1 | | 10 | | 1 | | | | | | | |
| | green, short, clustery; F | | | | | | | | | | | | | | | | | | | |
| | brown, fuzzy, thin leaf; G | | | | | | | | | | | | | | | | | | | |
| | dark green, 'mossy'; I | | | | | | | | | | | | | | | | | | | |
| | brown/tan, 'mossy'; J | | | | | | | | | | | | | | | | | | | |
| | brown/tan, thick, hairy; K | | | | | | | | | | | | 5 | | | | | | | |
| | orange encrusting algae; M | | | | | | | | | | | 5 | | | | | | | | |
| | pink encrusting algae; M | | | | | | | | | | | 10 | | | | | | | | |
| | red encrusting algae; M | | | 1 | | 2 | | | | | | 2 | 1 | | | | | | | |

Table 5. Species Index - Site 2

| Transect 6 (0m) | 0m-30m beachrock | | | | | | |
|---|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | | 1 | 2 | 3 | 4 | 5 |
| species name | description | | 4m | 8m | 22m | 26m | 28m |
| **Animalia** | | | | | | | |
| **P: Arthropoda; F: Alpheidae** | | | | | | | |
| | gray burrowing shrimp | | | | | | |
| *Nennalpheus sp.* | red burrowing shrimp | | | | | | |
| **P: Chordata; F: Labridae** | | | | | | | |
| *Halichoeres trimaculatus* | Three spot wrasse | | | | | | |
| **P: Chordata; F: Mullidae** | | | | | | | |
| *Parupeneus barberinus* | Dot & dash goatfish | | | | | | |
| **P: Chordata; F: Pinguiedidae** | | | | | | | |
| *Parapercis millepunctata* | Spotted sandperch-white | | | | | | |
| " | Spotted sandperch-gray | | | | | | |
| " | Spotted sandperch-black | | | | | | |
| **P: Chordata; F: Pomacentridae** | | | | | | | |
| unknown | black striped damsel | | | | | | |
| unknown | black damsel | | | | | | |
| unknown | black anemone fish, blue spots | | | | | | |
| **P: Chordata; F: Scorpaenidae** | | | | | | | |
| *Synanceja verrucosa* | Stonefish | | | | | | |
| **P: Chordata; F: Syngnathides** | | | | | | | |
| *Corythoichthys flavofasciatus* | Pipe fish | | | | | | |
| **P: Chordata; F: Tetraodontidae** | | | | | | | |
| *Canthigaster bennetti* | Bennett's sharpnose puffer | | | | | | |
| **P: Chordata; SubP: Urochorda** | | | | | | | |
| unknown | brown tunicate | | | | | | |
| **P: Cnidaria; O: Scleractinia** | | | | | | | |
| *Acropora sp.* | branching; bush-like form | | | | | | |
| *Fungia (cycloseris) costulata* | circular fungia | | | | | | |
| *Herpolitha limax* | elongated, mountain-like fungia | | | | | | |
| *Montipora undata* | plate-like; brown and/or purple | | | | | | |
| *Porites lobata and/or P. lutea* | massive; cream, yellow, brown | | 1 | | | | |
| *Porites solida* | brown or greenish yellow | | | | | | |
| unknown A. | pale cream, massive; 'swirly' | | | | | | |
| unknown B. | lt. yellow, branching; bush-like | | | | | | |
| **P: Cnidaria; O: Stichodactylidae** | | | | | | | |
| *Stichodactyla gigantea* | sea anemone | | | | | | |
| **P: Echinodermata** | | | | | | | |
| *Bohadschia argus* | sea cucumber | | | | | | 1 |
| *Culcita novaeguineae* | Cushion star | | | | | | |
| *Diadema savignyi* | black diadema | | | | | | |
| *Echinometra mathaei* | purple sea urchin | | 1 | 1 | 6 | | 1 |
| *Ophiocoma erinaceus* | black brittle star (also white) | | | | | 1 | |

| **Transect 6 (0m)** | | | | | | |
|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 3 | 4 | 5 |
| species name | description | | | | | |
| **P: Mollusca** | | | | | | |
| *Tridacna maximus* | giant clam | | | | | |
| unknown | bivalve-clam (all species) | | | | | |
| **P: Mollusca; C: Gastropoda** | | | | | | |
| *Hexabranchus sanguineus (eggs)* | Spanish dancer egg mass | | | | | |
| | snail (all species) | 2 | 50 | | | |
| | small crab (all species) 1-2cm | | | | | |
| | hermit crab (all species) | | | | | |
| **P: Porifera** | | | | | | |
| *Haliclona sp. (Haplosclerida Chalinidae)* | purple sponge | | | | 1 | |
| **P: Unknown** | | | | | | |
| *Gastrolepidia clavigera* | scale worm | | | | | |
| | unknown white worm | | | | | |
| P: Unknown- egg mass | unknown white egg mass | | | | | |
| **Planta** (in % coverage, except H) | | | | | | |
| **Green Algae** | | | | | | |
| *Caulerpa serrulata* | light green; unknown C | | | | | |
| *Halimeda micronesica* | coralline alga; unknown B | | 30 | | | |
| *Neomeris annulata* | Caterpillar weed; unknown H | | | | | |
| Valonia aegagropila | cluster of small green balls | | | | | |
| Valonia ventricosa | Sailor's eyeball | | | | | |
| **Red Algae** | | | | | | |
| *Dictyota sp.* | clumpy, brown: unknown A | | | | | |
| (possibly) *Lithothamnion prolifer* | coralline red alga; unknown L | | 5 | 2 | 2 | |
| **Red and Brown Algae** | | | | | | |
| *Padina gymnospora* | Funnelweed | 5 | | | | |
| *Sargassum sp.* | seaweed | | | 10 | | |
| *Turbinaria sp.* | Turbinweed | | | 1 | | |
| unknown red algae | red/brown thick cluster | | | | 4 | |
| **Unknown Algae** | | | | | | |
| | brown clumpy; unknown D | 5 | | | | |
| | green/brown, smooth; E | | | | | |
| | green, short, clustery; F | | | | | |
| | brown, fuzzy, thin leaf; G | | | | | |
| | dark green, 'mossy'; I | | | | | |
| | brown/tan, 'mossy'; J | | | | | |
| | brown/tan, thick, hairy; K | | | | | |
| | orange encrusting algae; M | | | | | |
| | pink encrusting algae; M | | | | | |
| | red encrusting algae; M | 1 | 5 | | | |
| **Substrate Type** (in % coverage) | | | | | | |
| | beachrock | 95 | 98 | 100 | 100 | 100 |
| | rubble | 50 | 75 | 30 | 2 | |
| | sand | 5 | 2 | | | |
| | boat anchor chain | 1 | | | | |

| Transect 7 (10m) | 0m-29m beachrock | | | | | | |
|---|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 3 | 4 | 5 | |
| species name | description | 0m | 6m | 10m | 13m | 24m | |
| **Animalia** | | | | | | | |
| **P: Arthropoda; F: Alpheidae** | | | | | | | |
| | gray burrowing shrimp | | | | | | |
| *Nennalpheus sp.* | red burrowing shrimp | | | | | | |
| **P: Chordata; F: Labridae** | | | | | | | |
| *Halichoeres trimaculatus* | Three spot wrasse | | | | | | |
| **P: Chordata; F: Mullidae** | | | | | | | |
| *Parupeneus barberinus* | Dot & dash goatfish | | | | | | |
| **P: Chordata; F: Pinguiedidae** | | | | | | | |
| *Parapercis millepunctata* | Spotted sandperch-white | | | | | | |
| " | Spotted sandperch-gray | | | | | | |
| " | Spotted sandperch-black | | | | | | |
| **P: Chordata; F: Pomacentridae** | | | | | | | |
| unknown | black striped damsel | | | 1 | | | |
| unknown | black damsel | | | 1 | | | |
| unknown | black anemone fish, blue spots | | | | | | |
| **P: Chordata; F: Scorpaenidae** | | | | | | | |
| *Synanceja verrucosa* | Stonefish | | | | | | |
| **P: Chordata; F: Syngnathides** | | | | | | | |
| *Corythoichthys flavofasciatus* | Pipe fish | 1 | | | | | |
| **P: Chordata; F: Tetraodontidae** | | | | | | | |
| *Canthigaster bennetti* | Bennett's sharpnose puffer | | | | | | |
| **P: Chordata; SubP: Urochorda** | | | | | | | |
| unknown | brown tunicate | | | 2% | | | |
| **P: Cnidaria; O: Scleractinia** | | | | | | | |
| *Acropora sp.* | branching; bush-like form | | | | 1 | | |
| *Fungia (cycloseris) costulata* | circular fungia | | | | | | |
| *Herpolitha limax* | elongated, mountain-like fungia | | | | | | |
| *Montipora undata* | plate-like; brown and/or purple | | | | | | |
| *Porites lobata and/or P. lutea* | massive; cream, yellow, brown | 3 | 1 | | | | |
| *Porites solida* | brown or greenish yellow | | | 1 | | | |
| unknown A. | pale cream, massive; 'swirly' | | | | | | |
| unknown B. | lt. yellow, branching; bush-like | | | | | | |
| **P: Cnidaria; O: Stichodactylidae** | | | | | | | |
| *Stichodactyla gigantea* | sea anemone | | | | | | |
| **P: Echinodermata** | | | | | | | |
| *Bohadschia argus* | sea cucumber | | | | | | |
| *Culcita novaeguineae* | Cushion star | | | | | | |
| *Diadema savignyi* | black diadema | | | | | | |
| *Echinometra mathaei* | purple sea urchin | 3 | 1 | 14 | 12 | 1 | |
| *Ophiocoma erinaceus* | black brittle star (also white) | | | | | | |

| Transect 7 (10m) | | | | | | |
|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 3 | 4 | 5 |
| species name | description | | | | | |
| **P: Mollusca** | | | | | | |
| *Tridacna maximus* | giant clam | | | | | |
| unknown | bivalve-clam (all species) | | | | | 1 |
| **P: Mollusca; C: Gastropoda** | | | | | | |
| *Hexabranchus sanguineus (eggs)* | Spanish dancer egg mass | | | | | |
| | snail (all species) | 1 | 1 | | | |
| | small crab (all species) 1-2cm | | | | | |
| | hermit crab (all species) | | | | | |
| **P: Porifera** | | | | | | |
| *Haliclona sp. (Haplosclerida Chalinidae)* | purple sponge | | | | | |
| **P: Unknown** | | | | | | |
| *Gastrolepidia clavigera* | scale worm | | | | | |
| | unknown white worm | | | | | |
| P: Unknown- egg mass | unknown white egg mass | | | 6 | | |
| **Planta** (in % coverage, except H) | | | | | | |
| **Green Algae** | | | | | | |
| *Caulerpa serrulata* | light green; unknown C | | 10 | | | |
| *Halimeda micronesica* | coralline alga; unknown B | 10 | 25 | 5 | 10 | |
| *Neomeris annulata* | Caterpillar weed; unknown H | | 4 | 7 | 1 | |
| Valonia aegagropila | cluster of small green balls | | | | | |
| Valonia ventricosa | Sailor's eyeball | | | | | |
| **Red Algae** | | | | | | |
| *Dictyota sp.* | clumpy, brown: unknown A | | | | | |
| (possibly) *Lithothamnion prolifer* | coralline red alga; unknown L | | | 15 | 5 | 5 |
| **Red and Brown Algae** | | | | | | |
| *Padina gymnospora* | Funnelweed | 1 | 1 | | | |
| *Sargassum sp.* | seaweed | | | | | |
| *Turbinaria sp.* | Turbinweed | | | | 25 | |
| unknown red algae | red/brown thick cluster | | | 15 | 10 | |
| **Unknown Algae** | | | | | | |
| | brown clumpy; unknown D | | 1 | 10 | | |
| | green/brown, smooth; E | | | | | |
| | green, short, clustery; F | | | | | |
| | brown, fuzzy, thin leaf; G | | | | | |
| | dark green, 'mossy'; I | | | | | |
| | brown/tan, 'mossy'; J | | | | | |
| | brown/tan, thick, hairy; K | | | | | |
| | orange encrusting algae; M | | | 20 | | |
| | pink encrusting algae; M | | | | | |
| | red encrusting algae; M | | 2 | 10 | 10 | |
| **Substrate Type** (in % coverage) | | | | | | |
| | beachrock | 100 | 100 | 95 | 100 | 100 |
| | rubble | | 20 | 2 | 50 | 100 |
| | sand | | | 80 | | |

| Transect 8 (20m) | 0m-23m beachrock | | | | | | |
|---|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 3 | 4 | 5 |
| species name | description | 0m | 3m | 7m | 10m | 22m |
| **Animalia** | | | | | | |
| **P: Arthropoda; F: Alpheidae** | | | | | | |
| | gray burrowing shrimp | | | | | |
| *Nennalpheus sp.* | red burrowing shrimp | | | | 1 | |
| **P: Chordata; F: Labridae** | | | | | | |
| *Halichoeres trimaculatus* | Three spot wrasse | | | | | |
| **P: Chordata; F: Mullidae** | | | | | | |
| *Parupeneus barberinus* | Dot & dash goatfish | | | | | |
| **P: Chordata; F: Pinguiedidae** | | | | | | |
| *Parapercis millepunctata* | Spotted sandperch-white | | | | | |
| " | Spotted sandperch-gray | | | | | |
| " | Spotted sandperch-black | | | | | |
| **P: Chordata; F: Pomacentridae** | | | | | | |
| unknown | black striped damsel | | | | | |
| unknown | black damsel | | | | | |
| unknown | black anemone fish, blue spots | | | | | |
| **P: Chordata; F: Scorpaenidae** | | | | | | |
| *Synanceja verrucosa* | Stonefish | | | | | |
| **P: Chordata; F: Syngnathides** | | | | | | |
| *Corythoichthys flavofasciatus* | Pipe fish | | | | | |
| **P: Chordata; F: Tetraodontidae** | | | | | | |
| *Canthigaster bennetti* | Bennett's sharpnose puffer | | | | | |
| **P: Chordata; SubP: Urochorda** | | | | | | |
| unknown | brown tunicate | 50% | 15% | | 1% | |
| **P: Cnidaria; O: Scleractinia** | | | | | | |
| *Acropora sp.* | branching; bush-like form | | | | | |
| *Fungia (cycloseris) costulata* | circular fungia | | | | | |
| *Herpolitha limax* | elongated, mountain-like fungia | | | | | |
| *Montipora undata* | plate-like; brown and/or purple | | | | | |
| *Pontes lobata and/or P. lutea* | massive; cream, yellow, brown | 1 | 1 | 1 | | |
| *Porites solida* | brown or greenish yellow | | | 1 | 1 | |
| unknown A. | pale cream, massive; 'swirly' | | | | | |
| unknown B. | lt. yellow, branching; bush-like | | | | | |
| **P: Cnidaria; O: Stichodactylidae** | | | | | | |
| *Stichodactyla gigantea* | sea anemone | | | | | |
| **P: Echinodermata** | | | | | | |
| *Bohadschia argus* | sea cucumber | | | | | |
| *Culcita novaeguineae* | Cushion star | | | | | |
| *Diadema savignyi* | black diadema | | | | | |
| *Echinometra mathaei* | purple sea urchin | 1 | 1 | 3 | | |
| *Ophiocoma erinaceus* | black brittle star (also white) | | | | | |

| **Transect 8 (20m)** | | | | | | |
|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 3 | 4 | 5 |
| species name | description | | | | | |
| **P: Mollusca** | | | | | | |
| *Tridacna maximus* | giant clam | | | | | |
| unknown | bivalve-clam (all species) | | | | | 2 |
| **P: Mollusca; C: Gastropoda** | | | | | | |
| *Hexabranchus sanguineus (eggs)* | Spanish dancer egg mass | | | | | |
| | snail (all species) | | | | | |
| | small crab (all species) 1-2cm | | | | 1 | 1 |
| | hermit crab (all species) | | | | | |
| **P: Porifera** | | | | | | |
| *Haliclona sp. (Haplosclerida Chalinidae)* | purple sponge | | | | | |
| **P: Unknown** | | | | | | |
| *Gastrolepidia clavigera* | scale worm | | | | | |
| | unknown white worm | | | | | |
| P: Unknown- egg mass | unknown white egg mass | | | | | |
| **Planta** (in % coverage, except H) | | | | | | |
| **Green Algae** | | | | | | |
| *Caulerpa serrulata* | light green; unknown C | | | | | |
| *Halimeda micronesica* | coralline alga; unknown B | 20 | 1 | | 2 | |
| *Neomeris annulata* | Caterpillar weed; unknown H | | | 2 | 3 | |
| Valonia aegagropila | cluster of small green balls | | | | | |
| Valonia ventricosa | Sailor's eyeball | | | | | |
| **Red Algae** | | | | | | |
| *Dictyota sp.* | clumpy, brown: unknown A | | | | | |
| (possibly) *Lithothamnion prolifer* | coralline red alga; unknown L | | 2 | 5 | 5 | |
| **Red and Brown Algae** | | | | | | |
| *Padina gymnospora* | Funnelweed | | | 1 | | |
| *Sargassum sp.* | seaweed | | | | | |
| *Turbinaria sp.* | Turbinweed | | | | | |
| unknown red algae | red/brown thick cluster | | | | 10 | |
| **Unknown Algae** | | | | | | |
| | brown clumpy; unknown D | | 2 | 5 | 2 | |
| | green/brown, smooth; E | | | | | |
| | green, short, clustery; F | | | | | |
| | brown, fuzzy, thin leaf; G | | | | | |
| | dark green, 'mossy'; I | | | | | |
| | brown/tan, 'mossy'; J | | | | | |
| | brown/tan, thick, hairy; K | | | | | |
| | orange encrusting algae; M | 1 | | | | |
| | pink encrusting algae; M | | | | | |
| | red encrusting algae; M | | | | 2 | |
| **Substrate Type** (in % coverage) | | | | | | |
| | beachrock | 100 | 60 | 80 | 70 | 70 |
| | rubble | | 40 | 20 | | 40 |
| | sand | | 10 | 10 | 30 | |

| Transect 9 (30m) | 0m-20.2m beachrock | | | | | |
|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 3 | 4 | 5 |
| species name | description | 5m | 8m | 17m | 18m | 19m |
| **Animalia** | | | | | | |
| **P: Arthropoda; F: Alpheidae** | | | | | | |
| | gray burrowing shrimp | | | | | |
| *Nennalpheus sp.* | red burrowing shrimp | 2 | | | | |
| **P: Chordata; F: Labridae** | | | | | | |
| *Halichoeres trimaculatus* | Three spot wrasse | | | | | |
| **P: Chordata; F: Mullidae** | | | | | | |
| *Parupeneus barberinus* | Dot & dash goatfish | | | | | |
| **P: Chordata; F: Pinguiedidae** | | | | | | |
| *Parapercis millepunctata* | Spotted sandperch-white | | | | | |
| " | Spotted sandperch-gray | | | | | |
| " | Spotted sandperch-black | | | | | |
| **P: Chordata; F: Pomacentridae** | | | | | | |
| unknown | black striped damsel | | | | | |
| unknown | black damsel | | | | | |
| unknown | black anemone fish, blue spots | | | | | |
| **P: Chordata; F: Scorpaenidae** | | | | | | |
| *Synanceja verrucosa* | Stonefish | | 1 | | | |
| **P: Chordata; F: Syngnathides** | | | | | | |
| *Corythoichthys flavofasciatus* | Pipe fish | | | | | |
| **P: Chordata; F: Tetraodontidae** | | | | | | |
| *Canthigaster bennetti* | Bennett's sharpnose puffer | | | | | |
| **P: Chordata; SubP: Urochorda** | | | | | | |
| unknown | brown tunicate | 35% | | | | |
| **P: Cnidaria; O: Scleractinia** | | | | | | |
| *Acropora sp.* | branching; bush-like form | | | | | |
| *Fungia (cycloseris) costulata* | circular fungia | | | | | |
| *Herpolitha limax* | elongated, mountain-like fungia | | | | | |
| *Montipora undata* | plate-like; brown and/or purple | | | | | |
| *Porites lobata and/or P. lutea* | massive; cream, yellow, brown | 1 | 1 | | | |
| *Porites solida* | brown or greenish yellow | | | | | |
| unknown A. | pale cream, massive; 'swirly' | | | | | |
| unknown B. | lt. yellow, branching; bush-like | | | | | |
| **P: Cnidaria; O: Stichodactylidae** | | | | | | |
| *Stichodactyla gigantea* | sea anemone | | | | | |
| **P: Echinodermata** | | | | | | |
| *Bohadschia argus* | sea cucumber | | | | | |
| *Culcita novaeguineae* | Cushion star | | | | | |
| *Diadema savignyi* | black diadema | | | | | |
| *Echinometra mathaei* | purple sea urchin | 10 | | | 1 | |
| *Ophiocoma erinaceus* | black brittle star (also white) | | | | | |

| Transect 9 (30m) | | | | | | |
|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 3 | 4 | 5 |
| species name | description | | | | | |
| **P: Mollusca** | | | | | | |
| *Tridacna maximus* | giant clam | | | | | |
| unknown | bivalve-clam (all species) | | | | | |
| **P: Mollusca; C: Gastropoda** | | | | | | |
| *Hexabranchus sanguineus (eggs)* | Spanish dancer egg mass | | | | | |
| | snail (all species) | | 1 | | | 70 |
| | small crab (all species) 1-2cm | | | | | |
| | hermit crab (all species) | | | | | 1 |
| **P: Porifera** | | | | | | |
| *Haliclona sp. (Haplosclerida Chalinidae)* | purple sponge | | | | | |
| **P: Unknown** | | | | | | |
| *Gastrolepidia clavigera* | scale worm | | | | | |
| | unknown white worm | | | | | |
| P: Unknown- egg mass | unknown white egg mass | | 1 | | | |
| **Planta** (in % coverage, except H) | | | | | | |
| **Green Algae** | | | | | | |
| *Caulerpa serrulata* | light green; unknown C | 4 | 1 | | | |
| *Halimeda micronesica* | coralline alga; unknown B | 5 | 5 | | | |
| *Neomeris annulata* | Caterpillar weed; unknown H | 26 | 10 | 2 | | |
| Valonia aegagropila | cluster of small green balls | | | | | |
| Valonia ventricosa | Sailor's eyeball | | | | | |
| **Red Algae** | | | | | | |
| *Dictyota sp.* | clumpy, brown: unknown A | | | | | |
| (possibly) *Lithothamnion prolifer* | coralline red alga; unknown L | 5 | 10 | | | |
| **Red and Brown Algae** | | | | | | |
| *Padina gymnospora* | Funnelweed | 1 | | 2 | | |
| *Sargassum sp.* | seaweed | | | | | |
| *Turbinaria sp.* | Turbinweed | | | | | |
| unknown red algae | red/brown thick cluster | | | 3 | | |
| **Unknown Algae** | | | | | | |
| | brown clumpy; unknown D | 2 | 5 | | | |
| | green/brown, smooth; E | | | | | |
| | green, short, clustery; F | | | | | |
| | brown, fuzzy, thin leaf; G | | | | | |
| | dark green, 'mossy'; I | | | | | |
| | brown/tan, 'mossy'; J | | | | | |
| | brown/tan, thick, hairy; K | | | | | |
| | orange encrusting algae; M | 5 | | | | |
| | pink encrusting algae; M | | | | | |
| | red encrusting algae; M | 1 | | | | |
| **Substrate Type** (in % coverage) | | | | | | |
| | beachrock | 90 | 80 | 100 | 100 | |
| | rubble | 50 | | 40 | 10 | 100 |
| | sand | 10 | 20 | | | |

| Transect 10 (40m) | 0m-17m beachrock | | | | | | |
|---|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 3 | 4 | 5 |
| species name | description | 3m | 5m | 6m | 9m | 16m |
| **Animalia** | | | | | | |
| **P: Arthropoda; F: Alpheidae** | | | | | | |
| | gray burrowing shrimp | | | | | |
| *Nennalpheus sp.* | red burrowing shrimp | | | | | |
| **P: Chordata; F: Labridae** | | | | | | |
| *Halichoeres trimaculatus* | Three spot wrasse | | | | | |
| **P: Chordata; F: Mullidae** | | | | | | |
| *Parupeneus barberinus* | Dot & dash goatfish | | | | | |
| **P: Chordata; F: Pinguiedidae** | | | | | | |
| *Parapercis millepunctata* | Spotted sandperch-white | | | | | |
| " | Spotted sandperch-gray | | | | | |
| " | Spotted sandperch-black | | | | | |
| **P: Chordata; F: Pomacentridae** | | | | | | |
| unknown | black striped damsel | | | | | |
| unknown | black damsel | | | | | |
| unknown | black anemone fish, blue spots | | | | | |
| **P: Chordata; F: Scorpaenidae** | | | | | | |
| *Synanceja verrucosa* | Stonefish | | | | | |
| **P: Chordata; F: Syngnathides** | | | | | | |
| *Corythoichthys flavofasciatus* | Pipe fish | | | | | |
| **P: Chordata; F: Tetraodontidae** | | | | | | |
| *Canthigaster bennetti* | Bennett's sharpnose puffer | | | | | |
| **P: Chordata; SubP: Urochorda** | | | | | | |
| unknown | brown tunicate | 20% | | | 1% | |
| **P: Cnidaria; O: Scleractinia** | | | | | | |
| *Acropora sp.* | branching; bush-like form | | | | | |
| *Fungia (cyclosenis) costulata* | circular fungia | | | | | |
| *Herpolitha limax* | elongated, mountain-like fungia | | | | | |
| *Montipora undata* | plate-like; brown and/or purple | | | | | |
| *Porites lobata and/or P. lutea* | massive; cream, yellow, brown | | | | | |
| *Porites solida* | brown or greenish yellow | | | | | |
| unknown A. | pale cream, massive; 'swirly' | | | | | |
| unknown B. | lt. yellow, branching; bush-like | | | | | |
| **P: Cnidaria; O: Stichodactylidae** | | | | | | |
| *Stichodactyla gigantea* | sea anemone | | | | | |
| **P: Echinodermata** | | | | | | |
| *Bohadschia argus* | sea cucumber | | | | | |
| *Culcita novaeguineae* | Cushion star | | | | | |
| *Diadema savignyi* | black diadema | | | | | |
| *Echinometra mathaei* | purple sea urchin | | 3 | 3 | 1 | |
| *Ophiocoma erinaceus* | black brittle star (also white) | | | | | |

| Transect 10 (40m) | | | | | | |
|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 3 | 4 | 5 |
| species name | description | | | | | |
| **P: Mollusca** | | | | | | |
| *Tridacna maximus* | giant clam | | | | | |
| unknown | bivalve-clam (all species) | | | | | 4 |
| **P: Mollusca; C: Gastropoda** | | | | | | |
| *Hexabranchus sanguineus (eggs)* | Spanish dancer egg mass | | | | | |
| | snail (all species) | | | 1 | | 2 |
| | small crab (all species) 1-2cm | | | | | |
| | hermit crab (all species) | | | | | 1 |
| **P: Porifera** | | | | | | |
| *Haliclona sp. (Haplosclerida Chalinidae)* | purple sponge | | | | | |
| **P: Unknown** | | | | | | |
| *Gastrolepidia clavigera* | scale worm | | | | | |
| | unknown white worm | | | | | |
| P: Unknown- egg mass | unknown white egg mass | | | | | |
| **Planta** (in % coverage, except H) | | | | | | |
| **Green Algae** | | | | | | |
| *Caulerpa serrulata* | light green; unknown C | 7 | | | | |
| *Halimeda micronesica* | coralline alga; unknown B | | | | | |
| *Neomeris annulata* | Caterpillar weed; unknown H | 2 | 6 | 5 | | |
| Valonia aegagropila | cluster of small green balls | | | | | |
| Valonia ventricosa | Sailor's eyeball | | | | | |
| **Red Algae** | | | | | | |
| *Dictyota sp.* | clumpy, brown: unknown A | | | | | |
| (possibly) *Lithothamnion prolifer* | coralline red alga; unknown L | 5 | | | 2 | |
| **Red and Brown Algae** | | | | | | |
| *Padina gymnospora* | Funnelweed | 5 | | | | |
| *Sargassum sp.* | seaweed | | | | | |
| *Turbinaria sp.* | Turbinweed | | | | | |
| unknown red algae | red/brown thick cluster | 4 | 20 | 20 | 10 | |
| **Unknown Algae** | | | | | | |
| | brown clumpy; unknown D | 4 | 4 | 1 | 1 | |
| | green/brown, smooth; E | | | | | |
| | green, short, clustery; F | | | | | |
| | brown, fuzzy, thin leaf; G | | | | | |
| | dark green, 'mossy'; I | | | | | |
| | brown/tan, 'mossy'; J | | | | | |
| | brown/tan, thick, hairy; K | | | | | |
| | orange encrusting algae; M | | | | | |
| | pink encrusting algae; M | | | | | |
| | red encrusting algae; M | | 2 | 5 | 5 | |
| **Substrate Type** (in % coverage) | | | | | | |
| | beachrock | 90 | 100 | 100 | 100 | 100 |
| | rubble | | | | | |
| | sand | 50 | 3 | | | |

Table 6. Species Index - Site 3

| Transect 11 (0m) | 0m-16.3m beachrock/sand | | | | | |
|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 3 | 4 | 5 |
| species name | description | 2m | 5m | 8m | 13m | 14m |
| **Animalia** | | | | | | |
| **P: Arthropoda; F: Alpheidae** | | | | | | |
| | gray burrowing shrimp | | | | | |
| *Nennalpheus sp.* | red burrowing shrimp | | | | | |
| **P: Chordata; F: Labridae** | | | | | | |
| *Halichoeres trimaculatus* | Three spot wrasse | | | | | |
| **P: Chordata; F: Mullidae** | | | | | | |
| *Parupeneus barberinus* | Dot & dash goatfish | | | | | |
| **P: Chordata; F: Pinguiedidae** | | | | | | |
| *Parapercis millepunctata* | Spotted sandperch-white | | | | | |
| " | Spotted sandperch-gray | | | | | |
| " | Spotted sandperch-black | | | | | |
| **P: Chordata; F: Pomacentridae** | | | | | | |
| unknown | black striped damsel | | | | | |
| unknown | black damsel | | | | | |
| unknown | black anemone fish, blue spots | | | | | |
| **P: Chordata; F: Scorpaenidae** | | | | | | |
| *Synanceja verrucosa* | Stonefish | | | | | |
| **P: Chordata; F: Syngnathides** | | | | | | |
| *Corythoichthys flavofasciatus* | Pipe fish | | | | | |
| **P: Chordata; F: Tetraodontidae** | | | | | | |
| *Canthigaster bennetti* | Bennett's sharpnose puffer | | | | | |
| **P: Chordata; SubP: Urochorda** | | | | | | |
| unknown | brown tunicate | | 2% | | | |
| **P: Cnidaria; O: Scleractinia** | | | | | | |
| *Acropora sp.* | branching; bush-like form | | | | | |
| *Fungia (cycloseris) costulata* | circular fungia | | | | | |
| *Herpolitha limax* | elongated, mountain-like fungia | | | | | |
| *Montipora undata* | plate-like; brown and/or purple | | | | | |
| *Pontes lobata and/or P. lutea* | massive; cream, yellow, brown | 1 | | | | |
| *Porites solida* | brown or greenish yellow | | 1 | 1 | | |
| unknown A. | pale cream, massive; 'swirly' | | | | | |
| unknown B. | lt. yellow, branching; bush-like | | | | | |
| **P: Cnidaria; O: Stichodactylidae** | | | | | | |
| *Stichodactyla gigantea* | sea anemone | | | | | |
| **P: Echinodermata** | | | | | | |
| *Bohadschia argus* | sea cucumber | | | | | |
| *Culcita novaeguineae* | Cushion star | | | | | |
| *Diadema savignyi* | black diadema | | | | | |
| *Echinometra mathaei* | purple sea urchin | | | 9 | 1 | |
| *Ophiocoma erinaceus* | black brittle star (also white) | | | | 1 | |

| **Transect 11 (0m)** | | | | | | |
|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 3 | 4 | 5 |
| species name | description | | | | | |
| **P: Mollusca** | | | | | | |
| *Tridacna maximus* | giant clam | | | | | |
| unknown | bivalve-clam (all species) | | | | 30 | 2 |
| **P: Mollusca; C: Gastropoda** | | | | | | |
| *Hexabranchus sanguineus (eggs)* | Spanish dancer egg mass | | | | | |
| | snail (all species) | | | | | |
| | small crab (all species) 1-2cm | | 1 | 1 | | |
| | hermit crab (all species) | | | | 1 | |
| **P: Porifera** | | | | | | |
| *Haliclona sp. (Haplosclerida Chalinidae)* | purple sponge | | | 1 | 1 | |
| **P: Unknown** | | | | | | |
| *Gastrolepidia clavigera* | scale worm | | | | | |
| | unknown white worm | | | | | |
| P: Unknown- egg mass | unknown white egg mass | | | | | |
| **Planta** (in % coverage, except H) | | | | | | |
| **Green Algae** | | | | | | |
| *Caulerpa serrulata* | light green; unknown C | 3 | | 2 | | |
| *Halimeda micronesica* | coralline alga; unknown B | 5 | 10 | 15 | | |
| *Neomeris annulata* | Caterpillar weed; unknown H | | 10 | 2 | 1 | |
| Valonia aegagropila | cluster of small green balls | | | | | |
| Valonia ventricosa | Sailor's eyeball | | | 1 | | |
| **Red Algae** | | | | | | |
| *Dictyota sp.* | clumpy, brown: unknown A | | | 4 | | |
| (possibly) *Lithothamnion prolifer* | coralline red alga; unknown L | 2 | 4 | 5 | | |
| **Red and Brown Algae** | | | | | | |
| *Padina gymnospora* | Funnelweed | 10 | 1 | 2 | | 1 |
| *Sargassum sp.* | seaweed | | | | | |
| *Turbinaria sp.* | Turbinweed | | | | | |
| unknown red algae | red/brown thick cluster | | 2 | 15 | 5 | |
| **Unknown Algae** | | | | | | |
| | brown clumpy; unknown D | | 4 | | | |
| | green/brown, smooth; E | | | | | |
| | green, short, clustery; F | | | 7 | | |
| | brown, fuzzy, thin leaf; G | | | | | |
| | dark green, 'mossy'; I | | | | | |
| | brown/tan, 'mossy'; J | | | | | |
| | brown/tan, thick, hairy; K | | | | | |
| | orange encrusting algae; M | | | 1 | | |
| | pink encrusting algae; M | | | | | |
| | red encrusting algae; M | 1 | | | | |
| **Substrate Type** (in % coverage) | | | | | | |
| | beachrock | 35 | 90 | 100 | 80 | 100 |
| | rubble | 10 | 20 | | 40 | 10 |
| | sand | 60 | 10 | 3 | 5 | 5 |

| Transect 12 (10m) | 0m-17.6m beachrock/sand | | | | | |
|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 3 | 4 | 5 |
| species name | description | 5m | 8m | 10m | 12m | 13m |
| **Animalia** | | | | | | |
| **P: Arthropoda; F: Alpheidae** | | | | | | |
| | gray burrowing shrimp | | | | | |
| *Nennalpheus sp.* | red burrowing shrimp | | | | | |
| **P: Chordata; F: Labridae** | | | | | | |
| *Halichoeres trimaculatus* | Three spot wrasse | | | | | |
| **P: Chordata; F: Mullidae** | | | | | | |
| *Parupeneus barberinus* | Dot & dash goatfish | | | | | |
| **P: Chordata; F: Pinguiedidae** | | | | | | |
| *Parapercis millepunctata* | Spotted sandperch-white | | | | | |
| " | Spotted sandperch-gray | | | | | |
| " | Spotted sandperch-black | | | | | |
| **P: Chordata; F: Pomacentridae** | | | | | | |
| unknown | black striped damsel | | | | | |
| unknown | black damsel | | | | | |
| unknown | black anemone fish, blue spots | | | | | |
| **P: Chordata; F: Scorpaenidae** | | | | | | |
| *Synanceja verrucosa* | Stonefish | | | | | |
| **P: Chordata; F: Syngnathides** | | | | | | |
| *Corythoichthys flavofasciatus* | Pipe fish | | | | | |
| **P: Chordata; F: Tetraodontidae** | | | | | | |
| *Canthigaster bennetti* | Bennett's sharpnose puffer | | | | | |
| **P: Chordata; SubP: Urochorda** | | | | | | |
| unknown | brown tunicate | 5% | | | | |
| **P: Cnidaria; O: Scleractinia** | | | | | | |
| *Acropora sp.* | branching; bush-like form | | | | | |
| *Fungia (cycloseris) costulata* | circular fungia | | | | | |
| *Herpolitha limax* | elongated, mountain-like fungia | | | | | |
| *Montipora undata* | plate-like; brown and/or purple | | | | | |
| *Porites lobata and/or P. lutea* | massive; cream, yellow, brown | 2 | | | | |
| *Pontes solida* | brown or greenish yellow | | 1 | | | |
| unknown A. | pale cream, massive; 'swirly' | | | | | |
| unknown B. | lt. yellow, branching; bush-like | | | | | |
| **P: Cnidaria; O: Stichodactylidae** | | | | | | |
| *Stichodactyla gigantea* | sea anemone | | | | | |
| **P: Echinodermata** | | | | | | |
| *Bohadschia argus* | sea cucumber | | | | | |
| *Culcita novaeguineae* | Cushion star | | | | | |
| *Diadema savignyi* | black diadema | | | | | |
| *Echinometra mathaei* | purple sea urchin | 3 | 7 | 6 | 11 | 2 |
| *Ophiocoma erinaceus* | black brittle star (also white) | | | | | |

| **Transect 12 (10m)** | | | | | | |
|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 3 | 4 | 5 |
| species name | description | | | | | |
| **P: Mollusca** | | | | | | |
| *Tridacna maximus* | giant clam | | | | | |
| unknown | bivalve-clam (all species) | | | | 22 | |
| **P: Mollusca; C: Gastropoda** | | | | | | |
| *Hexabranchus sanguineus (eggs)* | Spanish dancer egg mass | | | | | |
| | snail (all species) | | 50 | | 1 | |
| | small crab (all species) 1-2cm | | | | | |
| | hermit crab (all species) | | | 1 | | |
| **P: Porifera** | | | | | | |
| *Haliclona sp. (Haplosclerida Chalinidae)* | purple sponge | | | | | |
| **P: Unknown** | | | | | | |
| *Gastrolepidia clavigera* | scale worm | | | | | |
| | unknown white worm | | | | | |
| P: Unknown- egg mass | unknown white egg mass | | | | | |
| **Planta** (in % coverage, except H) | | | | | | |
| **Green Algae** | | | | | | |
| *Caulerpa serrulata* | light green; unknown C | | | | | |
| *Halimeda micronesica* | coralline alga; unknown B | 25 | 10 | 2 | 2 | |
| *Neomeris annulata* | Caterpillar weed; unknown H | 25 | 5 | | | 7 |
| Valonia aegagropila | cluster of small green balls | | | | | |
| Valonia ventricosa | Sailor's eyeball | | 1 | | | |
| **Red Algae** | | | | | | |
| *Dictyota sp.* | clumpy, brown: unknown A | | | | | |
| (possibly) *Lithothamnion prolifer* | coralline red alga; unknown L | | 10 | | | |
| **Red and Brown Algae** | | | | | | |
| *Padina gymnospora* | Funnelweed | | | | | |
| *Sargassum sp.* | seaweed | | | | | |
| *Turbinaria sp.* | Turbinweed | | | | | |
| unknown red algae | red/brown thick cluster | 10 | 10 | 2 | | |
| **Unknown Algae** | | | | | | |
| | brown clumpy; unknown D | | 2 | | | |
| | green/brown, smooth; E | | | | | |
| | green, short, clustery; F | | | | | |
| | brown, fuzzy, thin leaf; G | | | | | |
| | dark green, 'mossy'; I | | | | | |
| | brown/tan, 'mossy'; J | | | | | |
| | brown/tan, thick, hairy; K | | | | | |
| | orange encrusting algae; M | | | | | |
| | pink encrusting algae; M | | | | | |
| | red encrusting algae; M | | 2 | | 1 | |
| **Substrate Type** (in % coverage) | | | | | | |
| | beachrock | 30 | 40 | 95 | 60 | 100 |
| | rubble | | 60 | 5 | | |
| | sand | 40 | 60 | 5 | 10 | 10 |

| Transect 13 (20m) | 0m-16.5m beachrock/sand | | | | | |
|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 3 | 4 | 5 |
| species name | description | 0m | 3m | 5m | 6m | 8m |
| **Animalia** | | | | | | |
| **P: Arthropoda; F: Alpheidae** | | | | | | |
| | gray burrowing shrimp | | | | | |
| *Nennalpheus sp.* | red burrowing shrimp | | | | | |
| **P: Chordata; F: Labridae** | | | | | | |
| *Halichoeres trimaculatus* | Three spot wrasse | | | | | |
| **P: Chordata; F: Mullidae** | | | | | | |
| *Parupeneus barberinus* | Dot & dash goatfish | | | | | |
| **P: Chordata; F: Pinguiedidae** | | | | | | |
| *Parapercis millepunctata* | Spotted sandperch-white | | | | | |
| " | Spotted sandperch-gray | | | | | |
| " | Spotted sandperch-black | | | | | |
| **P: Chordata; F: Pomacentridae** | | | | | | |
| unknown | black striped damsel | | | | | |
| unknown | black damsel | | | | | |
| unknown | black anemone fish, blue spots | | | | | |
| **P: Chordata; F: Scorpaenidae** | | | | | | |
| *Synanceja verrucosa* | Stonefish | | | | | |
| **P: Chordata; F: Syngnathides** | | | | | | |
| *Corythoichthys flavofasciatus* | Pipe fish | | | | | |
| **P: Chordata; F: Tetraodontidae** | | | | | | |
| *Canthigaster bennetti* | Bennett's sharpnose puffer | | | | | |
| **P: Chordata; SubP: Urochorda** | | | | | | |
| unknown | brown tunicate | 5% | | | 15% | |
| **P: Cnidaria; O: Scleractinia** | | | | | | |
| *Acropora sp.* | branching; bush-like form | | | | | |
| *Fungia (cycloseris) costulata* | circular fungia | | | | | |
| *Herpolitha limax* | elongated, mountain-like fungia | | | | | |
| *Montipora undata* | plate-like; brown and/or purple | | | | | |
| *Porites lobata and/or P. lutea* | massive; cream, yellow, brown | | 1 | | 2 | |
| *Porites solida* | brown or greenish yellow | 1 | | 1 | 1 | |
| unknown A. | pale cream, massive; 'swirly' | | | | 1 | |
| unknown B. | lt. yellow, branching; bush-like | | | | | |
| **P: Cnidaria; O: Stichodactylidae** | | | | | | |
| *Stichodactyla gigantea* | sea anemone | | | | | |
| **P: Echinodermata** | | | | | | |
| *Bohadschia argus* | sea cucumber | | | | | |
| *Culcita novaeguineae* | Cushion star | | | | | |
| *Diadema savignyi* | black diadema | | | | | |
| *Echinometra mathaei* | purple sea urchin | 2 | 6 | 1 | 7 | 9 |
| *Ophiocoma erinaceus* | black brittle star (also white) | | | | | |

| Transect 13 (20m) | | | | | | |
|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 3 | 4 | 5 |
| species name | description | | | | | |
| **P: Mollusca** | | | | | | |
| *Tridacna maximus* | giant clam | | | | | |
| unknown | bivalve-clam (all species) | | | 2 | | |
| **P: Mollusca; C: Gastropoda** | | | | | | |
| *Hexabranchus sanguineus (eggs)* | Spanish dancer egg mass | | | | | |
| | snail (all species) | | | 2 | | |
| | small crab (all species) 1-2cm | | | 1 | | |
| | hermit crab (all species) | | | | | 1 |
| **P: Porifera** | | | | | | |
| *Haliclona sp. (Haplosclerida Chalinidae)* | purple sponge | | | | | |
| **P: Unknown** | | | | | | |
| *Gastrolepidia clavigera* | scale worm | 1 | | | | |
| | unknown white worm | | | | | |
| P: Unknown- egg mass | unknown white egg mass | | | | | |
| **Planta** (in % coverage, except H) | | | | | | |
| **Green Algae** | | | | | | |
| *Caulerpa serrulata* | light green; unknown C | | | | | |
| *Halimeda micronesica* | coralline alga; unknown B | 10 | 20 | 2 | 5 | 4 |
| *Neomeris annulata* | Caterpillar weed; unknown H | 1 | | 15 | 4 | 16 |
| Valonia aegagropila | cluster of small green balls | | | | | |
| Valonia ventricosa | Sailor's eyeball | | | | | |
| **Red Algae** | | | | | | |
| *Dictyota sp.* | clumpy, brown: unknown A | | | | | |
| (possibly) *Lithothamnion prolifer* | coralline red alga; unknown L | | 5 | 3 | 5 | 10 |
| **Red and Brown Algae** | | | | | | |
| *Padina gymnospora* | Funnelweed | | 2 | | | |
| *Sargassum sp.* | seaweed | | | | | |
| *Turbinaria sp.* | Turbinweed | | | | | |
| unknown red algae | red/brown thick cluster | | | 5 | 5 | 10 |
| **Unknown Algae** | | | | | | |
| | brown clumpy; unknown D | | | 2 | 5 | 4 |
| | green/brown, smooth; E | | | | | |
| | green, short, clustery; F | | | | | |
| | brown, fuzzy, thin leaf; G | | | | | |
| | dark green, 'mossy'; I | | | | | |
| | brown/tan, 'mossy'; J | | | | | |
| | brown/tan, thick, hairy; K | | | | | |
| | orange encrusting algae; M | 5 | 4 | 3 | | |
| | pink encrusting algae; M | | | | | |
| | red encrusting algae; M | 2 | 1 | 5 | 5 | 5 |
| **Substrate Type** (in % coverage) | | | | | | |
| | beachrock | 70 | 40 | 60 | 100 | 90 |
| | rubble | | | 40 | | |
| | sand | 30 | 60 | 20 | 2 | 10 |

| Transect 14 (30m) | 0m-20m beachrock/sand | | | | | |
|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 3 | 4 | 5 |
| species name | description | 6m | 8m | 13m | 17m | 18m |
| **Animalia** | | | | | | |
| **P: Arthropoda; F: Alpheidae** | | | | | | |
| | gray burrowing shrimp | | | | | |
| *Nennalpheus sp.* | red burrowing shrimp | | | | | |
| **P: Chordata; F: Labridae** | | | | | | |
| *Halichoeres trimaculatus* | Three spot wrasse | | | | | |
| **P: Chordata; F: Mullidae** | | | | | | |
| *Parupeneus barberinus* | Dot & dash goatfish | | | | | |
| **P: Chordata; F: Pinguiedidae** | | | | | | |
| *Parapercis millepunctata* | Spotted sandperch-white | | | | | |
| " | Spotted sandperch-gray | | | | | |
| " | Spotted sandperch-black | | | 1 | | |
| **P: Chordata; F: Pomacentridae** | | | | | | |
| unknown | black striped damsel | | | | | |
| unknown | black damsel | | | | | |
| unknown | black anemone fish, blue spots | | | | | |
| **P: Chordata; F: Scorpaenidae** | | | | | | |
| *Synanceja verrucosa* | Stonefish | | | | | |
| **P: Chordata; F: Syngnathides** | | | | | | |
| *Corythoichthys flavofasciatus* | Pipe fish | | | | | |
| **P: Chordata; F: Tetraodontidae** | | | | | | |
| *Canthigaster bennetti* | Bennett's sharpnose puffer | | | | | |
| **P: Chordata; SubP: Urochorda** | | | | | | |
| unknown | brown tunicate | 25% | | | | |
| **P: Cnidaria; O: Scleractinia** | | | | | | |
| *Acropora sp.* | branching; bush-like form | | | | | |
| *Fungia (cycloseris) costulata* | circular fungia | | | | | |
| *Herpolitha limax* | elongated, mountain-like fungia | | | | | |
| *Montipora undata* | plate-like; brown and/or purple | | | | | |
| *Porites lobata and/or P. lutea* | massive; cream, yellow, brown | 1 | | | | |
| *Porites solida* | brown or greenish yellow | | | | | |
| unknown A. | pale cream, massive; 'swirly' | | | | | |
| unknown B. | lt. yellow, branching; bush-like | | | | | |
| **P: Cnidaria; O: Stichodactylidae** | | | | | | |
| *Stichodactyla gigantea* | sea anemone | | | | | |
| **P: Echinodermata** | | | | | | |
| *Bohadschia argus* | sea cucumber | | | | | |
| *Culcita novaeguineae* | Cushion star | | | | | |
| *Diadema savignyi* | black diadema | | | | | |
| *Echinometra mathaei* | purple sea urchin | | 1 | 8 | 1 | |
| *Ophiocoma erinaceus* | black brittle star (also white) | | | | | |

| Transect 14 (30m) | | | | | | |
|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 3 | 4 | 5 |
| species name | description | | | | | |
| **P: Mollusca** | | | | | | |
| *Tridacna maximus* | giant clam | | | | | |
| unknown | bivalve-clam (all species) | | | | | |
| **P: Mollusca; C: Gastropoda** | | | | | | |
| *Hexabranchus sanguineus (eggs)* | Spanish dancer egg mass | | | | | |
| | snail (all species) | | | | | |
| | small crab (all species) 1-2cm | | | | | |
| | hermit crab (all species) | | | | | |
| **P: Porifera** | | | | | | |
| *Haliclona sp. (Haplosclerida Chalinidae)* | purple sponge | | | | | |
| **P: Unknown** | | | | | | |
| *Gastrolepidia clavigera* | scale worm | | | | | |
| | unknown white worm | | | | | |
| P: Unknown- egg mass | unknown white egg mass | | | | | |
| **Planta** (in % coverage, except H) | | | | | | |
| **Green Algae** | | | | | | |
| *Caulerpa serrulata* | light green; unknown C | 15 | | 5 | 3 | |
| *Halimeda micronesica* | coralline alga; unknown B | 15 | 7 | 10 | 5 | |
| *Neomeris annulata* | Caterpillar weed; unknown H | | | 11 | | |
| Valonia aegagropila | cluster of small green balls | | | | | |
| Valonia ventricosa | Sailor's eyeball | 1 | | | | |
| **Red Algae** | | | | | | |
| *Dictyota sp.* | clumpy, brown: unknown A | 5 | 20 | | | |
| (possibly) *Lithothamnion prolifer* | coralline red alga; unknown L | | 5 | 5 | | 2 |
| **Red and Brown Algae** | | | | | | |
| *Padina gymnospora* | Funnelweed | 1 | 2 | 1 | 30 | 40 |
| *Sargassum sp.* | seaweed | | | | | |
| *Turbinaria sp.* | Turbinweed | | | | | |
| unknown red algae | red/brown thick cluster | | 2 | 15 | 2 | |
| **Unknown Algae** | | | | | | |
| | brown clumpy; unknown D | 3 | | | | |
| | green/brown, smooth; E | | | | | |
| | green, short, clustery; F | | | | | |
| | brown, fuzzy, thin leaf; G | | | | | |
| | dark green, 'mossy'; I | | | | | |
| | brown/tan, 'mossy'; J | | | | | |
| | brown/tan, thick, hairy; K | | | | | |
| | orange encrusting algae; M | 5 | | | | |
| | pink encrusting algae; M | | | | | |
| | red encrusting algae; M | | 4 | 5 | | |
| **Substrate Type** (in % coverage) | | | | | | |
| | trash (plastic bottle) | | | | | 1 |
| | beachrock | 60 | 30 | 90 | 40 | 50 |
| | rubble | | | | | |
| | sand | 40 | 70 | 10 | 60 | 50 |

| Transect 15 (40m) | 0m-21m beachrock/sand | | | | | |
|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 3 | 4 | 5 |
| species name | description | 0m | 6m | 13m | 16m | 18m |
| **Animalia** | | | | | | |
| **P: Arthropoda; F: Alpheidae** | | | | | | |
| | gray burrowing shrimp | | | | | |
| *Nennalpheus sp.* | red burrowing shrimp | | | | | |
| **P: Chordata; F: Labridae** | | | | | | |
| *Halichoeres trimaculatus* | Three spot wrasse | | | | | |
| **P: Chordata; F: Mullidae** | | | | | | |
| *Parupeneus barberinus* | Dot & dash goatfish | | | | | |
| **P: Chordata; F: Pinguiedidae** | | | | | | |
| *Parapercis millepunctata* | Spotted sandperch-white | | | | | |
| " | Spotted sandperch-gray | | | | | |
| " | Spotted sandperch-black | | | | | |
| **P: Chordata; F: Pomacentridae** | | | | | | |
| unknown | black striped damsel | | | | | |
| unknown | black damsel | | | | | |
| unknown | black anemone fish, blue spots | | | | | |
| **P: Chordata; F: Scorpaenidae** | | | | | | |
| *Synanceja verrucosa* | Stonefish | | | | | |
| **P: Chordata; F: Syngnathides** | | | | | | |
| *Corythoichthys flavofasciatus* | Pipe fish | | | | | |
| **P: Chordata; F: Tetraodontidae** | | | | | | |
| *Canthigaster bennetti* | Bennett's sharpnose puffer | | | | | |
| **P: Chordata; SubP: Urochorda** | | | | | | |
| unknown | brown tunicate | 20% | | | | |
| **P: Cnidaria; O: Scleractinia** | | | | | | |
| *Acropora sp.* | branching; bush-like form | | | | | |
| *Fungia (cycloseris) costulata* | circular fungia | | | | | |
| *Herpolitha limax* | elongated, mountain-like fungia | | | | | |
| *Montipora undata* | plate-like; brown and/or purple | | | | | |
| *Porites lobata and/or P. lutea* | massive; cream, yellow, brown | 2 | | 1 | | |
| *Porites solida* | brown or greenish yellow | | | | | |
| unknown A. | pale cream, massive; 'swirly' | | | | | |
| unknown B. | lt. yellow, branching; bush-like | 2 | | | | |
| **P: Cnidaria; O: Stichodactylidae** | | | | | | |
| *Stichodactyla gigantea* | sea anemone | | | | | |
| **P: Echinodermata** | | | | | | |
| *Bohadschia argus* | sea cucumber | | | | | 1 |
| *Culcita novaeguineae* | Cushion star | | | | | |
| *Diadema savignyi* | black diadema | | | | | |
| *Echinometra mathaei* | purple sea urchin | | 1 | 3 | 4 | |
| *Ophiocoma erinaceus* | black brittle star (also white) | | | | | |

| Transect 15 (40m) | | | | | | |
|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 3 | 4 | 5 |
| species name | description | | | | | |
| **P: Mollusca** | | | | | | |
| *Tridacna maximus* | giant clam | | | | | |
| unknown | bivalve-clam (all species) | | | | | 2 |
| **P: Mollusca; C: Gastropoda** | | | | | | |
| *Hexabranchus sanguineus (eggs)* | Spanish dancer egg mass | | | | | |
| | snail (all species) | | 1 | 1 | | |
| | small crab (all species) 1-2cm | | | | 1 | 3 |
| | hermit crab (all species) | | | | 1 | |
| **P: Porifera** | | | | | | |
| *Haliclona sp. (Haplosclerida Chalinidae)* | purple sponge | | | | | |
| **P: Unknown** | | | | | | |
| *Gastrolepidia clavigera* | scale worm | | | | | |
| | unknown white worm | | | | | |
| P: Unknown- egg mass | unknown white egg mass | | | | | 3 |
| **Planta** (in % coverage, except H) | | | | | | |
| **Green Algae** | | | | | | |
| *Caulerpa serrulata* | light green; unknown C | | | 2 | 5 | 2 |
| *Halimeda micronesica* | coralline alga; unknown B | 5 | 20 | 5 | | |
| *Neomeris annulata* | Caterpillar weed; unknown H | | 1 | | 4 | |
| Valonia aegagropila | cluster of small green balls | | | | | |
| Valonia ventricosa | Sailor's eyeball | | | | | |
| **Red Algae** | | | | | | |
| *Dictyota sp.* | clumpy, brown: unknown A | | 15 | 5 | | |
| (possibly) *Lithothamnion prolifer* | coralline red alga; unknown L | | 10 | 5 | 7 | 5 |
| **Red and Brown Algae** | | | | | | |
| *Padina gymnospora* | Funnelweed | 10 | 20 | 5 | 1 | 10 |
| *Sargassum sp.* | seaweed | | | | | |
| *Turbinaria sp.* | Turbinweed | | | 1 | | |
| unknown red algae | red/brown thick cluster | | | | 5 | |
| **Unknown Algae** | | | | | | |
| | brown clumpy; unknown D | | 1 | | | |
| | green/brown, smooth; E | | | | | |
| | green, short, clustery; F | 20 | | | | |
| | brown, fuzzy, thin leaf; G | | | | | |
| | dark green, 'mossy'; I | | | | | |
| | brown/tan, 'mossy'; J | | | | | |
| | brown/tan, thick, hairy; K | | | | | |
| | orange encrusting algae; M | | 7 | | | |
| | pink encrusting algae; M | | | | | |
| | red encrusting algae; M | | 4 | | 4 | |
| **Substrate Type** (in % coverage) | | | | | | |
| | beachrock | 20 | 60 | 95 | 98 | 80 |
| | rubble | | | | | |
| | sand | 80 | 40 | 5 | 2 | 20 |

Table 7. Species Index - Site 4

| Transect 16 (0m) | 0m-25.2m rubble/sand | | | | | |
|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 3 | 4 | 5 |
| species name | description | 4m | 8m | 9m | 10m | 23m |
| **Animalia** | | | | | | |
| **P: Arthropoda; F: Alpheidae** | | | | | | |
| | gray burrowing shrimp | | | | | |
| *Nennalpheus sp.* | red burrowing shrimp | | | | | |
| **P: Chordata; F: Labridae** | | | | | | |
| *Halichoeres trimaculatus* | Three spot wrasse | | | | | |
| **P: Chordata; F: Mullidae** | | | | | | |
| *Parupeneus barberinus* | Dot & dash goatfish | | | | | |
| **P: Chordata; F: Pinguiedidae** | | | | | | |
| *Parapercis millepunctata* | Spotted sandperch-white | | | | | |
| " | Spotted sandperch-gray | | | | | |
| " | Spotted sandperch-black | | | | | |
| **P: Chordata; F: Pomacentridae** | | | | | | |
| unknown | black striped damsel | | | | | |
| unknown | black damsel | | | | | |
| unknown | black anemone fish, blue spots | | | | | |
| **P: Chordata; F: Scorpaenidae** | | | | | | |
| *Synanceja verrucosa* | Stonefish | | | | | |
| **P: Chordata; F: Syngnathides** | | | | | | |
| *Corythoichthys flavofasciatus* | Pipe fish | | | | | |
| **P: Chordata; F: Tetraodontidae** | | | | | | |
| *Canthigaster bennetti* | Bennett's sharpnose puffer | | | | | |
| **P: Chordata; SubP: Urochorda** | | | | | | |
| unknown | brown tunicate | | | 10% | 10% | |
| **P: Cnidaria; O: Scleractinia** | | | | | | |
| *Acropora sp.* | branching; bush-like form | | | | | |
| *Fungia (cycloseris) costulata* | circular fungia | | | | | |
| *Herpolitha limax* | elongated, mountain-like fungia | | | | | |
| *Montipora undata* | plate-like; brown and/or purple | | | | | |
| *Porites lobata and/or P. lutea* | massive; cream, yellow, brown | | 1 | | | |
| *Porites solida* | brown or greenish yellow | | 3 | 1 | | |
| unknown A. | pale cream, massive; 'swirly' | | | | | |
| unknown B. | lt. yellow, branching; bush-like | | | | | |
| **P: Cnidaria; O: Stichodactylidae** | | | | | | |
| *Stichodactyla gigantea* | sea anemone | | | | | |
| **P: Echinodermata** | | | | | | |
| *Bohadschia argus* | sea cucumber | | | | | |
| *Culcita novaeguineae* | Cushion star | | | | | |
| *Diadema savignyi* | black diadema | | | | | |
| *Echinometra mathaei* | purple sea urchin | | 6 | 2 | 1 | |
| *Ophiocoma erinaceus* | black brittle star (also white) | | | | | |

| Transect 16 (40m) | | | | | | |
|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 3 | 4 | 5 |
| species name | description | | | | | |
| **P: Mollusca** | | | | | | |
| *Tridacna maximus* | giant clam | | | | | |
| unknown | bivalve-clam (all species) | | | | | |
| **P: Mollusca; C: Gastropoda** | | | | | | |
| *Hexabranchus sanguineus (eggs)* | Spanish dancer egg mass | | | | | |
| | snail (all species) | | | | | |
| | small crab (all species) 1-2cm | | | | | |
| | hermit crab (all species) | | | | | |
| **P: Porifera** | | | | | | |
| *Haliclona sp. (Haplosclerida Chalinidae)* | purple sponge | | | | | |
| **P: Unknown** | | | | | | |
| *Gastrolepidia clavigera* | scale worm | | | | | |
| | unknown white worm | | | | | |
| P: Unknown- egg mass | unknown white egg mass | | | | | |
| **Planta** (in % coverage, except H) | | | | | | |
| **Green Algae** | | | | | | |
| *Caulerpa serrulata* | light green; unknown C | | | | | |
| *Halimeda micronesica* | coralline alga; unknown B | 15 | 5 | 4 | | |
| *Neomeris annulata* | Caterpillar weed; unknown H | | 5 | 15 | 2 | |
| Valonia aegagropila | cluster of small green balls | | | | | |
| Valonia ventricosa | Sailor's eyeball | | | | | |
| **Red Algae** | | | | | | |
| *Dictyota sp.* | clumpy, brown: unknown A | 5 | | | | |
| (possibly) *Lithothamnion prolifer* | coralline red alga; unknown L | 1 | 5 | | 5 | |
| **Red and Brown Algae** | | | | | | |
| *Padina gymnospora* | Funnelweed | 10 | | | | |
| *Sargassum sp.* | seaweed | | | | | |
| *Turbinaria sp.* | Turbinweed | | | | | |
| unknown red algae | red/brown thick cluster | | 10 | | 5 | |
| **Unknown Algae** | | | | | | |
| | brown clumpy; unknown D | 1 | 3 | 2 | | |
| | green/brown, smooth; E | | | | | |
| | green, short, clustery; F | | | | | |
| | brown, fuzzy, thin leaf; G | | | | | |
| | dark green, 'mossy'; I | | | | | |
| | brown/tan, 'mossy'; J | | | | | |
| | brown/tan, thick, hairy; K | | | | | |
| | orange encrusting algae; M | | | | | |
| | pink encrusting algae; M | | | | | |
| | red encrusting algae; M | | | | | |
| **Substrate Type** (in % coverage) | | | | | | |
| | beachrock | | | | | |
| | rubble | 30 | 60 | 90 | 90 | 100 |
| | sand | 100 | 40 | 10 | 10 | 100 |

| Transect 17 (10m) | 0m-27.7m rubble/sand | | | | | | |
|---|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 3 | 4 | 5 |
| species name | description | 2m | 4m | 7m | 23m | 26m |
| **Animalia** | | | | | | |
| **P: Arthropoda; F: Alpheidae** | | | | | | |
| | gray burrowing shrimp | | | | | |
| *Nennalpheus sp.* | red burrowing shrimp | | | | | |
| **P: Chordata; F: Labridae** | | | | | | |
| *Halichoeres trimaculatus* | Three spot wrasse | | | | | |
| **P: Chordata; F: Mullidae** | | | | | | |
| *Parupeneus barberinus* | Dot & dash goatfish | | | | | |
| **P: Chordata; F: Pinguiedidae** | | | | | | |
| *Parapercis millepunctata* | Spotted sandperch-white | | | | | |
| " | Spotted sandperch-gray | | | | | |
| " | Spotted sandperch-black | 1 | | | | |
| **P: Chordata; F: Pomacentridae** | | | | | | |
| unknown | black striped damsel | | | | | |
| unknown | black damsel | | | | | |
| unknown | black anemone fish, blue spots | | | | | |
| **P: Chordata; F: Scorpaenidae** | | | | | | |
| *Synanceja verrucosa* | Stonefish | | | | | |
| **P: Chordata; F: Syngnathides** | | | | | | |
| *Corythoichthys flavofasciatus* | Pipe fish | | | | | |
| **P: Chordata; F: Tetraodontidae** | | | | | | |
| *Canthigaster bennetti* | Bennett's sharpnose puffer | | | | | |
| **P: Chordata; SubP: Urochorda** | | | | | | |
| unknown | brown tunicate | | | | | |
| **P: Cnidaria; O: Scleractinia** | | | | | | |
| *Acropora sp.* | branching; bush-like form | | | | | |
| *Fungia (cycloseris) costulata* | circular fungia | | | | | |
| *Herpolitha limax* | elongated, mountain-like fungia | | | | | |
| *Montipora undata* | plate-like; brown and/or purple | | | | | |
| *Porites lobata and/or P. lutea* | massive; cream, yellow, brown | 3 | | 1 | | |
| *Porites solida* | brown or greenish yellow | | 1 | 3 | | |
| unknown A. | pale cream, massive; 'swirly' | | 1 | | | |
| unknown B. | lt. yellow, branching; bush-like | | | | | |
| **P: Cnidaria; O: Stichodactylidae** | | | | | | |
| *Stichodactyla gigantea* | sea anemone | | | | | |
| **P: Echinodermata** | | | | | | |
| *Bohadschia argus* | sea cucumber | | | | | |
| *Culcita novaeguineae* | Cushion star | | | | | |
| *Diadema savignyi* | black diadema | | | | | |
| *Echinometra mathaei* | purple sea urchin | | 1 | 3 | | |
| *Ophiocoma erinaceus* | black brittle star (also white) | | | | | |

| Transect 17 (10m) | | | | | | |
|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 3 | 4 | 5 |
| species name | description | | | | | |
| **P: Mollusca** | | | | | | |
| *Tridacna maximus* | giant clam | | | | | |
| unknown | bivalve-clam (all species) | | | | | |
| **P: Mollusca; C: Gastropoda** | | | | | | |
| *Hexabranchus sanguineus (eggs)* | Spanish dancer egg mass | | | | | |
| | snail (all species) | | | | | |
| | small crab (all species) 1-2cm | | | | | |
| | hermit crab (all species) | | | | | |
| **P: Porifera** | | | | | | |
| *Haliclona sp. (Haplosclerida Chalinidae)* | purple sponge | | | | | |
| **P: Unknown** | | | | | | |
| *Gastrolepidia clavigera* | scale worm | | | | | |
| | unknown white worm | | | | | |
| P: Unknown- egg mass | unknown white egg mass | | 25 | | | |
| **Planta** (in % coverage, except H) | | | | | | |
| **Green Algae** | | | | | | |
| *Caulerpa serrulata* | light green; unknown C | | | | | |
| *Halimeda micronesica* | coralline alga; unknown B | 5 | 20 | 4 | | |
| *Neomeris annulata* | Caterpillar weed; unknown H | | | | | |
| Valonia aegagropila | cluster of small green balls | | | | | |
| Valonia ventricosa | Sailor's eyeball | | | | | |
| **Red Algae** | | | | | | |
| *Dictyota sp.* | clumpy, brown: unknown A | | 5 | | | |
| (possibly) *Lithothamnion prolifer* | coralline red alga; unknown L | 2 | | 5 | | |
| **Red and Brown Algae** | | | | | | |
| *Padina gymnospora* | Funnelweed | 5 | 10 | 1 | | |
| *Sargassum sp.* | seaweed | | | | | |
| *Turbinaria sp.* | Turbinweed | | | | | |
| unknown red algae | red/brown thick cluster | | | 4 | | |
| **Unknown Algae** | | | | | | |
| | brown clumpy; unknown D | | | 5 | | |
| | green/brown, smooth; E | | | | | |
| | green, short, clustery; F | | | | | |
| | brown, fuzzy, thin leaf; G | | | | | |
| | dark green, 'mossy'; I | | | | | |
| | brown/tan, 'mossy'; J | | | | | |
| | brown/tan, thick, hairy; K | 5 | | | | |
| | orange encrusting algae; M | | 2 | | | |
| | pink encrusting algae; M | | | | | |
| | red encrusting algae; M | | 5 | | | |
| **Substrate Type** (in % coverage) | | | | | | |
| | beachrock | | | 95 | | |
| | rubble | 40 | 30 | | 60 | 50 |
| | sand | 80 | 90 | 5 | 40 | 50 |

| Transect 18 (20m) | 0m-26.5m rubble/sand | | | | | | |
|---|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 3 | 4 | 5 | |
| species name | description | 9m | 15m | 19m | 20m | 24m | |
| **Animalia** | | | | | | | |
| **P: Arthropoda; F: Alpheidae** | | | | | | | |
| | gray burrowing shrimp | | | | | | |
| *Nennalpheus sp.* | red burrowing shrimp | | | | | | |
| **P: Chordata; F: Labridae** | | | | | | | |
| *Halichoeres trimaculatus* | Three spot wrasse | | | | | | |
| **P: Chordata; F: Mullidae** | | | | | | | |
| *Parupeneus barberinus* | Dot & dash goatfish | | | | | | |
| **P: Chordata; F: Pinguiedidae** | | | | | | | |
| *Parapercis millepunctata* | Spotted sandperch-white | | | | | | |
| " | Spotted sandperch-gray | | | | | | |
| " | Spotted sandperch-black | 1 | | | | | |
| **P: Chordata; F: Pomacentridae** | | | | | | | |
| unknown | black striped damsel | | | | | | |
| unknown | black damsel | | | | | | |
| unknown | black anemone fish, blue spots | | | | | | |
| **P: Chordata; F: Scorpaenidae** | | | | | | | |
| *Synanceja verrucosa* | Stonefish | | | | | | |
| **P: Chordata; F: Syngnathides** | | | | | | | |
| *Corythoichthys flavofasciatus* | Pipe fish | | | | | | |
| **P: Chordata; F: Tetraodontidae** | | | | | | | |
| *Canthigaster bennetti* | Bennett's sharpnose puffer | | | | | | |
| **P: Chordata; SubP: Urochorda** | | | | | | | |
| unknown | brown tunicate | 5% | | | | | |
| **P: Cnidaria; O: Scleractinia** | | | | | | | |
| *Acropora sp.* | branching; bush-like form | | | | | | |
| *Fungia (cycloseris) costulata* | circular fungia | | | | | | |
| *Herpolitha limax* | elongated, mountain-like fungia | | | | | | |
| *Montipora undata* | plate-like; brown and/or purple | | | | | | |
| *Porites lobata and/or P. lutea* | massive; cream, yellow, brown | | | | | | |
| *Porites solida* | brown or greenish yellow | 1 | | 1 | | | |
| unknown A. | pale cream, massive; 'swirly' | | | | | | |
| unknown B. | lt. yellow, branching; bush-like | | | | | | |
| **P: Cnidaria; O: Stichodactylidae** | | | | | | | |
| *Stichodactyla gigantea* | sea anemone | | | | | | |
| **P: Echinodermata** | | | | | | | |
| *Bohadschia argus* | sea cucumber | | | | | | |
| *Culcita novaeguineae* | Cushion star | | | | | | |
| *Diadema savignyi* | black diadema | | | | | | |
| *Echinometra mathaei* | purple sea urchin | 4 | | | | | |
| *Ophiocoma erinaceus* | black brittle star (also white) | | 1 | | | | |

| Transect 18 (20m) | | | | | | |
|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 3 | 4 | 5 |
| species name | description | | | | | |
| **P: Mollusca** | | | | | | |
| *Tridacna maximus* | giant clam | | | | | |
| unknown | bivalve-clam (all species) | | | | 2 | |
| **P: Mollusca; C: Gastropoda** | | | | | | |
| *Hexabranchus sanguineus (eggs)* | Spanish dancer egg mass | | | | | |
| | snail (all species) | | | | | |
| | small crab (all species) 1-2cm | | | 1 | 1 | |
| | hermit crab (all species) | 1 | | | 1 | |
| **P: Porifera** | | | | | | |
| *Haliclona sp. (Haplosclerida Chalinidae)* | purple sponge | | 1 | | | |
| **P: Unknown** | | | | | | |
| *Gastrolepidia clavigera* | scale worm | | | | | |
| | unknown white worm | | | | | |
| P: Unknown- egg mass | unknown white egg mass | | | | | |
| **Planta** (in % coverage, except H) | | | | | | |
| **Green Algae** | | | | | | |
| *Caulerpa serrulata* | light green; unknown C | 3 | | | | |
| *Halimeda micronesica* | coralline alga; unknown B | 2 | | | 1 | |
| *Neomeris annulata* | Caterpillar weed; unknown H | 8 | | | | |
| Valonia aegagropila | cluster of small green balls | | | | | |
| Valonia ventricosa | Sailor's eyeball | | | | | |
| **Red Algae** | | | | | | |
| *Dictyota sp.* | clumpy, brown: unknown A | 10 | | | | |
| (possibly) *Lithothamnion prolifer* | coralline red alga; unknown L | 3 | 2 | 3 | 5 | |
| **Red and Brown Algae** | | | | | | |
| *Padina gymnospora* | Funnelweed | 10 | 5 | | | |
| *Sargassum sp.* | seaweed | | | | | |
| *Turbinaria sp.* | Turbinweed | | | | | |
| unknown red algae | red/brown thick cluster | 15 | | | | |
| **Unknown Algae** | | | | | | |
| | brown clumpy; unknown D | | | | | |
| | green/brown, smooth; E | | | | | |
| | green, short, clustery; F | | | | | |
| | brown, fuzzy, thin leaf; G | | | | | |
| | dark green, 'mossy'; I | | | | | |
| | brown/tan, 'mossy'; J | | | | | |
| | brown/tan, thick, hairy; K | | | | | |
| | orange encrusting algae; M | 2 | | | | |
| | pink encrusting algae; M | | | | | |
| | red encrusting algae; M | 2 | | | | |
| **Substrate Type** (in % coverage) | | | | | | |
| | beachrock | | | | | |
| | rubble | 50 | 100 | 98 | 100 | 100 |
| | sand | 50 | | 2 | | |

| Transect 19 (30m) | 0m-25.2m rubble/sand | | | | | |
|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 3 | 4 | 5 |
| species name | description | 4m | 8m | 13m | 22m | 23m |
| **Animalia** | | | | | | |
| **P: Arthropoda; F: Alpheidae** | | | | | | |
| | gray burrowing shrimp | | | | | |
| *Nennalpheus sp.* | red burrowing shrimp | | | | | |
| **P: Chordata; F: Labridae** | | | | | | |
| *Halichoeres trimaculatus* | Three spot wrasse | | | | | |
| **P: Chordata; F: Mullidae** | | | | | | |
| *Parupeneus barberinus* | Dot & dash goatfish | | | | | |
| **P: Chordata; F: Pinguiedidae** | | | | | | |
| *Parapercis millepunctata* | Spotted sandperch-white | | | | | |
| " | Spotted sandperch-gray | | | | | |
| " | Spotted sandperch-black | | | | | |
| **P: Chordata; F: Pomacentridae** | | | | | | |
| unknown | black striped damsel | | | | | |
| unknown | black damsel | | | | | |
| unknown | black anemone fish, blue spots | | | | | |
| **P: Chordata; F: Scorpaenidae** | | | | | | |
| *Synanceja verrucosa* | Stonefish | | | | | |
| **P: Chordata; F: Syngnathides** | | | | | | |
| *Corythoichthys flavofasciatus* | Pipe fish | | | | | |
| **P: Chordata; F: Tetraodontidae** | | | | | | |
| *Canthigaster bennetti* | Bennett's sharpnose puffer | | | | | |
| **P: Chordata; SubP: Urochorda** | | | | | | |
| unknown | brown tunicate | | | | | |
| **P: Cnidaria; O: Scleractinia** | | | | | | |
| *Acropora sp.* | branching; bush-like form | | | | | |
| *Fungia (cyclosens) costulata* | circular fungia | | | | | |
| *Herpolitha limax* | elongated, mountain-like fungia | | | | | |
| *Montipora undata* | plate-like; brown and/or purple | | | | | |
| *Porites lobata and/or P. lutea* | massive; cream, yellow, brown | | | | | |
| *Pontes solida* | brown or greenish yellow | 1 | | 1 | | |
| unknown A. | pale cream, massive; 'swirly' | | | | | |
| unknown B. | lt. yellow, branching; bush-like | | | | | |
| **P: Cnidaria; O: Stichodactylidae** | | | | | | |
| *Stichodactyla gigantea* | sea anemone | | | | | |
| **P: Echinodermata** | | | | | | |
| *Bohadschia argus* | sea cucumber | | | | | |
| *Culcita novaeguineae* | Cushion star | | | | | |
| *Diadema savignyi* | black diadema | | | | | |
| *Echinometra mathaei* | purple sea urchin | | 1 | | | 1 |
| *Ophiocoma erinaceus* | black brittle star (also white) | | | | | |

| Transect 19 (30m) | | | | | | |
|---|---|---|---|---|---|---|
| Quadrat Number ----- ----- ----- ----- ----- ----- ----- ----- ----- ----- -----> | | 1 | 2 | 3 | 4 | 5 |
| species name | description | | | | | |
| **P: Mollusca** | | | | | | |
| *Tridacna maximus* | giant clam | | | | | |
| unknown | bivalve-clam (all species) | | | | | |
| **P: Mollusca; C: Gastropoda** | | | | | | |
| *Hexabranchus sanguineus (eggs)* | Spanish dancer egg mass | | | | | |
| | snail (all species) | | | | | 3 |
| | small crab (all species) 1-2cm | | | | | |
| | hermit crab (all species) | | | | | |
| **P: Porifera** | | | | | | |
| *Haliclona sp. (Haplosclerida Chalinidae)* | cream sponge | | | 2 | | |
| **P: Unknown** | | | | | | |
| *Gastrolepidia clavigera* | scale worm | | | | | |
| | unknown white worm | | | | | |
| P: Unknown- egg mass | unknown white egg mass | | | | | |
| **Planta** (in % coverage, except H) | | | | | | |
| **Green Algae** | | | | | | |
| *Caulerpa serrulata* | light green; unknown C | | | | | |
| *Halimeda micronesica* | coralline alga; unknown B | 5 | 2 | 2 | | |
| *Neomeris annulata* | Caterpillar weed; unknown H | | | | | |
| Valonia aegagropila | cluster of small green balls | | | | | |
| Valonia ventricosa | Sailor's eyeball | | | | | |
| **Red Algae** | | | | | | |
| *Dictyota sp.* | clumpy, brown: unknown A | 5 | | | | 5 |
| (possibly) *Lithothamnion prolifer* | coralline red alga; unknown L | 2 | 5 | 10 | | |
| **Red and Brown Algae** | | | | | | |
| *Padina gymnospora* | Funnelweed | | 1 | | | |
| *Sargassum sp.* | seaweed | | | | | |
| *Turbinaria sp.* | Turbinweed | | | | | |
| unknown red algae | red/brown thick cluster | | 2 | | | |
| **Unknown Algae** | | | | | | |
| | brown clumpy; unknown D | | | | | |
| | green/brown, smooth; E | | | | | |
| | green, short, clustery; F | | | | | |
| | brown, fuzzy, thin leaf; G | | | | | |
| | dark green, 'mossy'; I | | | | | |
| | brown/tan, 'mossy'; J | | | | | |
| | brown/tan, thick, hairy; K | | | | | |
| | orange encrusting algae; M | | | | | |
| | pink encrusting algae; M | | | | | |
| | red encrusting algae; M | | 1 | | | |
| **Substrate Type** (in % coverage) | | | | | | |
| | beachrock | | | | | |
| | rubble | 50 | 60 | 100 | 50 | 100 |
| | sand | 50 | 40 | | 50 | |

# A benthic comparison of two tropical bays (Moorea, French Polynesia)

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ABSTRACT. In October and November of 1998 environmental sampling of the benthic habitat was performed in two tropical bays, on the island of Moorea, French Polynesia. The two bays appeared comparable in size and shape, but Cook's Bay has much more coastal development than Opunohu Bay. The goal of this study was to characterize the biological and physical changes along the depth gradient in each bay, and evaluate whether there was a significant difference in the benthic communities between the two bays. I took a single transect along the length of each bay, sampling every 5m in depth. Four replicate cores per depth were used for a biotic inventory, and two replicate cores per depth were used for a sediment analysis of particle size distribution and organic matter content. On one day in each bay I sampled bottom water along the transect, with two replicates per depth, measuring temperature, salinity, and dissolved oxygen content. The results of the survey of the physical benthic environment showed significant differences with depth, although only the bottom water data showed differences between the bays. The results of the survey of the macrobenthic communities in the two bays showed no differences with depth or between bays. Extremely low abundance was recorded, with comparatively high species richness. With such low abundance, the designation of dominant species in each bay from this data may not represent the reality in a larger-scale sampling. However, the dominant species in Cook's Bay were a stemaspid polychaete, an oligochaete, and an as-yet-unidentified polychaete. In Opunohu Bay the dominant species were a sipunculid, a phoronid, and a bivalve. Clearly, the dominant species (here representing 60% of the organisms in each bay) are completely different between the bays. In addition, many of their distributions varied with depth. At the scale of this study, there were no significant differences in the benthic community as a whole between bays or between depths within each bay. Further study of the benthos in these two bays is needed to adequately characterize the communities and their possible variations with depth, and to test conclusively whether coastal development has an effect on the macrobenthos.

## Introduction

Gradient studies have been useful for ecosystems ecologists to help identify the physical factors that control communities. Marine biologists have utilized the intertidal for such gradient studies, as well as the gradients offered in bay and estuary systems. Most of this work has been done in temperate zones. The gradients spanning typical bays include depth and pressure, salinity, temperature, organic matter, dissolved oxygen, and particle size distribution. Additionally, in developed bays there can be gradients of physical disturbance of the benthos, and of pollution. In a tropical system many of these gradients might be altered significantly from those expected based on temperate work, since in tropical waters the thermocline is depressed considerably, and reefs can be present as a secondary source of larger particles and organic matter.

In Moorea, French Polynesia, two adjacent bays of similar shape and size dominate the northern side of the island. These bays present a natural laboratory for characterizing gradients in tropical bays and assessing how they effect the macrobenthic community. Additionally, one bay is moderately developed along its shores while the other remains mostly pristine. In this way they also offer a system in which to test the relative effects of shoreline development on the benthos.

Previous studies have examined distributions of organisms both along the lengths of these two bays, including plankton (Houston 1995), and corals (Muto 1997; Adjeroud and Salvat 1996), and differences in biota between the bays, including plankton (Canepa 1996). However, no previous study has focused on the macrobenthos in these two bays. My goal was to characterize how the physical gradients differ in these two tropical bays with depth and between bays, and to determine how the benthic community responds to these differences

## Materials and Methods

### *Study site*

The island of Moorea lies at 17°30′ S, 149°50′W in the middle of the South Pacific Ocean, in the Society Islands of French Polynesia. It is a high volcanic island surrounded by both fringing and barrier coral reefs. There are two adjacent bays on the north side of the island with similar bathymetry, shape, orientation, and non-agricultural vegetation (Figure 1). Both bays exchange water with the ocean through passes in the barrier reef and both have

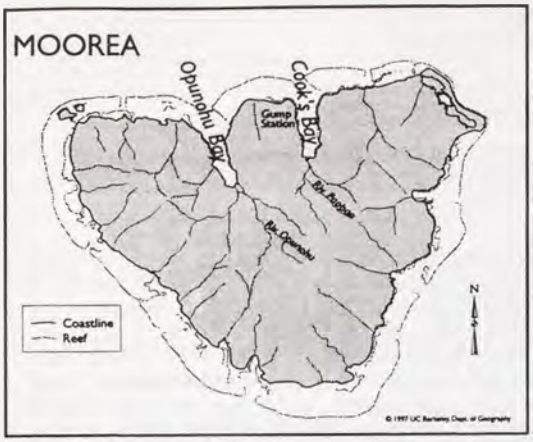


Figure 1. Moorea, French Polynesia.

fringing reefs along the majority of their coastlines. Opunohu Bay is a relatively undeveloped bay, with most of its shoreline remaining unmodified from its natural state. It has some habitations around it and a few small markets, but no larger developments. Cook's Bay is a moderately developed bay, with very little natural shoreline left. There are five hotels around the bay, numerous stores and markets, a fish cooperative, a school, a pineapple juice factory, and comparatively dense housing all the way around the bay. Although the watershed in Opunohu bay is approximately twice the size of that of Cook's Bay (Opunohu Valley drainage is 15.98km$^2$ while the Paopao Valley drainage is 7.59 km$^2$; Ferris 1992), Paopao River actually has a much higher discharge rate than Opunohu River except in major storm events (London and Tucker 1992). The total sediment loading between the two bays is very similar (London and Tucker 1992). Pineapple plantations dominate the development of the Cook's Bay watershed while the Opunohu watershed is mostly pastureland, with a secondary use for fruit trees (Recherché Etudes Environnement Developpement 1990). So although Opunohu Bay is not pristine, it poses as an acceptable control site for the effects of shoreline development on the benthos.

To characterize the benthic communities of each the bays, I performed a transect along the middle of each bay and located sampling stations at every five meters of depth up to 35m in Cook's Bay and 40m in Opunohu Bay (Figures 2 and 3). I performed all sampling from boats above my sampling stations.

*Biological sampling*

I collected benthic samples using a WILDCO Gravity-Stratification core sampler (WILDCO Wildlife Supply Company, Michigan, USA). This corer sampled approximately 22cm$^2$, and I used only the top 10cm of each core. I took four replicates per depth station, recording the exact depth of each the sample using a hand-held depth sounder (model # 718370, Speedtech Instruments, Virginia, USA). Each sample was refrigerated and sieved through a 500μm sieve within 24 hours. This portion was then stained with rose bengal, sorted under a dissecting microscope, and stored in ethanol for return to Berkeley and further taxonomic identification.

All Opunohu biological sampling was done on October 28$^{th}$, 1998, while biological sampling in Cook's Bay occurred from October 6$^{th}$ through October 26$^{th}$, 1998.

*Sediment sampling*

Using the same corer described above, I collected two replicates per depth station. Sediment cores were taken at the same time as the biological cores. The samples were refrigerated, then allowed to air-dry, although drying was not complete at time of transport. The samples were then dried in a drying oven in Berkeley at 60° C until dry. I used a subsample of one replicate from each station for particle size analysis. I sieved the subsample through a nested range of sieves (2mm, 1mm, 500μm, 250μm, 125μm, and 63μm), dried each fraction, and weighed to determine the relative percentages in the initial sample. Percent organic matter was determined by combustion for five hours in a 550°C muffle furnace.

*Bottom water sampling*

I retrieved two bottom water samples per depth station using a WILDCO Kemmerer Water Sampler bottle (1200 Series). This sampler holds 1200ml of water. I tested each sample immediately upon recovery. I used a Leica Handheld Refractometer (Model 10419/10423, Leica Inc.., New York, USA) to measure salinity, and a YSI Model 55 Dissolved Oxygen System (YSI Incorporated, Ohio, USA) to measure both temperature and dissolved oxygen.

All samples within each bay were collected on the same day, and the sampling of the two bays was separated by eleven days. Sampling begun at the same time of day, at the same point in the tidal cycle, on days with similar conditions.

*Analysis Methods*

Initially I graphed the data for each variable against depth, and compared graphs between bays. In order to compare the data statistically between the two bays I used Mann-Whitney U tests (Siegal 1956). To compare variables within each bay I used

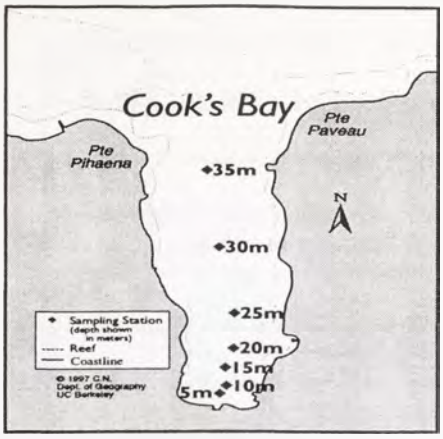


Figure 2. Locations of sampling stations in Cook's Bay.

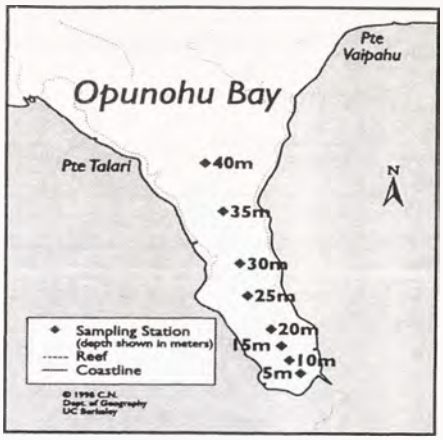


Figure 3. Locations of sampling stations in Opunohu Bay.

Kruskal-Wallis one way ANOVAs when the sample number was greater than one per station. In all statistical tests I set the minimum value for significance at $\alpha = 0.05$. In addition, I performed cluster analyses of the raw biological data for each bay, using each of the species found as a variable. I also performed cluster analyses for the two bays' data for bottom water characteristics, and for sediment particle size distribution, using the seven different particle size fractions as the variables. Cluster analysis was done using NTSYS™, using hierarchical clustering, with UPGMA as the parameter for water and sediment trees, and the Manhattan coefficient used to calculate similarity for the biological data.

## Results

*Biological sampling*

There was low organism abundance with an average of 3.3 organisms per sample. Species found included polychaetes, oligochaetes, nematodes, sipunculids, bivalves, and gastropods. In twenty-six total cores in Cook's Bay I found one hundred and five individuals comprising twenty species. The three dominant species (accounting for 61% of the organisms) were a sternaspid polychaete, a species of oligochaete (oligochaete sp. A), and a species of polychaete (polychaete sp. C). In Opunohu Bay a total of thirty-one cores yielded eighty-seven individuals and eighteen species. The three dominant species in Opunohu (accounting for 57% of the organisms) were a sipunculid, a phoronid, and a bivalve. Eleven species were found in common between the two bays.

In addition to comparing bays and depth stations based on the numbers of organisms and species per core, I also calculated the diversity index for each sample using the Shannon diversity function:

$$H' = \sum p_j \times \log p_j$$

where H' is the diversity index, with a higher H value representing a more diverse community, and $p_j$ is the proportion each species is of the total number of organisms in the sample. The diversity value thus quantifies both the number of species and their relative proportions in each sample. Although it is normal to proceed from diversity to evenness calculations, which quantify the degree of evenness of the distribution of organisms among the species present, with my extremely low abundance the evenness tends to oscillate unnaturally between 0 and 1 and so would not provide new, useful interpretations of the data.

Data for abundance, species richness, and diversity versus depth shows very low $R^2$ values in both bays (Figures 4 - 9). The high variability in the data caused a lack of any clear simple relationship for abundance, species richness, or diversity with depth in either bay. Kruskal-Wallis one way ANOVAs showed no significant statistical difference between the depth stations in Opunohu Bay. Using organism abundance data, Kruskal-Wallis showed that $p > 0.50$. Using species richness values, $p > 0.10$, and calculated with species difference $p > 0.10$. A cluster analysis using the abundance data for the eighteen species present created 100 different tied trees! This is likely due to low abundance values, since low numbers of organisms is all the species provides only low resolution for tie-breaking. With such a huge

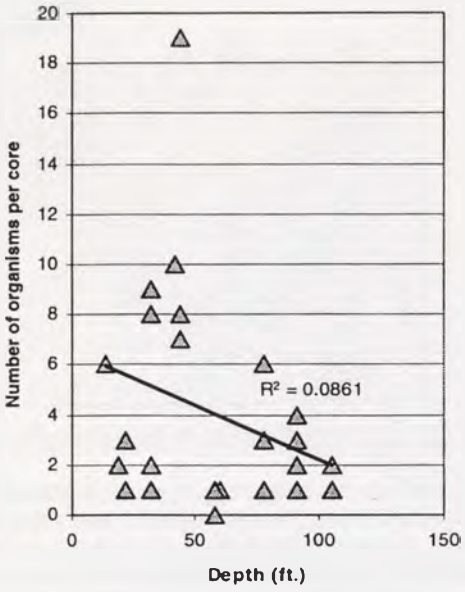


Figure 4. Organism abundance per core along the depth gradient of Cook's Bay.

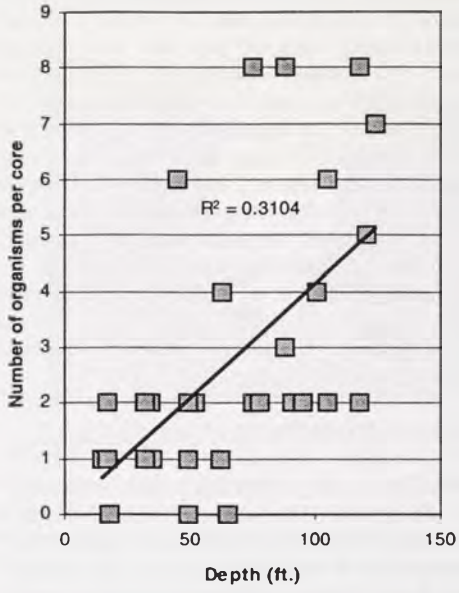


Figure 5. Organism abundance per core along the depth gradient of Opunohu Bay.

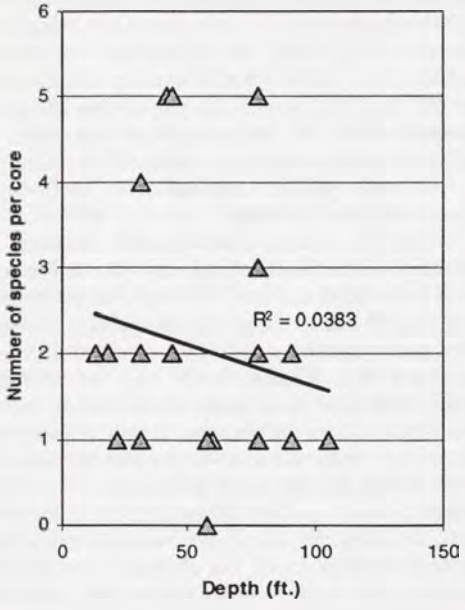


Figure 6. Species richness per core along the depth gradient of Cook's Bay.

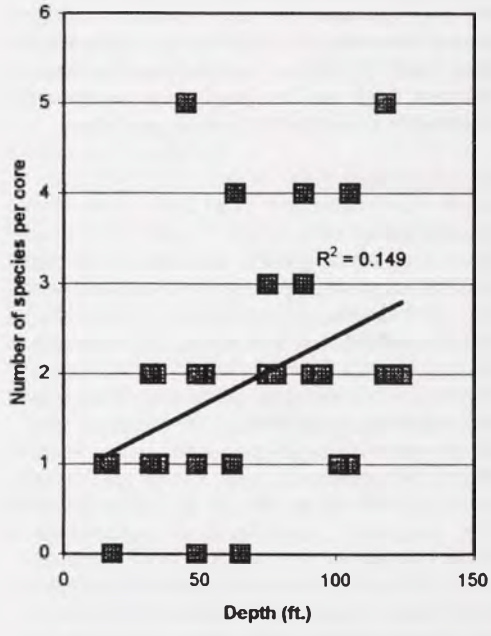


Figure 7. Species richness per core along the depth gradient of Opunohu Bay.

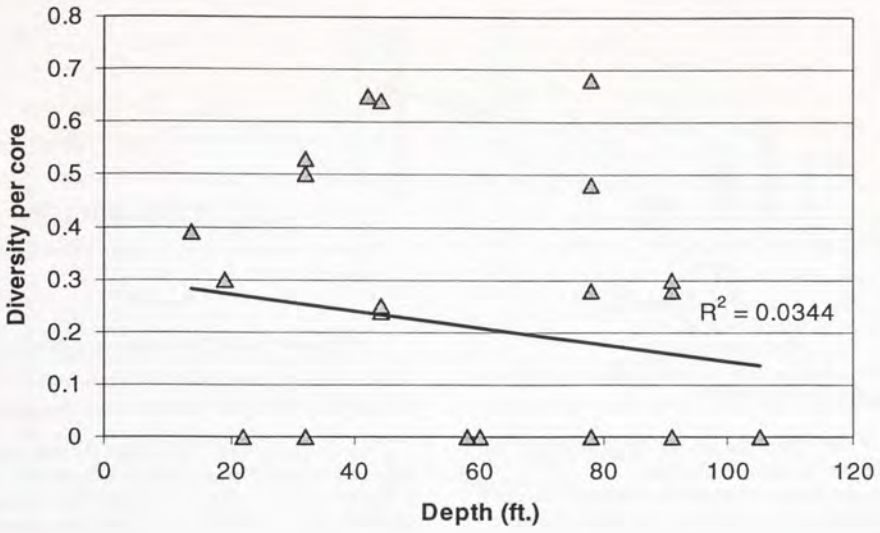


Figure 8. Diversity values (calculated using the Shannon Diversity function) per core along the depth gradient in Cook's Bay.

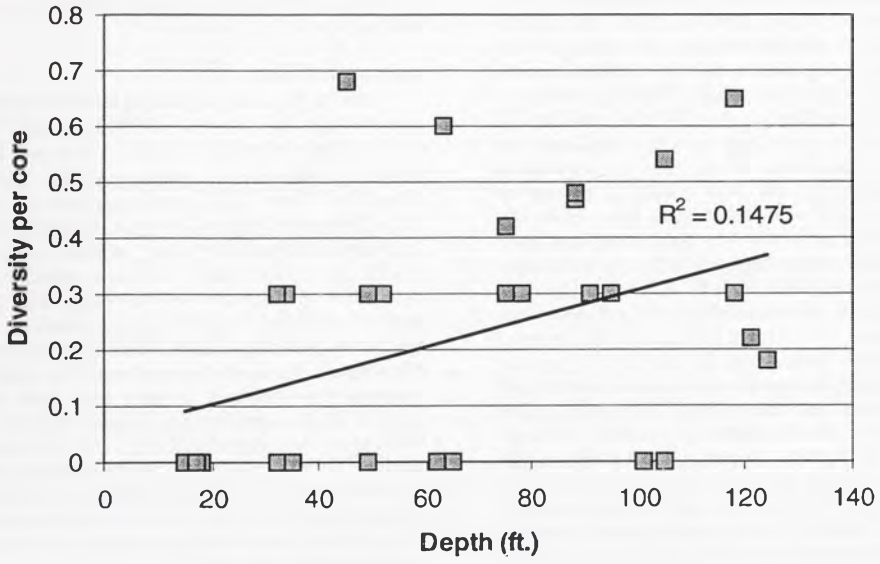


Figure 9. Diversity values (calculated using the Shannon Diversity function) per core along the depth gradient in Opunohu Bay.

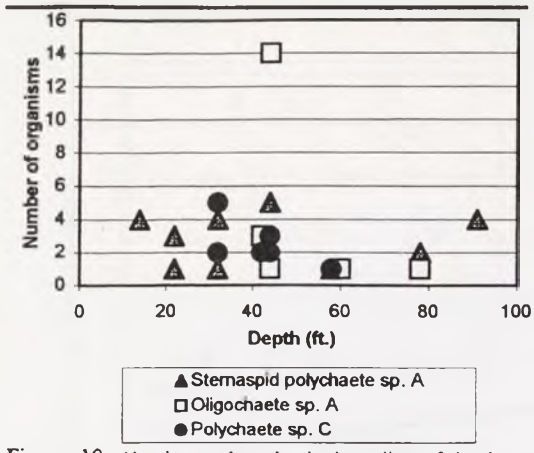


Figure 10. Abundances along the depth gradient of the three most dominant species in Opunohu Bay.

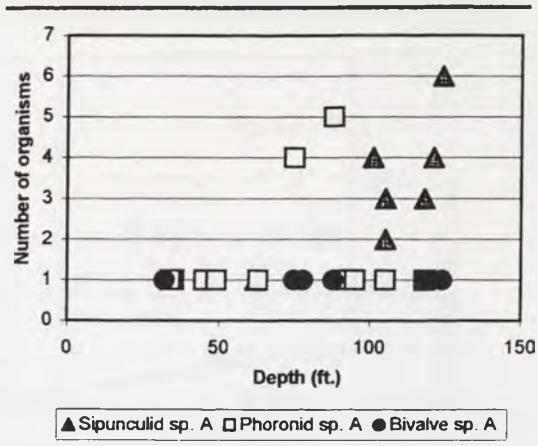


Figure 11: Abundances along the depth gradient of the three most dominant species in Cook's Bay.

number of tied trees, the cluster analysis is not a meaningful way to interpret this data.

When the focus is narrowed, however, and the distribution of the three dominant species in Opunohu is plotted against depth (Figure 10), there is some indication of differences along the depth gradient. While the bivalve is distributed uniformly in very low numbers, the Phoronids' cosmopolitan distribution seems to be interrupted by a peak between 50 and 70 ft. of depth. However, because of the low organism numbers the significance of this peak is not very robust. The Sipunculid does show a clearly uneven distribution along the depth gradient of the bay, being present only at depths of greater than 100 ft., and then at comparatively high numbers.

In Cook's Bay, Kruskal-Wallis calculations showed more promising results. Analyzed by organism abundance, there was a significant difference between the depth stations of the bay at $0.05 > p$. The same low p value is found when the statistical test is done on the species richness data. By species diversity values, the difference with depth is not significant but at $p > 0.10$. A cluster analysis of the Cook's Bay abundance data produced more than 100 tied trees, and so again the result is that that type of analysis is meaningless for this data. When the distribution of the three dominant species are focused in on there are clear changes in abundance with depth (Figure 11). The Sternaspid polychaete, although found to 90 ft. deep, clusters predominantly in the shallower depths between 10 and 40 ft. The oligochaete is limited to the middle depths sampled between 40 and 80 ft., with polychaete sp. C showing a similar distribution, occurring only between 30 and 60 ft.

In comparing the biota between the two bays, the most striking difference is the lack of overlap in the dominant species. When I plotted the abundance, species richness and diversity with depth there was no clear difference in the data sets between the two bays. The Mann-Whitney U test also showed no statistically significant difference in the organism abundance, species richness, or species diversity per core between the two bays. Calculated using organism abundance, the Mann-Whitney U test produced a $p = 0.17$, using species richness $p = 0.43$, and with species diversity $p = 0.33$.

*Sediment sampling*

Particle size analysis showed a predominance of particles less than 63µm at all depths in both bays. Silt is defined as particles between 50µ and 2µ in diameter, while clay is anything smaller than 2µ (Brady and Weil 1996), but sieving does not allow for a distinction between the two. Therefore I can only say that the majority of my sediment was either a silt or a silt loam. Sediment particle size distribution is similar between bays. The three smallest size fractions plotted against depth for each bay shows generally similar trends (Figures 12 and 13) although the curve is considerably smoother for Opunohu Bay sediment. In both bays there is an increase in the smallest size fraction between the shallowest two depth stations, and a decrease between the two deepest stations. In Opunohu Bay the trend is clearly increasing silt/clay content to 15m, a plateau until 30m, and then a decline to 40m. In Cook's Bay there is no clear plateau, with irregular data between 10m and 30m.

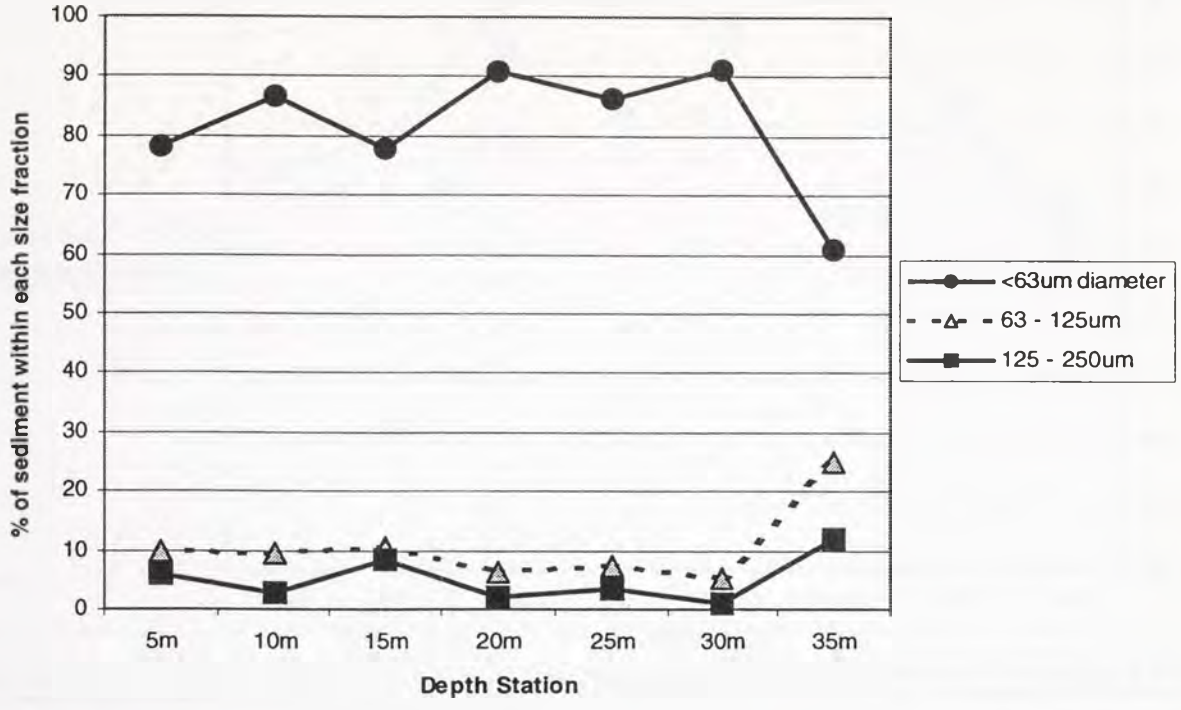


Figure 12. Sediment particle size distributions along the depth gradient in Cook's Bay; particles larger than 500μm accounted for less than 5% of all samples.

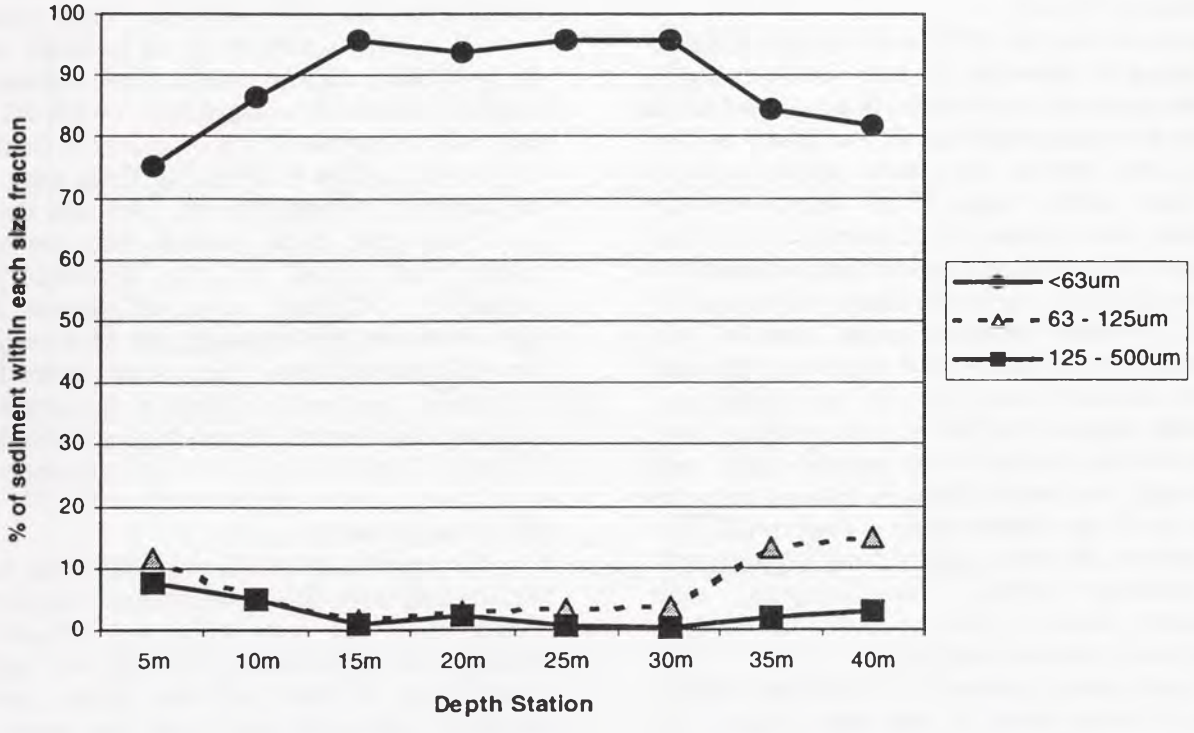


Figure 13. Sediment particle size distributions along the depth gradient in Opunohu Bay; particles larger than 500μm accounted for less than 5% of all samples.

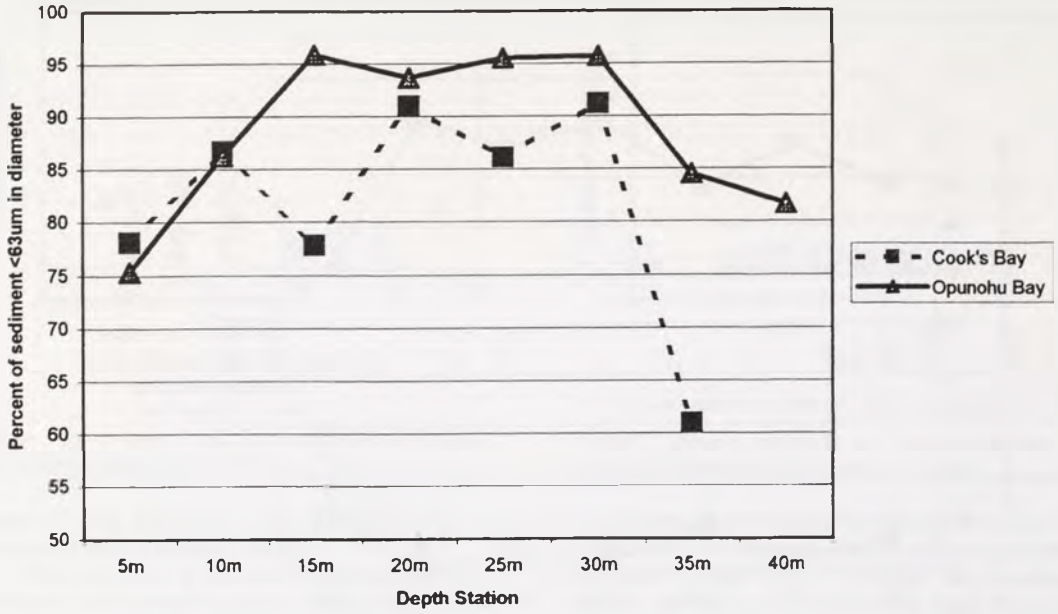


Figure 14. A comparison of the percentage of sediment less than 63μm in diameter along the depth gradients in Opunohu and Cook's Bays.

The percentage of silt/clay in the Opunohu Bay was generally higher than in Cook's Bay (Figure 14). When I applied a Mann-Whitney U test to this difference, I found that the difference was not significant ($p = 0.116$).

A cluster analysis of the sediment data using all size classes to determine similarity between depths and bays produced mixed results (Figure 15). Overall the data was interspersed and did not cluster by bay, showing that stations were more similar between bays than within bays. There was a notable exception, with stations O (Opunohu) 15m, 20m, 25m, and 30m clustering together. The cladogram did show very limited cohesion by depth, with no first or second groupings spanning more than a 15m difference. One important result from the cladogram was the discovery that by particle size distribution, the middle depths of the two bays are generally more similar to each other than to the extreme depths. And surprisingly, the deepest Opunohu stations are more similar to all the shallow stations than to the mid-depth stations. However, despite some suggestions in the clustering patterns, this cladogram most prominently shows a thorough mixing of the bays and depths by similarity analysis.

The organic matter analysis of the sediment samples showed a similar trend in both bays (Figure 16). Organic matter peaked at the 10m station at approximately 34%, then decreased steadily with depth to less than 10% at the deepest stations. Although Opunohu Bay had generally higher organic content across depth, this difference was not significant with the Mann-Whitney p-value of 0.168.

Lastly, the color of the sediment was characterized using Munsell color charts (Appendix 1). Colors were described for dry sediment and for the post-ashing mineral portion of the sediment. For the dry sediment they ranged from 10 YR 3/2 at the head of both bays to 10 YR 7/2 at 35m in Cook's and 10 YR 6/2 at 40m in Opunohu. These were colors ranging from a blackish-brown color near the heads to a beige-gray at the mouths. After the organic matter was burned off the sediment looked dramatically different; across all stations it had become redder, but the change was more dramatic in the shallower sediments. The mineral portion ranged from a dark brick red 2.5 YR 4/6 at the heads of both bays to a slightly pinkish gray-beige at the mouth, 10 YR 6/2 in Cook's Bay and 5 YR 6/4 in Opunohu.

*Bottom water sampling*

There was considerable variability in the salinity data for both bays. When plotted against depth the $R^2$ values were not particularly high (Figure 17), although the coherence of the data was higher in Cook's Bay. In both bays the salinity generally increased with depth, and Cook's Bay seems to be more saline than Opunohu although there is overlap in the data sets. The Mann-Whitney U test showed that the difference in the salinity of the two bays was

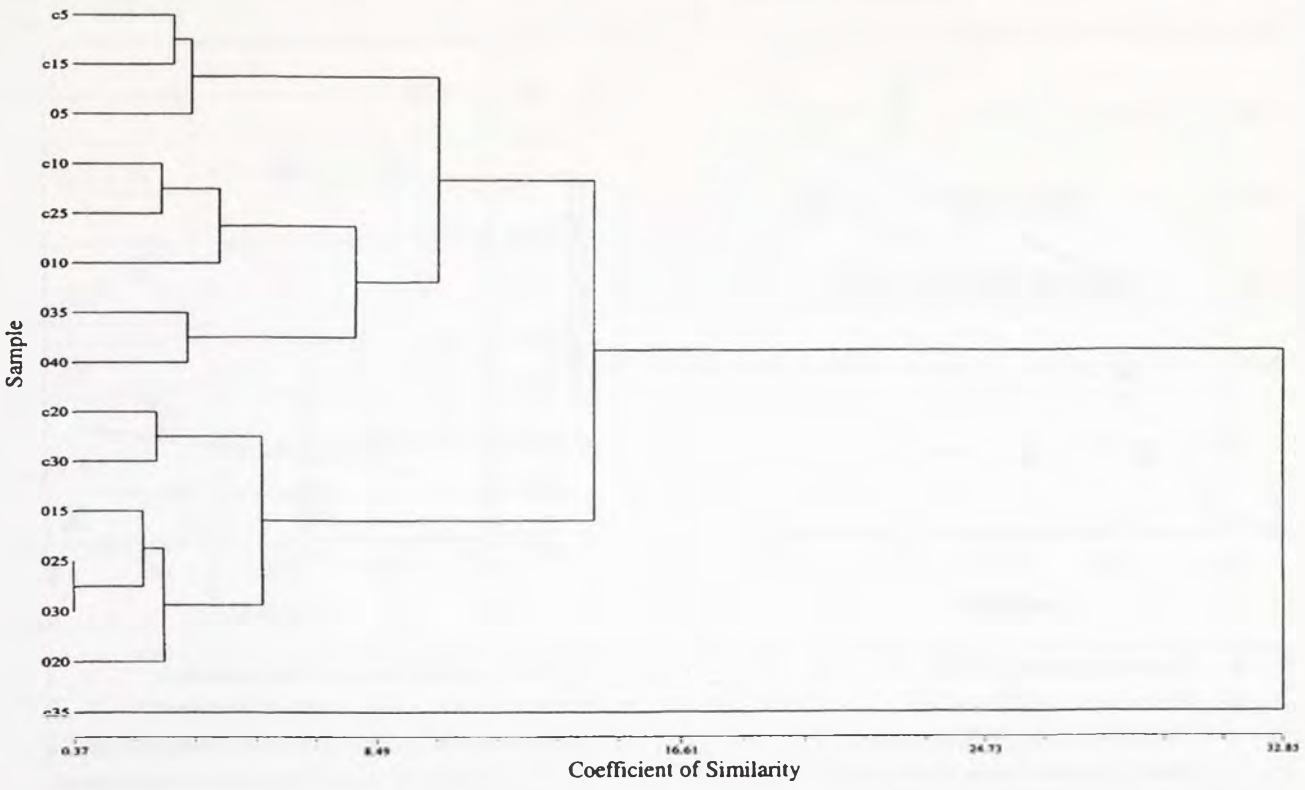


Figure 15. Results of a cluster analysis of the sediment data (using all particle size classes) to determine similarity between depth stations and between bays. The stations are designated by either "O" for Opunohu or "c" for Cook's, and by their depth in meters. (So "O25" is the 25m station in Opunohu Bay.)

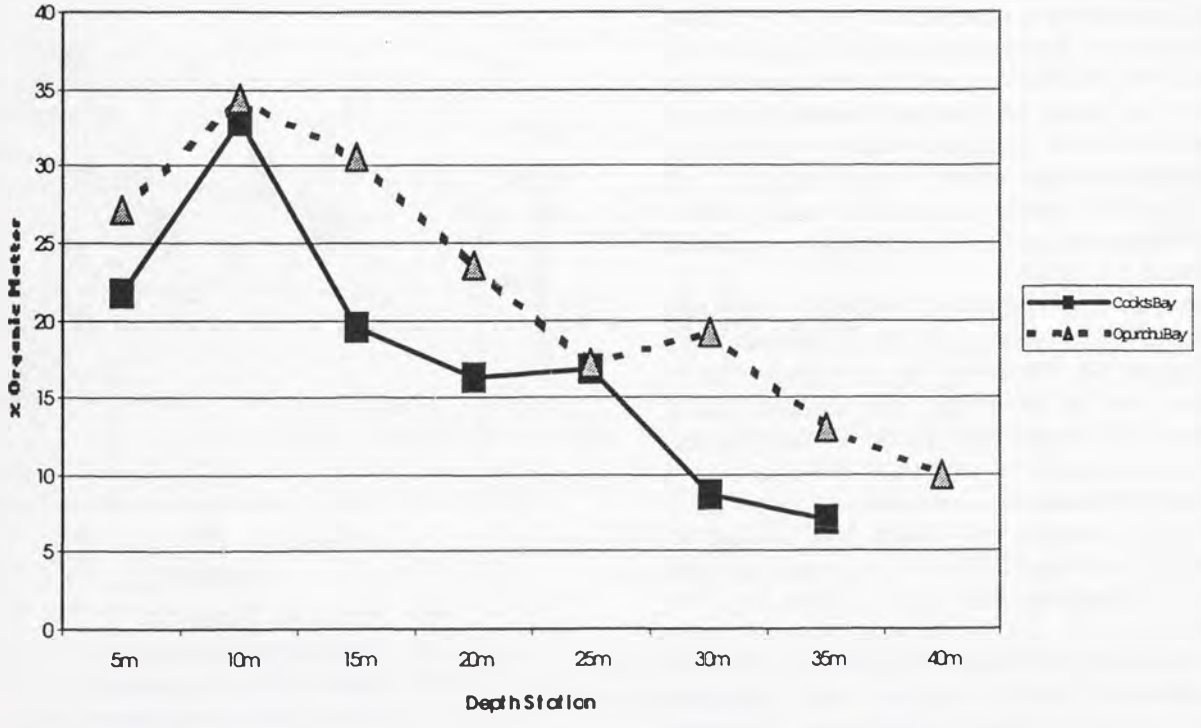


Figure 16. Percent organic matter in the sediment along the depth gradients in Opunohu and Cook's Bays.

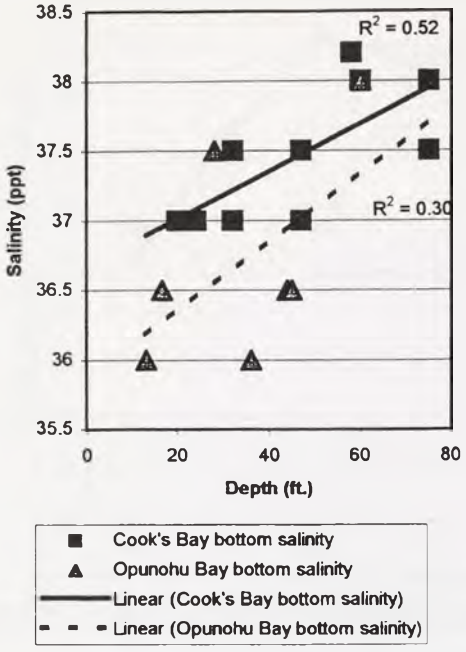


Figure 17. Bottom water salinities in upper Cook's Bay (11/16/98) and upper Opunohu Bau (11/26/98).

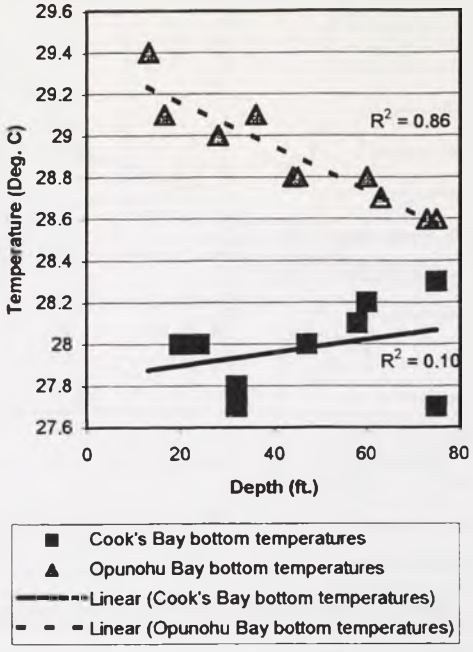


Figure 18. Bottom water temperatures in upper Cook's Bay (11/16/98) and Opunohu Bay (11/26/98).

not significant with p = 0.12.

The plot of temperature versus depth shows a powerful regression in Opunohu Bay at $R^2$ = 0.8648, with temperature decreasing with depth (Figure 18). In Cook's Bay the much lower $R^2$ value represents an extremely low slope of relation between depth and temperature as well as slightly more variable data. The Opunohu bottom water is much warmer at all depths than the Cook's Bay bottom water, with a Mann-Whitney test giving a statistically significant difference at p = 0.001.

There are relatively low $R^2$ values for the linear regression of dissolved oxygen versus depth for both bays (Figure 19). However, this is mostly due to variability, and in both bays the oxygen clearly increases with depth. The Mann-Whitney U test shows that the dissolved oxygen in the two bays is significantly different with p = 0.001.

A cluster analysis for Cook's Bay pooling all three of the measured bottom water characteristics showed no clustering with depth (Figure 20). For Opunohu Bay, a cluster analysis showed some limited clustering with depth (Figure 21). The two 15m replicates cluster together with complete similarity, as do the two 20m replicates. However, the 5m and 10m replicates are highly dissimilar, which perhaps implies a greater heterogeneity in the

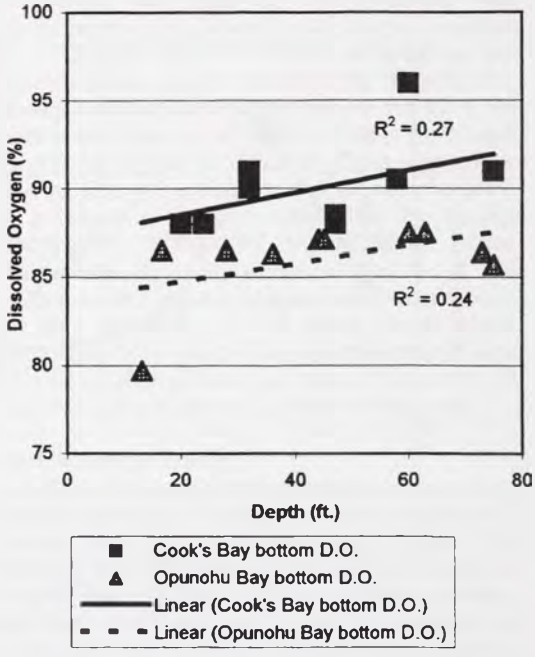


Figure 19. Bottom water dissolved oxygen contents in upper Cook's Bay (11/16/98) and Opunohu Bay (11/26/98).

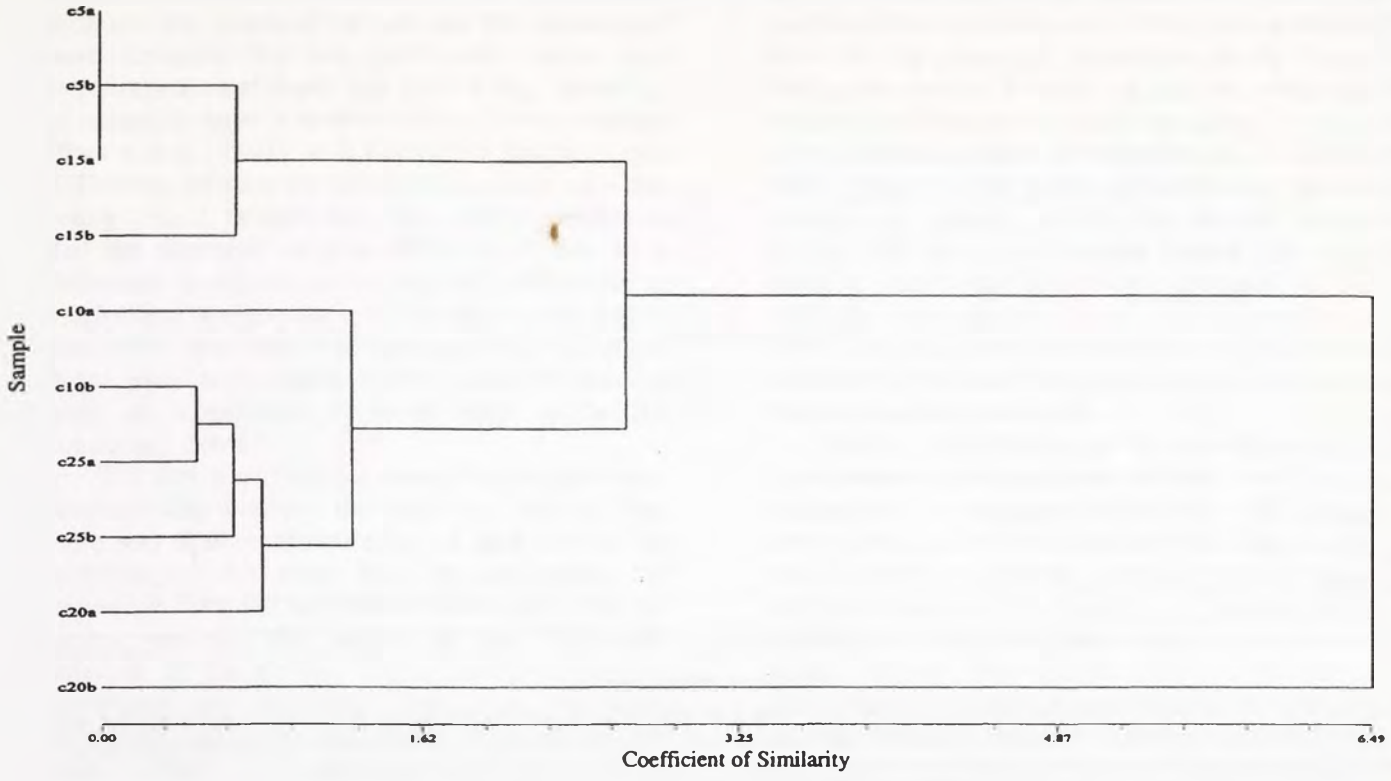


Figure 20. Results of a cluster analysis of the pooled bottom water data for Cook's Bay, to test clustering of stations with depth based on bottom water characteristics. The samples are designated by the initial "c" for Cook's Bay, their meter depth, and the replicate, "a" or "b".

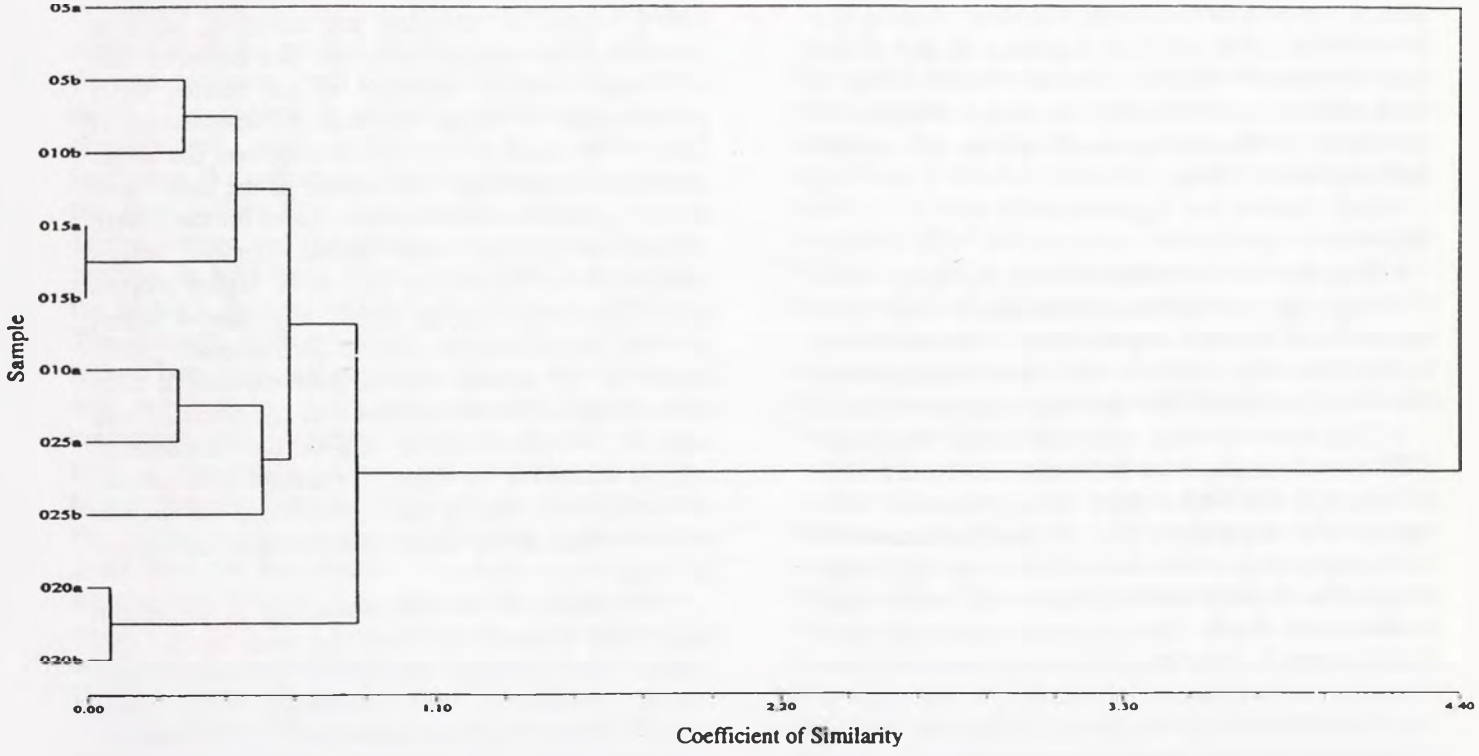


Figure 21. Results of a cluster analysis of the pooled bottom water data for Opunohu Bay, to test clustering of stations with depth based on bottom water characteristics. The samples are designated by the initial "O" for Opunohu Bay, their meter depth, and the replicate, "a" or "b".

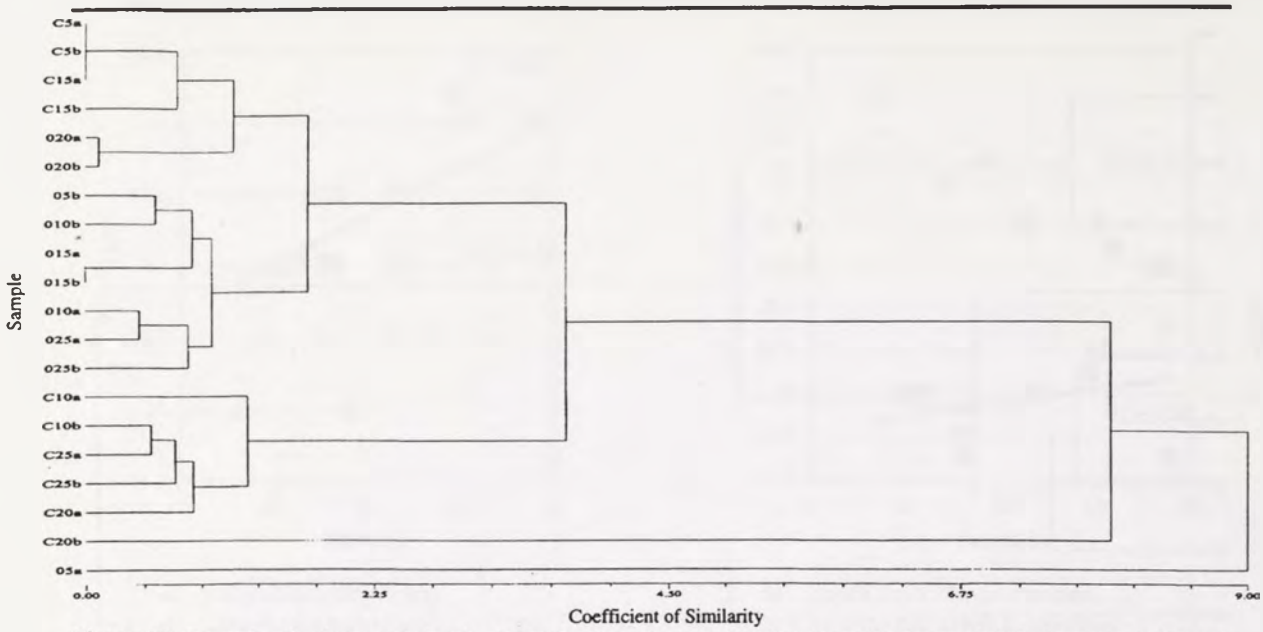


Figure 22. The results of a cluster analysis using the bottom water data from both bays to test the degree of similarity among stations and between bays. Each sample is designated by a letter, "O" for Opunohu and "C" for Cook's Bay, a number representing the depth station the sample is from, and a final letter, either "a" or "b" denoting the replicate (two replicates were taken at each depth station).

bottom waters at shallower depths. When a cladogram was created using bottom water data from both the bays (Figure 22), large scale clustering by bay (to third and fourth degrees of similarity) was seen for twelve of the twenty stations. Among the other stations, four showed clustering by bay to the second degree of similarity. When only comparing to the first degrees of similarity, we see that 9 out of 10 stations in each bay are most similar to another station(s) within the same bay.

**Discussion**

The physical data collected from this study show a limited degree of difference with depth along each bay, with more robust depth-related differences seen in Opunohu Bay, and that there is some difference between the physical environments of the two bays.

The bottom water showed some important differences with depth in both bays. In Cook's Bay, salinity and dissolved oxygen (D.O.) increased with depth while temperature was variable but showed a slight increase. In Opunohu, salinity and D.O. also increased with depth, and temperature showed a clear decrease with depth. These patterns agree well with those expected for a bay, where freshwater inflow creates lower salinity at the head. A decrease in temperature with depth is expected based the physics of heating and mixing , and on the idea that open-seawater is colder and so proximity to a pass should correlate with colder temperatures at depth where the saltier sea water enters the bay. The slight increase and high variability of temperature with depth seen in Cook's Bay could be a result of sampling duration. While I began sampling both bays at the same time of day, in Cook's Bay I was considerably slower and it took 2.5 hours to complete my sampling, while in Opunohu I was finished in 1 hour. The Opunohu data is a more accurate snapshot of the bottom water profile, and the slight increase in temperature in Cook's Bay could be due to warming over the longer sampling duration into the middle of the day. There are two potential non-exclusive causes for the pattern of increasing D.O. with depth. Organic matter brought in by the stream can drive higher oxygen consumption near the bay head. Also, deeper waters can hold more dissolved oxygen (Brown et al. 1995). Based on the organic matter data showing a clear peak of organic matter content near the heads of both bays, it is reasonable to expect the biochemical oxygen demand to be higher at the head. This permits the conclusion that in these two bays, the organic matter profiles do correlate with the dissolved oxygen gradients.

The results of the cluster analysis of the bottom water data showed no clustering with depth. This implies that although individual parameters may change consistently and observably with depth, overall (by the three parameters studied here) there is not a clear and definable difference in the bottom water along the depth gradient.

Comparing the bottom water data between the bays shows interesting differences. Although the

salinity of the two bays was not significantly different, the dissolved oxygen and the temperature were. Opunohu Bay was significantly warmer and less oxygenated at depth than Cook's Bay. Solubility of oxygen in water is inversely related to temperature (Brown et al. 1995), so it is possible that these two differences between the two bays represent only one acting control, temperature. The other possibility is that the dissolved oxygen difference is due to a difference in organic matter and so a difference in biochemical oxygen demand, but the organic matter data refute this. There was no significant difference in the percentage organic matter present in the two bays, so temperature is more likely to be the controlling factor.

The cluster analysis for comparing bottom water characteristics between the two bays showed that there was significant clustering of each bay to the exclusion of the other bay. By comparing the regression lines for the bottom water data with the cluster analysis, the source of the substantial cohesion of the stations within each bay can be interpreted as stemming from the dissimilar temperature and dissolved oxygen values in the two bays. Where the cladogram shows limited intermingling of the two bays' stations, this is likely due to the variable and overlapping salinity data.

The sediment data showed a difference with depth but not between bays. There was no significant difference between the two bays in organic matter content or in the percent of sediment in the <63µm fraction. However, both of these factors change with depth. The change in relative percentages of the clay/silt and sand fractions in the profiles is intriguing. We expect larger particles to settle out of the river inflow first, and smaller particles to be carried further, and this appears to be reflected in the profiles. In both bays, there is an initial increase in the clay/silt fraction between the first two stations. The fringing reefs are fairly uniformly distributed around both bays, and so we would not expect to see any gradient in their potential contribution of calcareous sand. However, there are also the barrier reefs at the mouth of each bay, which are much bigger than the fringing reefs and whose effects on the benthic environment should be seen in a gradient away from the bay mouth. The drop in percent of silt/clay and increase in percent sands at the deeper stations in both bays may represent the gradient in coral sands brought into the bay from the barrier reef. One way to test this and determine the relative impact of reef-derived particles on the gradient would be to treat the ashed mineral portion of the sediment with concentrated hydrochloric acid, which would dissolve any calcium carbonate sands (as per Smith and Kukert 1996). Another way to glimpse the effects of the reef is by the color of the mineral portion of the sediment. As is easily seen in the bare soils of the pineapple plantations in the Paopao Valley, the soils of Moorea are very red, while coral sand ranges from creamy tan to light gray. The colors of the mineral portion of the sediments in each bay were deep red in the shallower depths near the river inflow. At deeper stations the mineral portion dramatically lost its red hue and became light beige-gray. In Cook's Bay this change happened at 25m, while in Opunohu the change in color occurred at 30m. This loss of red color coinciding with the small increase in the sand fraction suggests a contribution from reef-derived sediment.

Finally, the difference in the smoothness of the two particle size gradients in the two bays is suggestive. The roughness in the Cook's Bay silt/clay curve compared to the smooth curve in Opunohu Bay could possibly due to the potentially higher mixing and disturbance of the Cook's Bay benthos due to higher boat and cruise ship density and associated anchor scarring. Although this difference between the bays is logical, it would be very difficult to prove that there is a quantifiable result to the bay floor. Using an ROV with a camera to directly observe potential scarring sites in both bays might lend data to the argument, but even then it might be difficult to prove that recorded furrows on the bay floor were definitely anthropogenic.

The cluster analysis for the combined sediment particle size data reflected the similarity of the two bays and a fundamental lack of distinctiveness among depth stations despite the general trends shown in the graphs. By feel the deeper stations seemed significantly sandier, and so despite the cladogram's result of relative homogeneity, I feel strongly that an organism could perceive the deeper stations as very different; a slight change in percent sand can make a disproportionate difference to texture.

The organic matter was one of the more convincing gradients obtained in this study, although again there was no significant difference between the bays. Hypothetically, the agriculture-dominated Cook's Bay watershed would retain less of its organic matter of all sizes due to rapid runoff from swathes of bare soil, and the lack of an established litter layer with the associated microbial loop ready to consume litter quickly. This seems to be true, because although the absolute amounts of organic matter in the two bays are similar, the Cook's Bay since it's watershed is half the size and so the relative amount of organic matter entering the bay is higher (Ferris 1992). The delay in the organic matter peak to the 10m station rather than the 5m one in both bays is interesting, and perhaps represents both an average particle size for the organic matter and an average density which

carry it past the mouth of the river outflow.

The location of the organic matter peak at 10m in both bays is somewhat unexpected since the different watershed usage might be expected to create different types of organic matter with different settling qualities. The comparative lack of litter-trapping and -retaining mechanisms in Cook's Bay watershed would suggest a larger average organic matter particle size, while the predominance of livestock in the Opunohu watershed would be expected to produce small particulate organic matter. If this were true and the different types of organic matter had the same density, then based purely on size considerations the Cook's peak should be closer to the river mouth than the Opunohu peak. While some of the hypothetically smaller particles produced in the Opunohu watershed from livestock feces would be "new" carbon and still be rich in the lighter organic molecules, pastures are predominantly associated with erosion, and with the displaced sediment comes partially degraded particulate organic matter. This partially degraded matter has higher density (due to consumption of lighter molecules first) than the fresher organic matter brought into Cook's Bay. So by this reasoning, the larger, lighter particles in Cook's Bay might tie in their settling distance with the smaller denser particles in Opunohu Bay.

My data is in agreement the London and Tucker data (1992), which showed comparable sediment loading between the two bays. Through the surrogates of similar organic matter contents and silt/clay distributions, my data implies similar sediment loading. The only troubling discrepancy is that the London and Tucker research showed very different Secchi disk readings for water clarity at the mouths of the two rivers. Paopao River outflow was consistently murkier than Opunohu River outflow, which should indicate some difference in the nature of the inflowing sediment. Such a difference was not uncovered by my data.

Overall the physical data shows evidence for both differences with depth and between bays in the physical environment of the benthic habitat. These physical differences were not clearly reflected in the biological data.

The overall distribution of organisms by number, species richness, and diversity did not show a pattern with depth or between bays. With the majority of the species in each bay represented by only one individual, the numbers were simply too small for larger-scale trends to be revealed. The data reflect a patchiness and heterogeneity across the bay, which at the scale sampled overwhelm any larger patterns that might be present. The core used was particularly small, but my abundance was extremely low even for tropical waters. A study of the benthic macrofauna of a tropical lagoon bottom in Hawaii, sampled from 12 – 16m deep using a 35cm$^2$ corer, and retrieved organism densities ranging from 150 – 350 individuals per core (Smith and Kukert, 1996). With a 22cm$^2$ corer, I retrieved 192 total individuals in 57 cores! In the Hawaiian study there were reefs present, and freshwater inflow. However, a clue to the possible problem lies in a preliminary study done by Smith and Kukert, where they found that at the Hawaiian site, most of the macrobenthic abundance was concentrated in small individuals that pass through a 500μm sieve. Because of their preliminary work they were able to use a 300μm sieve instead. From a personal comparison with previous benthic sorting experience, I noticed that my organisms were generally much smaller than those I have seen in temperate sediments. So, it is possible that the organisms were there and a smaller sieve and larger corer were necessary.

I did not find low species diversity along with the low abundance. I found 27 species in 197 individuals, while the Hawaiian study found 8 – 13 species per 100 individuals. In Sanders' (1968) study of four tropical shallow-water habitats he found 15 – 45 macrobenthic species per 100 individuals. This would suggest that given the low abundance, the patchiness of the community, and the evidence that I did not completely sample or characterize the community, perhaps in the Moorea data there might actually be unusually high species richness. A conclusion will have to wait for a further study.

I also analyzed the data for just the three most dominant species in each bay in an attempt to glean some information from my biological data. The validity of this given the low abundance is questionable; although in each bay the three represent approximately 60% of the organisms, with such low numbers it may be a false classification and not representative of the community as a whole. Assuming that it is a valid way of looking at the data, there are very striking patterns. The three dominant organisms are completely different between the two bays, so 60% of one bay's biota is totally different from 60% of the other bay's. The only differences evidenced between the bays in the physical data were dissolved oxygen and temperature. It is possible that the difference in biota is due to these physical differences, or it might be due to the difference in coastal development, that factor I was initially interested in examining. Opunohu is still the best control site for testing Cook's, so I would do further testing to determine the accuracy of the bottom water differences, which here represent only one sampling date in each bay. Also, I would recreate the bottom water and sediment of the two bays in a laboratory

setting and test the survival and fitness of the six species dominant in the two bays, to test if the bottom water differences are directly controlling the organisms present. I would also examine the plankton in each bay for the larvae of the dominants to see if the same larvae are being distributed throughout each bay.

The difference of the communities with depth is suggested by the distributions of some of the dominant species, although again, with such low organism numbers, conclusions drawn from such data are weak. Overall, the biological data from this study show no clear trends, and only by making assumptions of dubious validity about the adequate characterization of dominants can any patterns be seen along depth or differences be found between bays.

**Conclusion**

Ideally in a future benthic study of this area, time and money would be available to do preliminary research to determine the most appropriate core and sieve size and sample number to adequately characterize these communities. In this study the communities were not thoroughly described, as is evidenced by the extremely low abundance and considerable heterogeneity of replicates at each depth. I suspect that a smaller sieve, larger core, and moderately higher sample number at each depth would help significantly in creating clearer data that accurately represent the community. Using a corer with a core catcher would permit coring all the way along the transects into the passes of each bay, where the sandy sediment fell out of the corer used in this study. Increasing the length of the transect might improve the regression with depth for the variables measured. Longer-term bottom water sampling would permit more robust conclusions about habitat differences along and between bays. In addition, it would be useful to measure the levels of a range of pollutants across the depth gradients of the two bays to quantify the direct effects of the differences in shoreline development.

My study shows that there are potentially important differences in the physical environment with depth and between bays. From my biological data I am unable to refute the null hypothesis that the macrobenthic communities do not change with depth or between bays. However, from the difference in dominant organisms between bays and their uneven distribution with depth, other investigators should be encouraged to continue the bays characterization of these two bays; I expect that further larger-scale research efforts will show overall community differences with depth and between bays.

**Acknowledgements**

This research would not have been possible without the tireless core-hauling efforts of my field assistant and good friend Kathleen Sims. I am also indebted to the Amundson and Weston labs for sharing their facilities and equipment with me, and to Dr. Lindberg for assisting in the cluster analyses. Amy Lesen and Virginia Matzek were extremely helpful with technical consulting. From my fellow students Joe Talavera and Eric Crandall I received astute criticism of ideas and writing, as well as their remarkable friendship. Each student in this group was ready to lend an ear and offer suggestions, and it was a pleasure to be a part of!

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**Appendix 1**
Munsell colors of bottom sediment along the depth gradients of Cook's and Opunohu Bays, of both the dry unaltered sediment and the dry post-ashing sediment.

| Bay | Depth Station | Dry Soil Color | Mineral Portion Color |
|---|---|---|---|
| Cook's Bay: | 5m | 10 YR 3/2 | 2.5 YR 4/6 |
| | 10m | 10 YR 3/3 | 2.5 YR 4/6 |
| | 15m | 10 YR 3/3 | 2.5 YR 4/6 |
| | 20m | 10 YR 5/2 - 4/2 | 5 YR 5/6 |
| | 25m | 10 YR 6/3 - 5/3 | 7.5 YR 6/4 |
| | 30m | 10 YR 6/2 | 7.5 YR 6/4 |
| | 35m | 10 YR 7/2 | 10 YR 6/2 |
| Opunohu Bay: | 5m | 10 YR 3/2 | 2.5 YR 4/6 |
| | 10m | 10 YR 3/1 | 2.5 YR 4/6 |
| | 15m | 10 YR 3/1 | 2.5 YR 5/6 |
| | 20m | 10 YR 4/2 | 5 YR 5/6 |
| | 25m | 10 YR 4/2 | 5 YR 5/4 |
| | 30m | 10 YR 5/2 | 5 YR 6/4 |
| | 35m | 10 YR 6/2 | 5 YR 6/4 |
| | 40m | 10 YR 6/2 | 5 YR 6/4 |

# Seagrass, *Halophila decipiens* Ostenfeld, populations in Moorea, French Polynesia, and their response to herbivory and light.

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**Abstract**

There are three seagrass beds of *Halophila decipiens* Ostenfeld in lagoon, estuary, and near shore (strand) habitats, in Pao Pao Bay, Moorea, French Polynesia. The lagoon bed is separated from the barrier reef by a conspicuous band of sand, 24 m. wide. To test whether light conditions or herbivory from reef fish is inhibiting growth of *H. decipiens*,, I constructed four treatments on the back-reef slope, 1) no shade, herbivory; 2) shade, herbivory; 3) no shade, no herbivory; and 4) shade, no herbivory. Transplants from the lagoon and estuary beds, placed into the treatment containers, were monitored for leaf growth, death, and herbivory. Herbivory by reef fish was found to be prohibiting seagrass survival, while light conditions also caused mortality at the top of the back-reef slope.

Transplants under caged and open treatments were placed at 5 intervals along a transect from the top of the back-reef slope (1.37 m. deep) to the seagrass bed (6.1 m. deep). Herbivory caused mortality at the top of the slope, had a minor effect in the middle of the slope, and caused mortality under the caged transplants only at the bottom of the slope.

I compared the morphologies of the lagoon, estuary, and strand seagrass beds. Along an increasing depth gradient, growth rate increased from 0.27 +-0.05 internodes/d at the strand bed, to 0.55 +-0.17 internodes/d. Leaf lengths and widths appeared to decline along an increasing salinity gradient.

## 1. Introduction

Seagrasses are highly adapted flowering monocot plants forming extensive underwater meadows in the shallow-water coastal areas of the world. Seagrass meadows operate primarily on detritus based food webs, and to a lesser extent on herbivore webs (Phillips and Menez, 1988). Historically, herbivory has been thought to be modest on most seagrasses (den Hartog, 1970), however, new research has revealed a greater impact of herbivory on some seagrass species by tropical urchins (Vadas et.al., 1982), fish, e.g. bucktooth parrotfish (Lobel and Ogden, 1981), green sea turtles (Bjorndal, 1980), and sirenians (Thayer et. al., 1984).

Within the last half century, seagrasses have been recognized as important marine resources. Wood, Odum, and Zieman (1969) list the major functions of seagrasses as: (1) sediment stabilization even through the stresses of hurricanes and temperate storms; (2) slowing of water currents and waves, promoting sedimentation and inhibiting resuspension of organic and inorganic matter; (3) refuge for adult and juvenile animals, particularly juvenile fish, many of which have commercial and recreational value; (4) herbivore and detrital pathways are supported by high productivity (leaves of some species can grow up to 1cm/day); (5) internal nutrient cycles keep organic matter and nutrients within the system.

There are approximately 48 species of these grass-like plants, derived from two families, Potamogetonaceae (9 genera, 34 species), and Hydrocharitaceae (3 genera, 14 species) (Phillips, and Menez, 1988). The genus *Halophila*, in the family Hydrocharitaceae, contains 11 species of seagrass, one of which, *Halophila decipiens* Ostenfeld, is the topic of this paper.

### 1.2 Characteristics of *Halophila Decipiens* Ostenfeld

*Halophila decipiens* Ostenfeld, the only pantropical seagrass species, is found in the tropical regions of the Pacific, Atlantic, and Indian Oceans. In the Society Islands *H. decipiens* is the only known seagrass (den Hartog, 1970) (Phillips and Menez, 1988). The species possesses a number of characteristics which allow it to grow in deep, turbid, or shaded marine environments. These characteristics include a high ratio of leaf tissue to non-photosynthetic tissue, a low

leaf area index (reduces self shading), high turnover rate, and the ability to rapidly colonize suitable sandy bottoms (Josselyn et. al., 1986). The species usually occurs between 10-30 m. deep though it grows anywhere from sheltered low tide level sites to 85 m. deep (Phillips and Menez, 1988).

**Figure 1:** *H. decipiens* Ostenfeld. Global distribution. Modified from Phillips and Menez (1988)

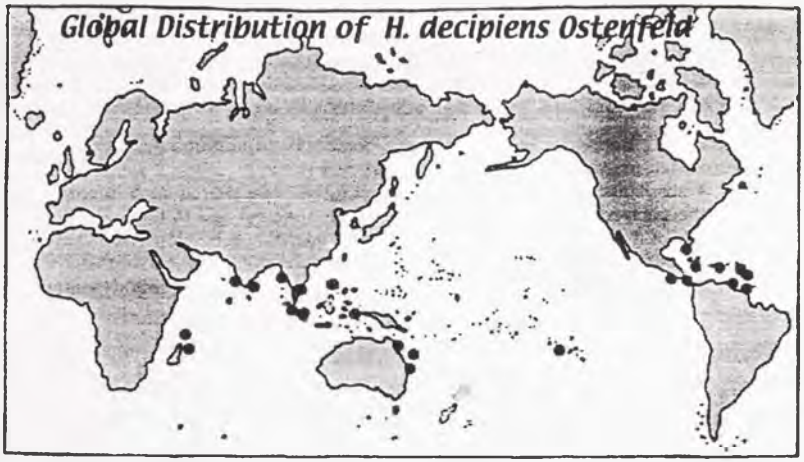
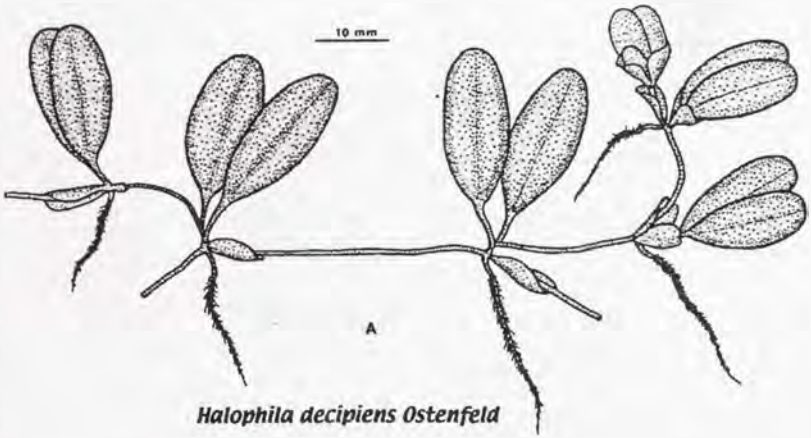


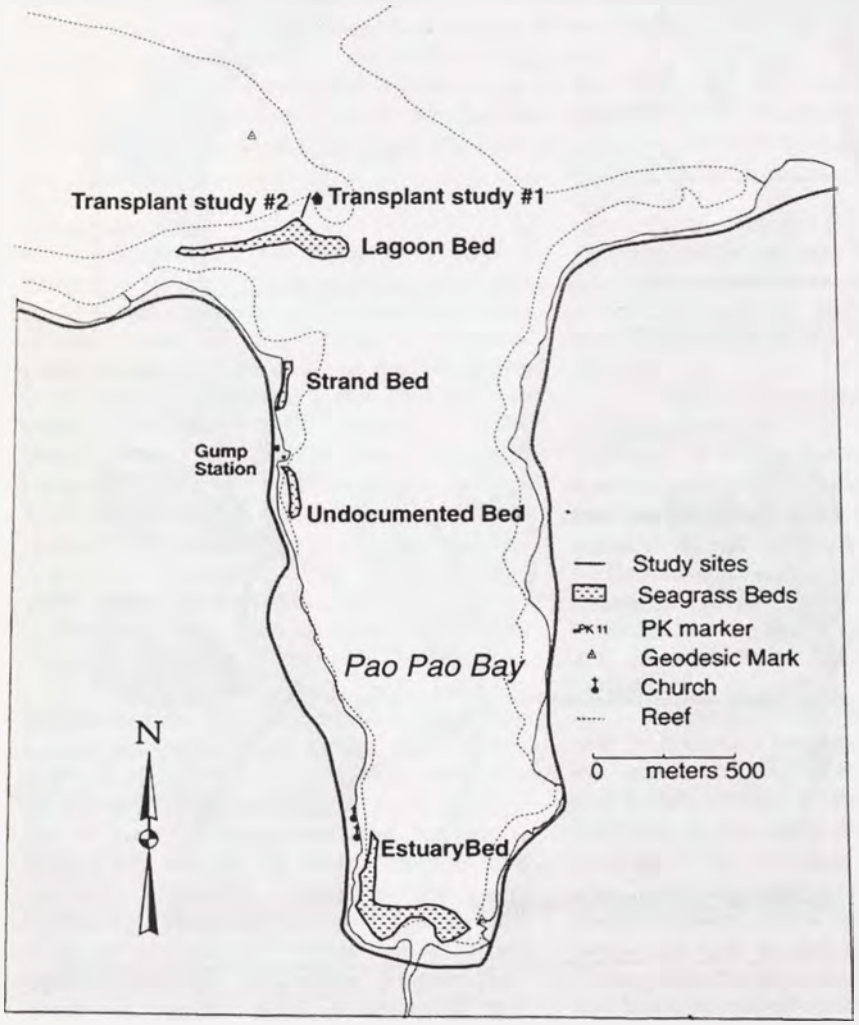

**Figure 2:** Habit of sterile plant. Modified from Phillips and Menez (1988).



### 1.3 Site Information

Previous to this study, there were two documented *H. decipiens* meadows in Pao Pao Bay (Emmett 1996). The habitats of the two meadows, as well as the morphologies of the seagrass growing in them are remarkably different. The estuarine meadow is located at the mouth of Pao Pao river, where sedimentation is high, and the water shallow (0.5 -5 meters). The lagoon meadow begins behind the barrier reef where the back-reef slope levels off at 6.1 meters depth, and continues down a gradual slope to 20 meters (Emmett, 1996). Emmett reported variations in seagrass morphology corresponding to differences in the physical environment of the *H. decipiens* meadows. Compared to the seagrass growing in the lagoon bed, the estuarine *H. decipiens* has longer internodes, and smaller leaf surface area. Emmett's results suggested physical adaptability to gradients of salinity, depth, light, temperature, and substrate. During my research, I located a third bed, 0.5 hectares area, and growing in .5m of water under the shade of some trees along the edge of Pao Pao Bay. This third bed does not fall into either

**Figure 3:** Map of Pao Pao Bay, Moorea, showing study sites and locations of *H. decipiens* beds.



of the two categories described by Elliot, and will be referred to as the strand bed. (Figure 3)

Of particular interest is the location of the lagoon meadow in relation to the reef. Between the reef and *H. decipiens* bed, on the back reef slope, lies a 24 meter stretch of bare sand, occasionally dotted by a patch reef . Halos of sand separating reefs from *Thalasia testudinum* seagrass beds have been attributed to herbivory from reef fish (Randall, 1965). However, this case is unusual in that the sand is the back-reef slope, and the species of seagrass is different. It was unclear weather the apparent herbivory halo was caused by herbivory, light intolerance of *H. decipiens*, or sediment movement along the back-reef slope.

**1.4 Objectives**

The objectives of this study are

(1) to understand the factors prohibiting *H. decipiens* growth on the back reef slope;

(2) to understand the gradients in those factors along the reef to seagrass bed transect, and

(3) to compare *H. decipiens* characteristics and morphology in the strand bed to the estuarine and lagoon beds.

## 2. Methods and Materials

**2.1 Transplant Study 1**

***Site selection and Habitat description***

The site selected for relocating the transplants in the first light/herbivory study lies on the lagoon side of the barrier reef, at the top of the back reef slope, and adjacent to the lagoon *H. decipiens* bed (See Map). The advantages of this site include proximity to the reef, herbivory by reef fishes, and a shallow, high light environment. The water depth at this site is 1.5m.

I chose to take transplants from the lagoon and estuary sites described by Elliot (1996). By including the estuarine H. decipiens in this study, a wider range of variability within the species is accounted for. One obvious difference between plants from the two sites was that the amount of silt, and epiphytes covering the leaves was far greater on the estuarine plants. Herbivores may prefer seagrass with more, or less epiphytes. In addition, by including the estuarine plants, I was able to test herbivore preference for plants with different leaf specific growth rates (SGR). *H. decipiens* growing in the lagoon bed have a higher SGR than the *H. decipiens* in the estuarine bed (Emmett, 1996). While herbivores have been shown to prefer seagrass species with higher SGR, an index of leaf nutritional quality (Cebrian, and Duarte, 1998), it is uncertain whether the trend in herbivory relating to SGR is maintained between two populations of the same species. Finally, more sediment in the water column at the estuarine site translates into more sediment incorporating into the algal mat or epiphytic community of the seagrass (Heijs, 1984). This in turn may effect palatability, manifested as herbivore preference for *H. decipiens* from the lagoon bed. Separating SGR and sediment incorporation in the epiphyte community as they both effect herbivore preference is beyond the scope of this study.

***Transplant and Collection Methods***

Transplants were made into plastic containers measuring 14 x 21 x 6cm. With a gardening trowel, I cut around an area of seagrass equal to the size of the transplant container, and placed the plants, plus two to three inches of sediment into the plastic containers. Placing a second container face down on top of the transplant minimized sediment loss while surfacing. To keep the number of leaves per sample between 40 and 150, one quarter of each transplant was randomly selected for sampling. Quarter sections were delineated using green gardening ribbon tied around the transplant containers. I then "planted" the transplants in sediment so that the entire container was underground.

***Treatments***

I collected a total of sixteen transplants, eight from each of two seagrass meadows. Two transplants from the deep water lagoon meadow and two transplants from the shallow water estuary meadow were provided for each of four treatments. The treatments were 1) herbivory and no shade, 2) no herbivory and shade, 3) No

herbivory and no shade, and 4) herbivory and shade. A 0.5 cm mesh chicken wire was chosen as an herbivory block on treatments 2 and 3 because it kept the largest grazers out, while allowing sufficient current to penetrate the cages. Three layers of black window screening provided shading in treatments 2 and 4. The transplants under treatment 1 were left in the open. Other materials used in constructing the treatments included string and wooden stakes for anchoring the cages to the sediment, and wire for fastening the screening to the cages.

*Data Collection*

The number of dead and living leaves in the quarter transplant samples were counted at the initiation of the study, and at regular intervals of 2-4 days for approximately two weeks. If herbivory was present, evidenced by clipped leaves, a negative trend in number of leaves was attributed to herbivory. When no herbivory sign was detected, missing leaves were assumed to have died and fallen off. A positive trend in number of leaves indicated new growth.

**2.2 Transplant Study 2**

Twenty transplants were taken from the lagoon *H. decipiens* meadow. I placed the transplants along a transect running from the lagoon edge of the back reef at 1.37 m. deep, down a sandy slope to the beginning of the seagrass meadow at 6.1 m. deep. At each of five intervals (0, 9.25, 16.15, 19.81, and 23.7 m from the reef) two transplants were placed under chicken wire cages to eliminate large herbivores, and two transplants were left open to herbivory. Rather than providing shading, the increasing depth of the transplants provided a light gradient down to the seagrass bed margins.

*Data collection*

Again, I counted the number of living and dead leaves on one quarter of each transplant at the initiation of the study. However, during the study, observations were made, but no further leaf counts were taken until the 14th day. This minimized disturbance associated with leaf counts, which without the use of SCUBA, required surfacing with each transplant. This method also allowed plant growth beyond the borders of the transplant container.

**2.3 Seagrass Bed Comparison**

This segment of the study utilizes the methods employed by Emmet (1996) to describe the estuarine and lagoon seagrass beds in Pao Pao Bay. Data was collected for percent cover, growth rate, internode length, biomass, leaf length, leaf width, and leaf surface area of the strand *H. decipiens* bed. Averages of these data were then compared between beds to determine which characteristics were statistically different.

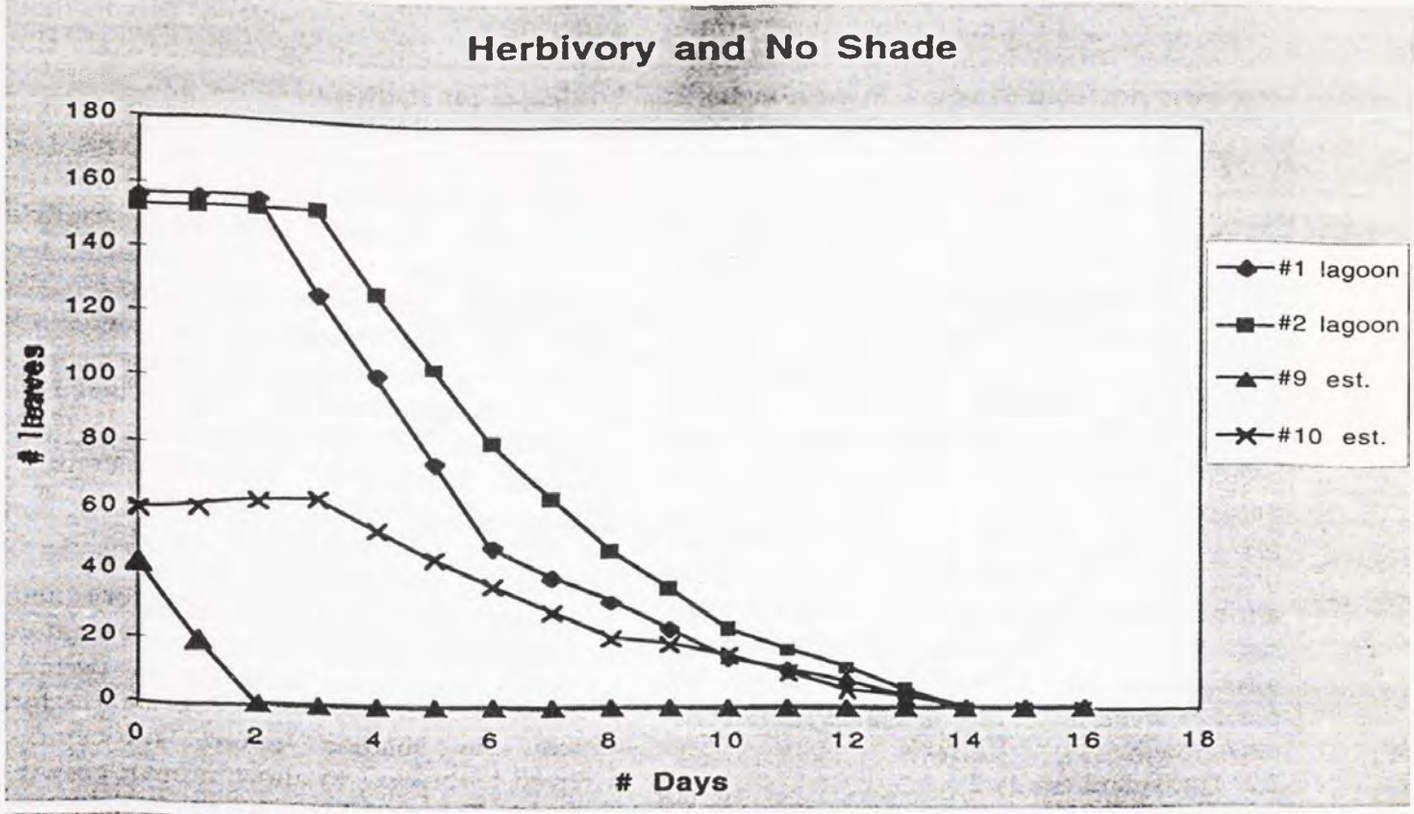
## 3. Results and Data

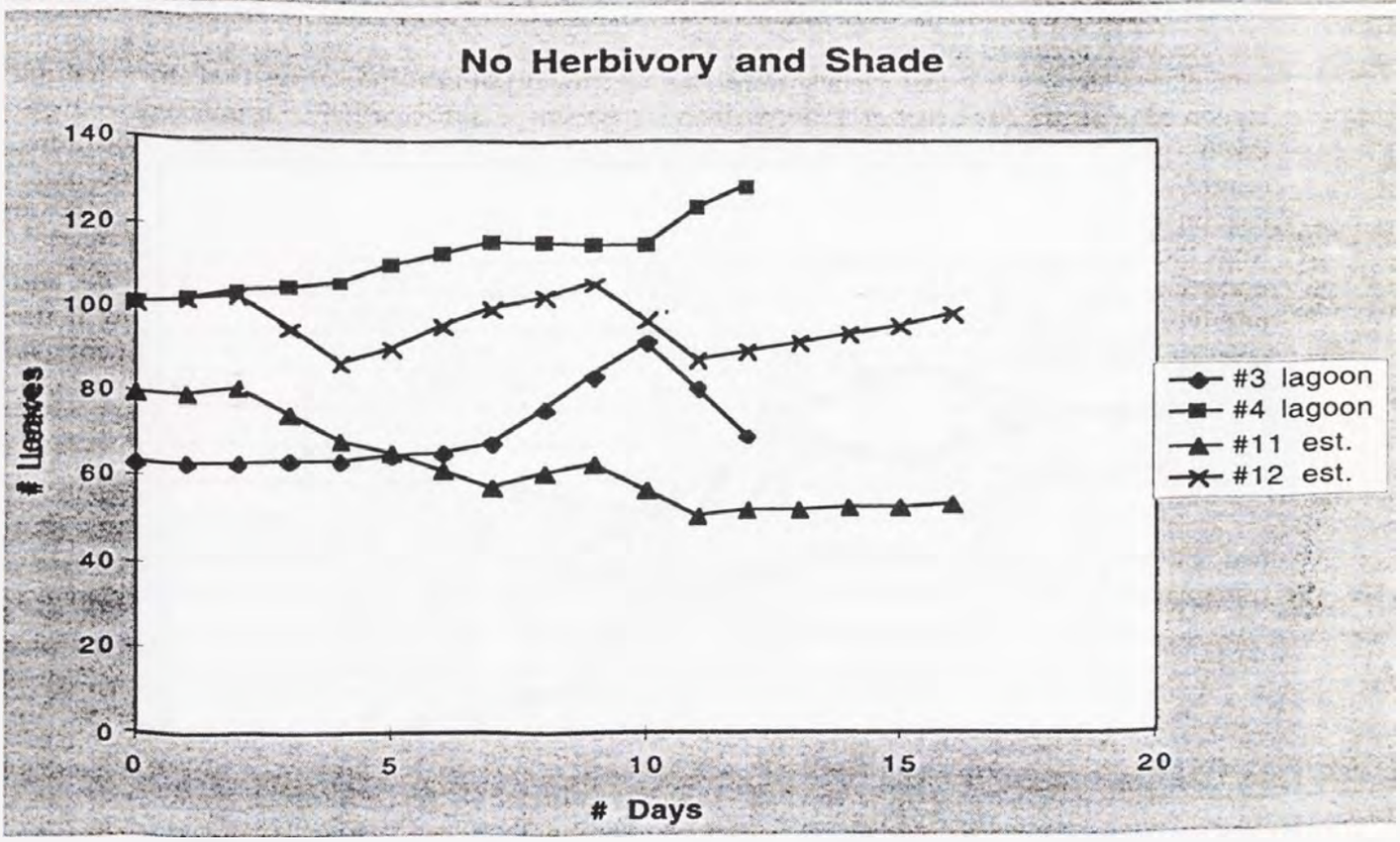
**3.1 Transplant study 1** (Figures 4-7)

Transplants open to herbivory and normal light (#s 1,2,9,10) were eaten completely within the two week period. This excludes transplants 7,8,15, and 16 for which the shading screen sufficiently deterred herbivory to allow normal growth to occur. Transplants under shade with no herbivory (#s 3,4,11, and 12) showed a normal growth pattern, indicating that the shading screen sufficiently mimicked light characteristics at both seagrass bed locations. The number of leaves in transplants under normal light conditions and without herbivory (#s 5,6,13, and 14) declined slowly.

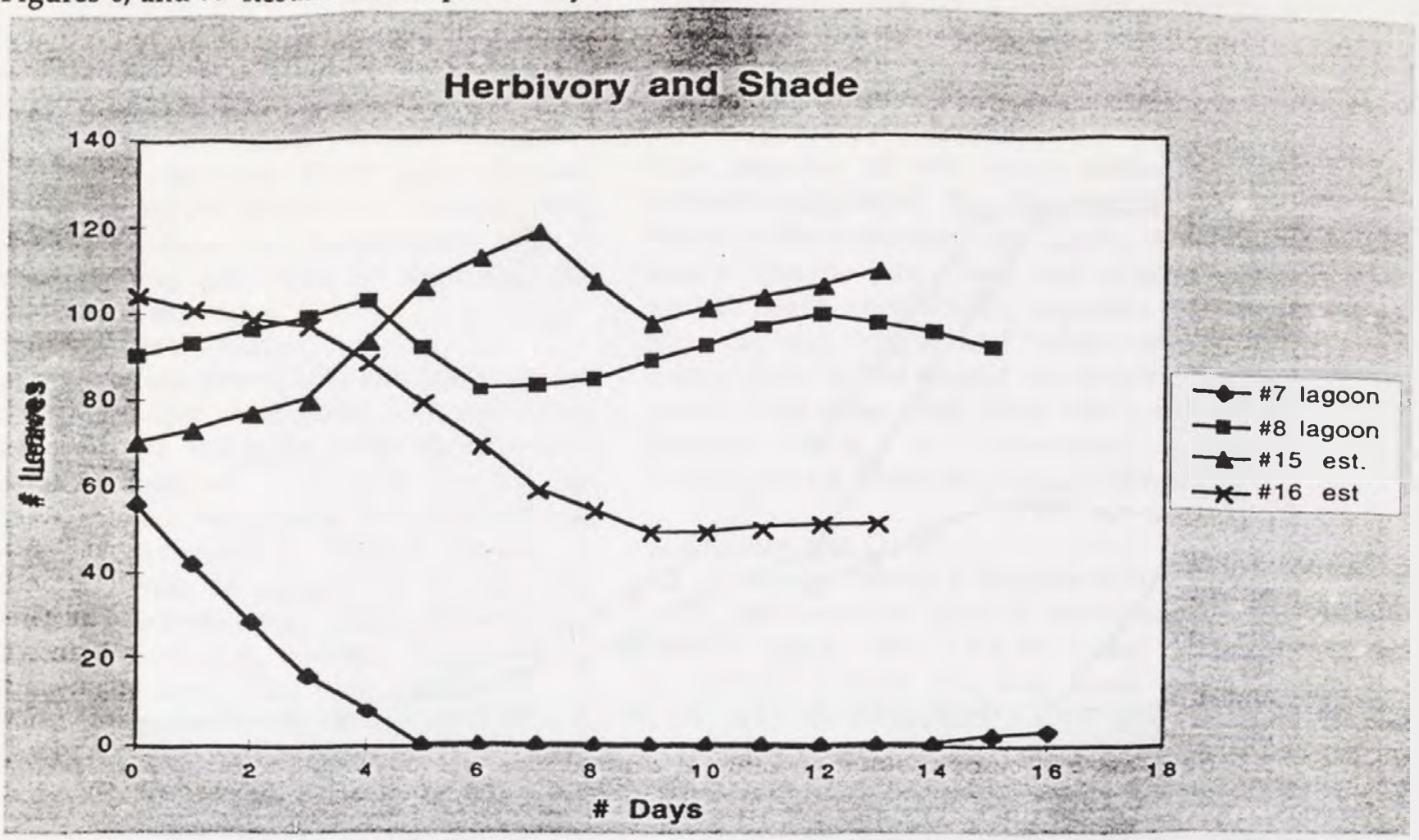
Transplants from the estuarine and lagoon beds responded differently only under the no herbivory and no shade treatment (#s 5,6,13, and 14). While the lagoon plants showed a continual decline until the end of the treatment period, the estuarine plants declined initially before they began to recover after nine days. Of the four transplants left in the open (#s 1, 2, 9, and 10), herbivores preferred neither the lagoon nor estuarine seagrasses.

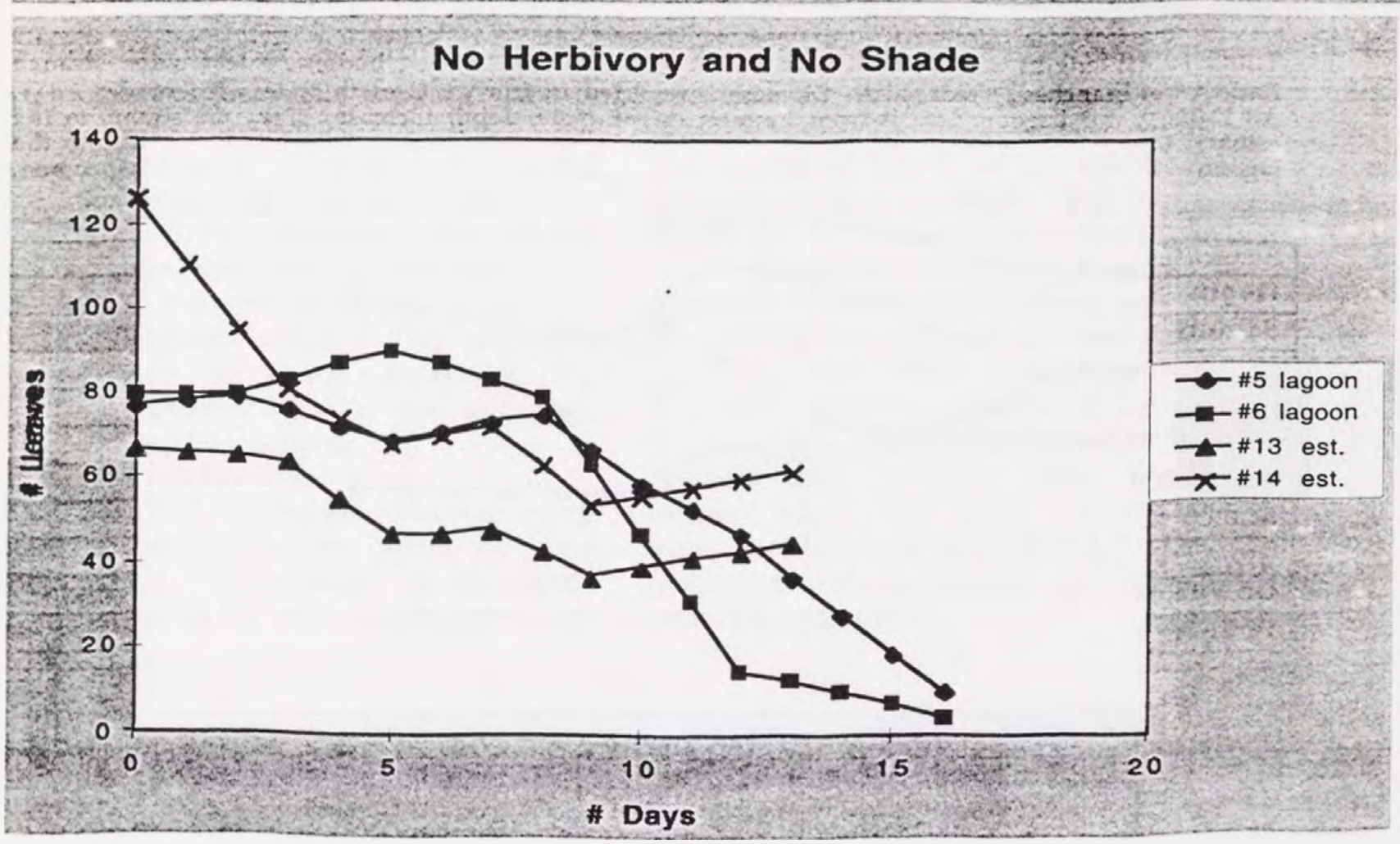
Figures 4-5: Results of Transplant study #1. Note four transplants for each treatment



Figures 6, and 7: Results of transplant study #1 continued..




3.2 **Transplant study 2** (Figures 7 and 8)

Uncaged transplants at 0 m. (a, and f), were eaten to the ground after 4 days. At the 9.25 m. site, uncaged transplants(b, and g) were completely eaten after 5, and 9 days respectively. Uncaged transplants from 16.15 m. (c, and h) survived with 61% and 54% of their original number of leaves. Transplant i, from19.81m, survived with 47% of its original leaves while the replicate transplant, d, was eaten to the ground after 12 days. At 23.7 m (e, and j), survived with 30%, and 90% of their leaves

With two exceptions, the caged transplants all survived during the study period. At 0m.,transplants A, and F, both ended with 40% of their original leaves. Transplants B, and G, from 9.25 m., finished with only 11%, and 17%., and at 16.15 m., transplants C, and H, retained 47%, and 78% of their leaves. Transplant D, from 19.81 m. retained only 5%, and transplant E, from 23.7 m., retained 0% of its leaves. However, the replicates from these depths, transplants I, and J, both survived with quite different percentages, 81%, and 106% respectively.

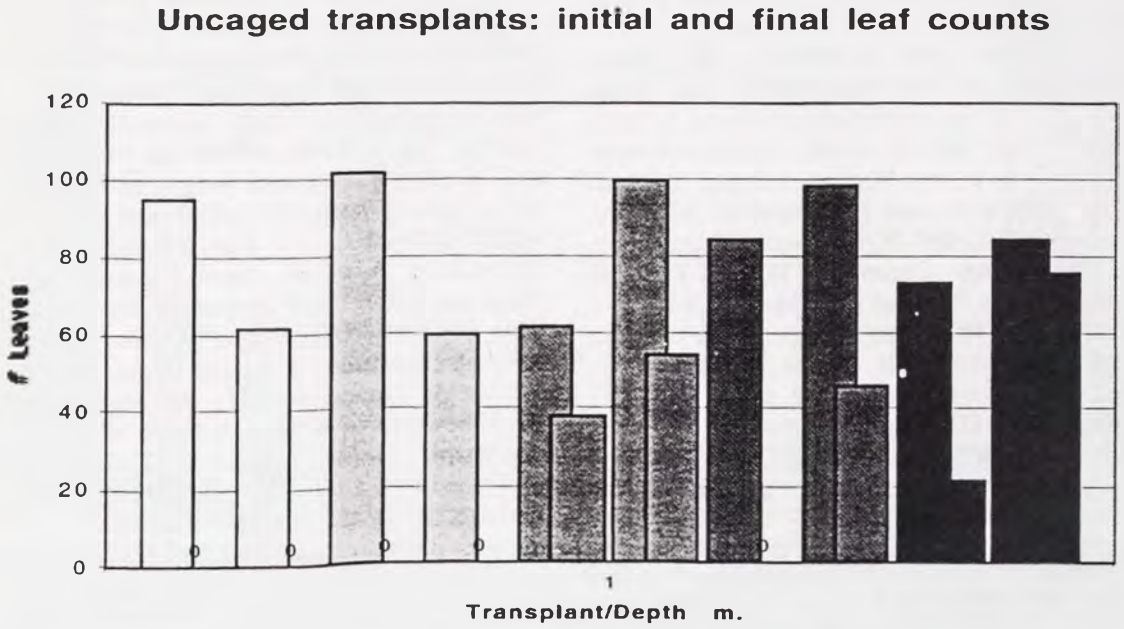
**3.3 Seagrass bed comparison** (See Table 1)

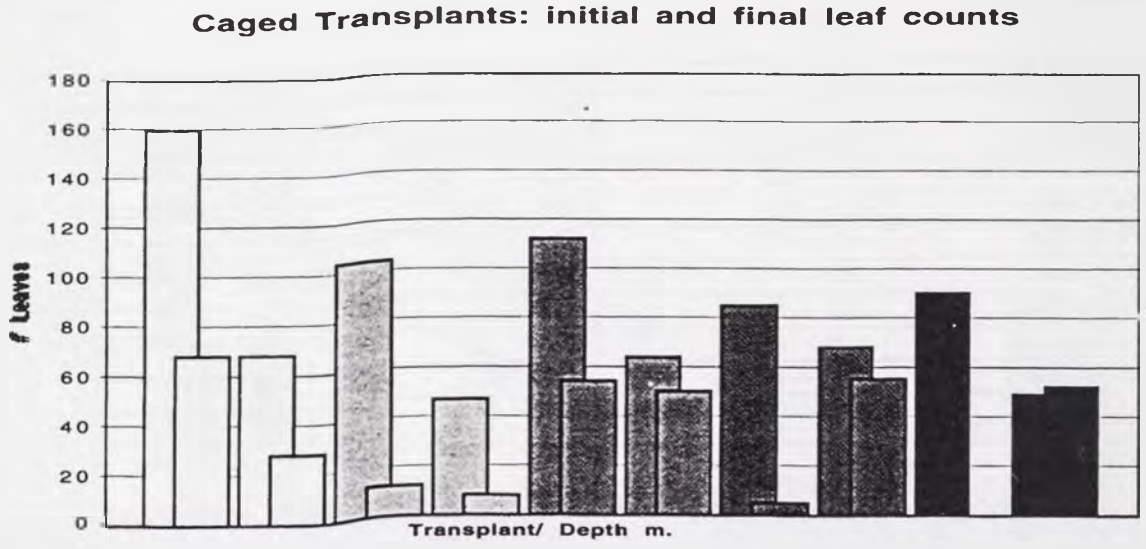
When compared to the estuarine and lagoon beds, the strand bed has several distinguishing characteristics. Percent cover at the strand bed (77 +- 17%) was higher than both the lagoon (47 +- 17%) and estuary (47 +- 15%) beds. Biomass at the strand site (76 +- 30g/$m^2$ ) more than doubled the biomass at the lagoon (27 +- 11 g/$m^2$ ) or estuary (29 +- 14 g/$m^2$ ) sites. Despite higher biomass and % cover, internode growth rate was lower at the strand site (0.27 +- 0.06 internodes/d) than at the lagoon ( 0.55 +- 0.11 internodes/d) and the estuary sites (0.37 +- 0.11 internodes/d). Both internode length and leaf width were smallest at the strand site. Values for internode length are 16.36 +- 6.07, 20.5 +- 6, and 24 +-8.05 and for leaf width, 4.33 +-0.77, 5 +- 0.69, and 6.2 +- 1.11, respectively for the strand, lagoon, and estuarine beds. Leaf length at the strand sight (16.31 +- 3.07) is smaller than at the estuarine site (22 +- 4.1), and larger than at the lagoon site (15 +- 2.1) All lagoon and estuary data from this section are from Emmet (1996).

**Table 1: All lengths are reported in mm.. Fruit ratio = # of fruiting bodies / # leaf pairs. Branch Ratio = # of branches / # leaf pairs. Biomass is reported in g/m sq. Growth Rate = Internodes / day. All Estuary and Lagoon data is from Emmett (1996). Note, depth increases from the strand, to the estuary, to the lagoon bed, while assumed salinity increases from the estuary to the strand, to the lagoon bed.**

| Seagrass Bed | Estuary | Strand | Lagoon |
|---|---|---|---|
| Depth | 0.5 - 5 m. | 0.5 m. | 6.1 - 20 m. |
| Salinity | Assumed low | Assumed medium | Assumed high |
| Internode Length | 24 +- 8.05 | 16.36 +- 6.07 | 20.5 +- 6 |
| Leaf Length | 22 +- 4.1 | 16.31 +- 3.08 | 15 +- 2.1 |
| Leaf Width | 6.2 +- 1.11 | 4.32 +- 0.77 | 5 +- 0.69 |
| Fruit Ratio | 0.08 +- 0.12 | 0.71 +- 0.29 | 0.15 +- 0.21 |
| Branch Ratio | 0.33 +- 0.23 | 0.21 +- 0.24 | 0.29 +- 0.25 |
| Biomass | 0.29 +- 0.14 | 0.76 +- 0.29 | 0.27 +- 0.11 |
| Growth Rate | 0.37 +- 0.11 | 0.27 +- 0.06 | 0.55 +- 0.17 |
| % Cover | 0.48 +- 0.15 | 0.77 +- 0.17 | 0.47 +- 0.17 |

Figures 8 and 9: Results of transplant study #2. Note that depth and distance from the reef increase as the columns become darker to the right. Also note that each set of two bars represent initial, and final leaf counts for one transplant. For the uncaged transplant figure, all four transplants on the left go to zero.



## 4.0 Discussion

### 4.1 Transplant study 1

At the top of the back reef slope, herbivory is the major factor preventing *H. decipiens* colonization. Light intensity also plays a role in decreasing the fitness of growing plants. The caged and unshaded transplants, 13 and 14, demonstrate that light may not be completely interrupting growth at 1.5 meters depth. Between days 9 and 13 , transplant #13 increased from 37 to 45 leaves, and transplant #14 increased from 54 to 62 leaves. It is uncertain whether this increase indicates an actual recovery or just a short term trend in a continuing decline. However, if recovery is assumed, these results suggest that the estuary plants may be better adapted to large fluctuations of light intensity associated with sediment load during the flood, and drought of Pao Pao river.

Observation of all of the transplants under a no shade and no herbivory treatment indicated extensive competition by epiphytic algae. Epiphytes may have actually supported new seagrass growth by providing a canopy of shade under which new shoots could grow. This observation was made for all of the no herbivory no shade transplants (#s 5,6,13, and14). Transplant under shading screens had very little or no epiphytic algae.

### 4.2 Transplant study 2

Some trends reflecting the effect of herbivory and light gradients along the back-reef slope were observed. Herbivory decreased from the top of the back-reef slope to the edge of the seagrass bed. With the exception of the middle site, at 16.15 m from the reef, the caged transplants fared better than the uncaged transplants. Uncaged transplants c, and h, may be the exception due to their extreme exposure in the middle of the sandy slope, where herbivores are furthest away from any refuge. Herbivory completely overwhelmed uncaged transplants at the top, and near the top of the back reef slope (a, b,f, and g). At the bottom of the back-reef slope, a small difference between caged and uncaged transplants indicated low herbivory.

Herbivory by small fish which could fit through the chicken wire mesh was evident in two transplants, D and E, at the bottom of the slope. By providing forage, and cover from large predators, the cages may have actually encouraged herbivory by small fish which were observed in the cages, and near the seagrass bed. However, the replicate caged transplants I and J showed no such small fish herbivory, and reflected a normal growth pattern. Some grazing by small herbivores is likely occurring at the lagoon seagrass bed. However, Ogden (1990) notes that small grazers do little to effect seagrass community structure, while the larger herbivores such as manatees and turtles profoundly effect both structure and function of seagrass communities.

A gradient in the % leaves retained for the caged transplants reveals the effects of diminishing light on *H. decipiens* . The number of leaves on the four caged transplants nearest the top of the back-reef slope (A,B,F, and G) decreased by at least 60% during the study. Caged transplants in the middle of the slope (C, and H) decreased by less,53%, and 22% respectively. The caged transplant (I), between the middle and bottom of the slope, which was not grazed upon by small fish, decreased by only 19%, while at the bottom of the slope, transplant J, was the only transplant to increase its number of leaves, ending with 106%.

### 4.3 Seagrass bed comparison

Morphogeographic variations in seagrass species have been documented by Phillips (1960), McMillan and Moseley (1967), Strawn (1961), and McMillan (1978). McMillan (1978) concluded that:

1) seagrass leaf length and width can be modified by interaction with changing environmental conditions, though ecoplastic limits are genetically controlled.

2) Seagrass species may contain local populations with distinct genetic limits of ecoplasticity.

3)Within local populations, individual clones may have distinct limits of endogenous plasticity.

McMillan, (1978), found two genetically dissimilar populations of *Halophila engelmannii* which showed a trend from wide to narrow leaves along an environmental gradient of increasing depth. Similarly, this study finds that along the same depth gradient, growth rate increases for *H. decipiens*. Growth rate is the sole characteristic measured here, which relates the strand bed more closely to the estuarine bed. By all of the other characteristics, the strand bed appears to be more closely related morphologically to the lagoon bed. This association may represent an assumed salinity gradient which begins with low salinity at the estuarine bed, medium to high salinity at the strand bed, and high salinity at the deep water lagoon bed. To make any conclusions, the salinities of the strand and lagoon beds, must be more similar than the salinities of the strand and estuary beds. Whereas Phillips (1960) reports shorter and narrower leaves in low salinities for *Thalassia testudinium* , this study finds the opposite for *H. decipiens*. The higher salinity sights (lagoon and strand), had significantly smaller leaf lengths, and widths.

Visual observations made during the study suggest that each *H. decipiens* bed supports a unique assemblage of flora and fauna. For example, the flying guinard was only seen at the estuary bed, and the *H. decipiens* mimicking algae, *Caulerpa taxifola* , was only found at the strand bed. Though identifications of fish fauna were not completed, obvious differences in the juvenile and adult fish using each seagrass bed were observed.

## 5. Conclusion

This study has contributed the following conclusions to the understanding of *H. decipiens* populations, and their response to light and herbivory in Pao Pao Bay, Moorea.

(1) Herbivory and light both affect the ability of *H. decipiens* to survive in an environment such as the back-reef slope.

(2) The ability of *H. decipiens* to survive on the back-reef slope increases with depth and distance from the reef, and is caused by gradients in light and herbivory.

(3) Three morphologically distinct *H. decipiens* beds exist in Pao Pao Bay.

Understanding habitat partitioning of *H. decipiens* has consequences for local people and conservation. Coastal development has the potential to eradicate at least some of the diverse *H. decipiens* habitats currently found on Moorea. Without further research, the consequences for local fisheries will continue to be unknown, and will go unnoticed. It is thus of primary importance to gain a comprehensive understanding of the flora, fauna, and ecosystem dynamics of each unique *H. decipiens* habitat.

Use of SCUBA would have allowed multiple leaf counts during the transect study. I also recommend that light under any shades, and at the seagrass sights, as well as salinity be quantified in the future. This data would allow gradients and trends in seagrass morphology to be conclusive rather than assumed.

### 5.3 Suggestions for Future Work

I observed several other seagrass beds in Pao Pao Bay which are not discussed in this paper. Due to lack of time, I was not able to analyze these in the manner of Emmet (1996). It would be interesting to look further into the relationship between the variable physical habitats, meadow characteristics, and *H. decipiens* morphologies of these beds. It is unclear weather each *H. decipiens* population is genetically distinct, or weather the morphological differences observed are within the genetic plasticity of a single populations. Furthermore, little is known about the infauna, epifauna, and macrofauna of *H. decipiens* meadows in French Polynesia. The map shows the location of an undocumented *H. decipiens* bed.

## 6. Acknowledgments

Thanks to UC Berkeley for the use of the Gump Research Station, to Michael Emmett for his initial research on *H. decipiens* in Moorea, to my professors, Dr. Vince Resh, Dr. Jere Lipps, Dr. David Stoddart, and Dr. David Lindberg, to the dedicated teaching assistants, Tegan Churcher, Virginia Matzek , and Amy Lesen, and to my 21 fellow colleagues without whom all would have failed.

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# Distribution and host preference of the parasitic vine *Cassytha filiformis* (Lauraceae) growing on Motu Tiahura, Moorea, French Polynesia

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ABSTRACT. Host preference and patterns of infestation by the parasitic angiosperm *Cassytha filiformis* (Lauraceae) were examined on Motu Tiahura, Moorea, French Polynesia (149°55'W, 17°30'S). Infestation rates (measured as percent of individuals or ramets infested) varied with habitat, significantly higher in the broadleaf forest than the sparser vegetation immediately adjacent to the beach. *Cassytha* preferentially infested herbs, shrubs, and trees over grasses, sedges, and ferns, and preferentially infested shrubs and trees over herbs. Among species with similar growth forms, *Cassytha* showed significant preferences for certain species, namely *Lepturus repens* and *Cenchrus echinatus* among grasses and sedges, *Emilia fosbergii* and *Passiflora foetida* among herbs, and *Scaevola taccada* among shrubs and trees. *Cassytha* displayed great generality in host range as well, infesting 19 out of 21 potential host species examined. Possible explanations for the observed infestation patterns include distributional limits imposed by *Cassytha*'s own physiological requirements, the distribution and abundance of host plants, and the size and age of potential host plants. Comparing patterns in infestation rates (in all species) across habitats to infestation rates in a single widespread species (*Lepturus repens*) did not support the hypothesis that physiological constraints played a major role in generating the observed habitat preference. Comparing patterns in overall infestation rates to the distribution of preferred hosts supported the hypothesis that the observed patterns could in part be explained by the distribution of host plants. Analysis of the role of host plant size in influencing infestation rates was inconclusive.

## Introduction

*Cassytha filiformis* (Lauraceae) is a parasitic angiosperm with a pantropical distribution. *Cassytha* is largely restricted to coastal habitats, possibly because it depends on ocean currents to disperse its fruits and seeds (Wiens 1962). On Moorea, French Polynesia (149°50' W, 17°30' S), *Cassytha* is found in three habitats. Small populations persist in fragments of coastal strand vegetation along the coast of the main island. Patches of *Cassytha* also grow at low (< 100m) elevations on hills along the north coast of the island, usually in disturbed environments. The largest populations are found on the surrounding motu, islets formed by the accumulation and cementation of coral rubble on top of the barrier reef.

*Cassytha* parasitizes xylem fluid of its hosts via haustoria which penetrate the host plants' vascular tissues (Burch 1992). This parasitism may significantly reduce the fitness of host plants (Burch 1992; Schmutterer 1998). *Cassytha* is a perennial and a single plant often infests multiple hosts, such that an individual *Cassytha* need not die following the death of a host plant.

Host preference in *Cassytha* has received little study. Kujit (1969) states that herbaceous plants often serve as "starters" for *Cassytha* seedlings (which germinate independently in the soil), but *Cassytha* finds its full development in woody plants. As a xylem parasite, *Cassytha* might be expected to display "relatively unspecialized" host selection (Burch 1992). Some studies of ecologically similar (Kujit 1969) dodders of the genus *Cuscuta* have found distinct host preferences (Pennings and Callaway 1996), but this is not true of all species. A study of five species of *Cuscuta* found restricted host ranges in two species but wide host ranges in three others (Beliz 1987).

This study examined the host preference of *Cassytha filiformis* growing in Moorea. Host infestation rates were investigated as a function of habitat, growth habit of hosts, species of host, and size of individuals within selected host species.

## Methods

Field sampling was carried out during October and November 1998 on an 80m stretch of publicly - accessible beach on the northwest coast of Motu Tiahura (149°55'W, 17°30'S, Figure 1). This site was chosen because it offered the most diverse plant community with the least human traffic of all potential sites.

Within approximately 10 - 12m of the high tide line, the beach consists predominately of bare coral sand. From approximately 12 - 22m inland plant cover increases, with grasses and sedges (e.g., *Lepturus repens* and *Fimbristylis cymosa*) and small herbs (e.g., *Chamaesyce prostrata*) dominant. A broadleaf forest grows further inland, with dominant overstory plants including *Cocos nucifera* and *Pandanus tectorius*, an intermediate canopy of plants such as *Hibiscus tiliaceus*, *Morinda citrifolia*, and *Premna serratifolia*,

and groundcover including *Passiflora foetida, Emilia fosbergii,* and *Phymatosorus* sp. (Figure 2).

**Figure 1.** Location of Motu Tiahura, the study site.

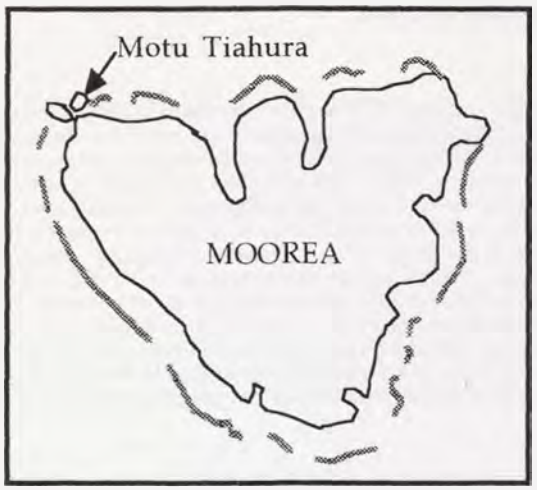
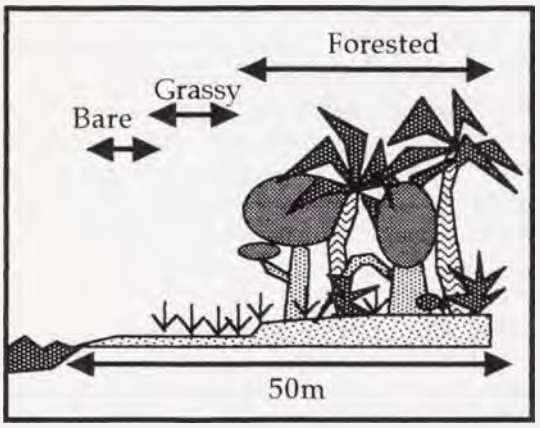



**Figure 2.** Cross-sectional profile of study site.




Within this site, three areas containing infestations of *Cassytha* were chosen. These areas spanned 37m of coastline. Eight points were selected at random along the high tide line within these zones, and from each point a transect was run 50m inland. Along each transect, every individual (or ramet for clonal plants) rooting within 1m to either side was identified (using morphospecies criteria if necessary). For each individual or ramet, the species identification, distance from the high tide line, and presence or absence of *Cassytha* infestation (as determined by the attachment and apparent penetration of haustoria) was recorded. In areas with dense grass cover, grass ramet numbers were estimated in $1m^2$ blocks. Many grass ramets lacked reproductive structures and so identification was attempted based only on vegetative characteristics.

Each individual or ramet was classified into one of four growth forms based on its growth habit - grasses, ferns, herbs (plants lacking woody stems), and shrubs/trees. Sedges were grouped with grasses based on their similar growth habits. Seedlings of shrubs and trees that had not yet developed secondary stem hardening were classified as herbs, and *Cocos nucifera* and *Pandanus tectorius* plants over 20cm tall were classified as shrubs and trees because their stems are hardened and their growth habit resembles other shrubs and trees. For *Morinda citrifolia, Hibiscus tiliaceus,* and *Scaevola taccada* plants, stem length was recorded as well.

Patterns in infestation rates as a function of habitat were examined by describing each plant sampled as growing in either the open shore habitat or the broadleaf forest habitat. Infestation rates (defined as percent of individuals or ramets infested) in the open habitat were compared to infestation rates in the forest using a Chi-square test. Composition of each habitat was examined in terms of the relative abundance of each growth form in each habitat. A Chi-square test was used to compare the compositions of the two habitats.

A Chi-square test followed by a Tukey type test for comparison of multiple proportions (Zar 1996) was used to compare infestation rates among different growth forms. Infestation rates were compared among species within a growth form category using a Pearson Chi-square test followed by a Tukey type test, excluding rare species (< 10 individuals or ramets in all transects combined) so that Cochran's criterion for sparseness was not exceeded (Sall and Lehman 1996). Logistic regression (Sall and Lehman 1996) was used to examine the effect of host plant stem length on infestation rates.

## Results

*Habitat comparison*

Overall infestation rates were more than four times higher in the broadleaf forest than in the open shore habitat (Figure 3a, $\chi^2 = 378$, df = 1, $p < .001$). Considering only infestation on *Lepturus repens*, the most widespread species, infestation rates did not differ significantly between habitats (Figure 3b, $\chi^2 = 2.82$, $p = .093$).

The two habitat types differed significantly in their composition (Table 1, $\chi^2 = 2030$, df =3, $p < .001$).

The open shore habitat was almost entirely grass (93% of all individuals or ramets). Grasses were also the most abundant growth form in the forest (48% of all individuals or ramets), but other growth forms were several times more abundant than in the open shore habitat.

**Figure 3a.** Infestation rates (percent individuals or ramets of all species infested) by habitat type. Error bars represent 95% confidence intervals.

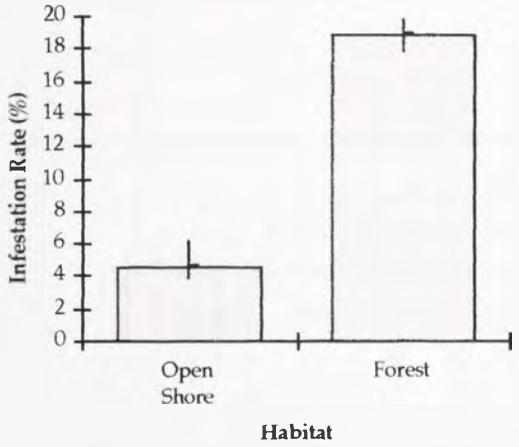



**Figure 3b.** Infestation rates on *Lepturus repens* by habitat type. Error bars represent 95% confidence intervals.

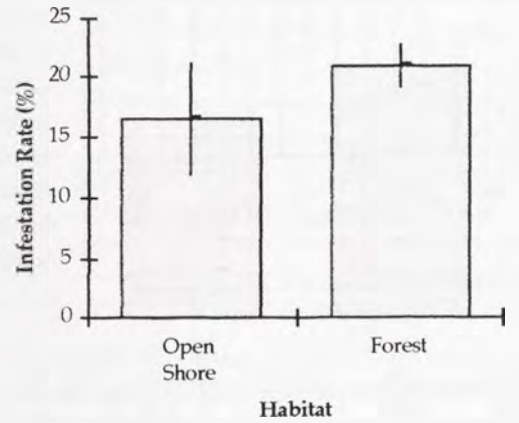



**Table 1.** Composition of each habitat (percent total individuals / ramets falling into each growth form category) with 95% confidence intervals.

| | Open Shore | Forest |
|---|---|---|
| Grasses | 93 % ± 0.98% | 48% ± 1.8% |
| Ferns | 0% | 11% ± 2.4% |
| Herbs | 6.5% ± 3.6% | 34% ± 2.1% |
| Shrubs / Trees | 0.57% ± 3.7% | 6.9% ± 2.4% |

*Growth forms*

Infestation rates varied significantly among growth forms (Figure 4, $\chi^2$ = 138, df =3, p < .001). Infestation rates did not differ significantly between ferns (10%) and grasses (12%); but herbs (20%) and shrubs/trees (23%) were infested at significantly higher rates than any other growth forms, and shrubs/trees were infested at a significantly higher rate than herbs (Tukey type post test, Table 2).

**Figure 4.** Infestation rates (percent of individuals or ramets infested) of different growth forms. Error bars represent 95% confidence intervals.

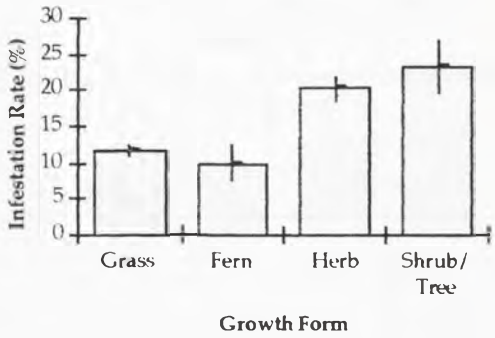



**Table 2.** Results (p values) of Tukey type test for comparison of multiple proportions comparing infestation rates among different growth forms.
n.s. = not significant.

| | Grasses | Herbs | Shrubs/ Trees |
|---|---|---|---|
| Ferns | n.s. | <.001 | <.001 |
| Grasses | | <.001 | <.001 |
| Herbs | | | <.05 |

*Species*

Only one species of fern (*Phymatosorus* sp.) was found. For all other growth forms, different species were infested at significantly different rates (Figures 5a-5c, Pearson Chi-square, p < .001 in all cases). Among grasses, both *Lepturus repens* and *Cenchrus echinatus* were infested significantly more often than the other grass species, and *Lepturus* was infested at a significantly higher rate than *Cenchrus* (Tukey type post test, Table 3a). Among herbs, infestation rate was significantly higher for *Emilia fosbergii* and *Passiflora foetida* than for any other species, and infestation rates did not differ significantly between *Emilia* and *Passiflora* (Table 3b). Among shrubs and trees, *Scaevola taccada* was infested significantly more often than any other species (Table 3c). *Scaevola*

**Figure 5a.** Infestation rates of different grass species, with 95% confidence intervals. See Appendix 1 for key to species abbreviations.

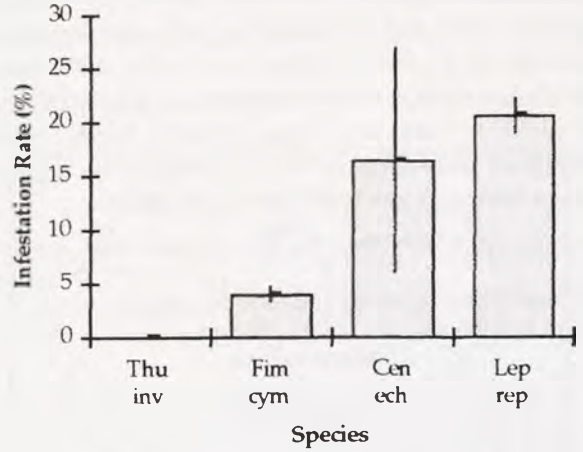



**Table 3a.** Results (p values) of Tukey type post test comparing infestation rates among different grass species. n.s. = not significant. See Appendix 1 for key to species abbreviations.

| | Fim cym | Cen ech | Lep rep |
|---|---|---|---|
| Thu inv | n.s. | <.001 | <.001 |
| Fim cym | | <.001 | <.001 |
| Cen ech | | | <.025 |

**Figure 5b.** Infestation rates of different herb species, with 95% confidence intervals. See Appendix 1 for key to species abbreviations.

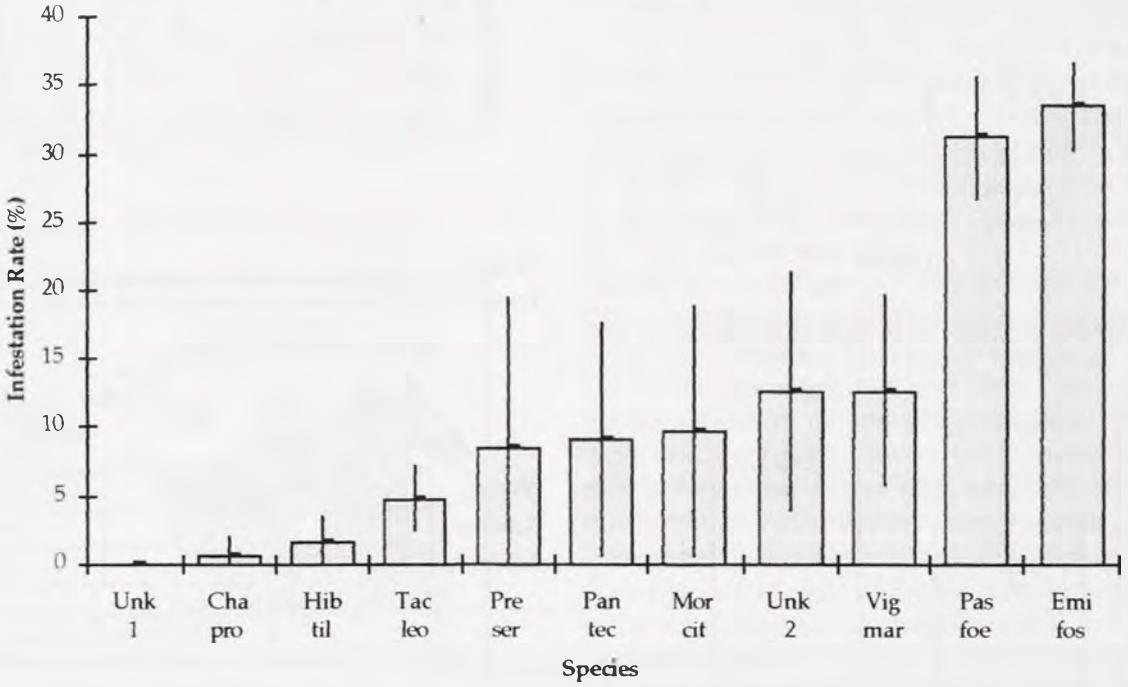



**Table 3b.** Results (p values) of Tukey type post test comparing infestation rates among different herb species. n.s. = not significant, DNT = did not test. See Appendix 1 for key to species abbreviations.

| | Cha pro | Hib til | Tac leo | Mor cit | Pre ser | Pan tec | Unk 2 | Vig mar | Pas foe | Emi fos |
|---|---|---|---|---|---|---|---|---|---|---|
| Unk 1 | n.s. | n.s. | n.s. | <.05 | <.05 | <.01 | <.001 | <.001 | <.001 | <.001 |
| Cha pro | | DNT | DNT | <.001 | <.005 | <.001 | <.001 | <.001 | <.001 | <.001 |
| Hib til | | | DNT | <.01 | <.05 | <.001 | <.001 | <.001 | <.001 | <.001 |
| Tac leo | | | | n.s. | n.s. | n.s. | <.005 | <.001 | <.001 | <.001 |
| Mor cit | | | | | DNT | DNT | n.s. | n.s. | <.001 | <.001 |
| Pre ser | | | | | | DNT | DNT | DNT | <.001 | <.001 |
| Pan tec | | | | | | | DNT | DNT | <.001 | <.001 |
| Unk 2 | | | | | | | | DNT | <.001 | <.001 |
| Vig mar | | | | | | | | | <.001 | <.001 |
| Pas foe | | | | | | | | | | n.s. |

**Figure 5c.** Infestation rates of different shrub / tree species, with 95% confidence intervals. See Appendix 1 for key to species abbreviations.

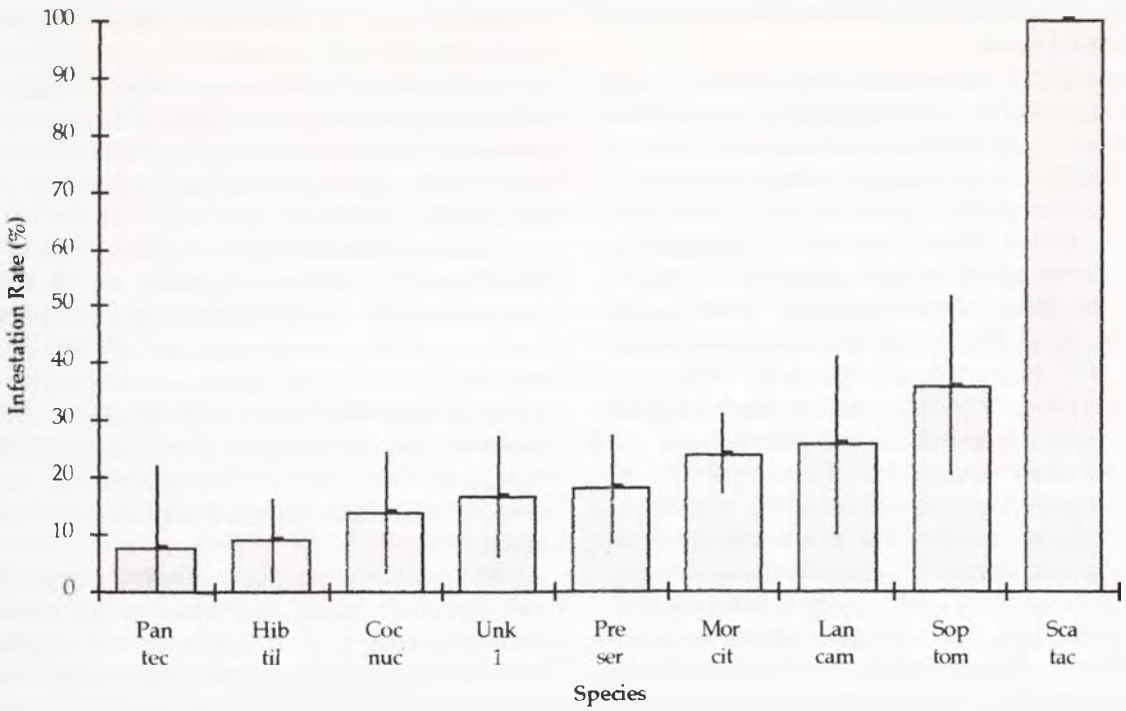



**Table 3c.** Results (p values) of Tukey type post test comparing infestation rates among different shrub / tree species. n.s. = not significant, DNT = did not test. See Appendix 1 for key to species abbreviations.

| | Hib til | Cocnuc | Unk 1 | Pre ser | Mor cit | Lan cam | Sop tom | Sca tac |
|---|---|---|---|---|---|---|---|---|
| Pan tec | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | <.005 | <.001 |
| Hib til | | DNT | DNT | DNT | DNT | DNT | <.005 | <.001 |
| Cocnuc | | | DNT | DNT | DNT | DNT | <.005 | <.001 |
| Unk 1 | | | | DNT | DNT | DNT | n.s. | <.001 |
| Pre ser | | | | | DNT | DNT | DNT | <.001 |
| Mor cit | | | | | | DNT | DNT | <.001 |
| Lan cam | | | | | | | DNT | <.001 |
| Sop tom | | | | | | | | <.001 |

had the highest infestation rate of all species (100% of plants large enough to qualify as shrubs/trees, 77% including seedlings).

Logistic regression on infestation rates as a function of *Morinda citrifolia* stem length was inconclusive ($p = .030$, $r^2 = .0262$). Despite an apparently significant p value the $r^2$ measure of fit was very low. The data for *Hibiscus tiliaceus* did not show a significant effect of stem length on infestation rates ($p = .17$, $r^2 = .039$). The data for *Scaevola taccada* strongly suggest an effect of stem length on infestation rates ($p < .001$, $r^2 = 1.00$). For this species, 7/7 plants under 8cm tall were uninfested and 24/24 plants over 12cm tall were infested.

## Discussion

*Habitat comparison*

Overall infestation rates showed a clear effect of habitat (Figure 3a), with infestation rates higher in the forest. Possible explanations for this pattern fall into two general categories. The reduced infestation rate in the open shore habitat may be the result of physiological constraints which reduce *Cassytha* fitness and hence infestation rates. For example,

infestation might be inhibited by desiccation stress, salt spray, or wind stress. Alternatively, this pattern in infestation rates could be explained by the distribution of hosts, if preferred host plants were more abundant in the forest.

Analyzing infestation rates on *Lepturus repens* does not support the hypothesis that physiological constraints are responsible for the observed pattern in infestation rates. If physiological stress reduced the infestation rate on plants outside the forest, infestation of *Lepturus* should be similarly reduced outside the forest. However, infestation rates on *Lepturus* did not differ significantly between habitats. The small, statistically insignificant difference observed does not preclude the existence of a small effect of physiological constraints, but if such an effect exists at all it is probably less important than other factors.

As mentioned earlier, not all grasses observed had reproductive structures present, possibly leading to misidentifications. Some of the plants described as *Lepturus* might actually be *Stenotaphrum micranthum*, which is often confused with *Lepturus* but generally much less abundant where the two species co-occur (Whistler 1992). Unless *Lepturus* and *Stenotaphrum* differed significantly in both infestation rates and distribution, this is unlikely to substantially affect the validity of this conclusion. It seems unlikely that *Lepturus* and *Stenotaphrum* should differ drastically in infestation susceptibility given their high degree of morphological similarity. In addition, *Lepturus* may be so much more abundant than *Stenotaphrum* that the contribution of *Stenotaphrum* to overall patterns is insignificantly small.

The distribution of plants of different growth forms is consistent with the hypothesis that the distribution of preferred hosts is an important factor in generating higher infestation rates inside the forest. Grasses, which were infested at a relatively low rate, dominate the open shore habitat where infestation rates were low (Table 1). More frequently infested herbs, shrubs, and trees are proportionately 5-12 times more abundant in the forest. The distribution of ferns, infested at a relatively low rate but found only in the forest, is not consistent with this hypothesis. However, ferns should make relatively little contribution to overall patterns in infestation rates, as they make up only a small fraction of the potential host pool (677 fern ramets vs. 8224 individuals or ramets of all the other growth forms).

*Growth forms*

Consistent with Kujit's (1969) observation that *Cassytha* finds its full development on woody plants, infestation rates did vary significantly among growth forms, with shrubs and trees the most highly infested (Figure 4, Table 2). Since transects were deliberately placed in areas of *Cassytha* infestation, relative infestation rates are more meaningful than absolute rates, which are not representative of infestation rates on the entire motu. Herbs were infested at nearly twice the rate of grasses and ferns, while shrubs and trees were infested approximately 20% more often than herbs. This suggests a strong host preference at the level of growth forms.

This preference for certain growth forms could arise from the preferred growth forms occurring predominately in areas well suited for the growth of *Cassytha*. This could account for the higher infestation rates of herbs, shrubs and trees, which were concentrated in the broadleaf forest where *Cassytha* infestation rates were highest. This seems unlikely, at least on a coarse scale, since infestation rates on *Lepturus repens* did not differ significantly between habitats.

The apparent preference for shrubs and trees may result from their larger size, which should lead to an increased probability of encounter by a growing *Cassytha*. In addition, larger plants offer a larger area upon which to photosynthesize, possibly contributing to greater growth and survivorship. Larger plants would generally be older, allowing more time for encounter and infection.

Experiments meant to test this hypothesis were inconclusive. Consistent with this hypothesis, stem length had a very strong effect on infestation rates for *Scaevola*, with every plant over 12cm tall infested and none of the smaller plants. Increasing stem length did not seem to increase infestation rates in either *Morinda* or *Hibiscus*, however. It is possible that the surface area and degree of branching of a plant could have a greater effect than stem length and be a more relevant measure of host size from the perspective of *Cassytha*. Although area could be expected to increase with stem length, at least within a species, further testing of the effects of size on infestation rates using different measures of host size may be merited.

*Species*

*Cassytha* displayed varying degrees of host preference at the species level. Among grasses, three of four species found were infested at significantly different rates (Table 3a). Interpretation of this result must take into account issues of species identification as discussed earlier. Even if not all species were not properly identified, however, there is clearly a difference in infestation rates among species. Only two of eleven herb species and one of nine shrub/tree species were infested at significantly different rates than all

other species of the same growth form (Tables 3b and 3c). These results suggest that *Cassytha* is a relative specialist in infesting grasses and a relative generalist in infesting herbs, shrubs, and trees.

As discussed earlier, the hypothesis that increasing host plant size would increase infestation rates received little support, making host size an unlikely explanation for the observed species preferences. The observed preferences might arise from greater average age of preferred species, but this is not consistent with small and presumably short lived herbs like *Emilia fosbergii* and *Passiflora foetida* being infested at higher rates than all of the shrub and tree species with the exception of *Scaevola* and *Sophora tomentosa*.

Other explanations for observed species preferences appear more likely and merit further testing. It may be that the preferred species share *Cassytha*'s microhabitat or disturbance regime preferences. *Cassytha*, *Emilia*, and *Passiflora* were all abundant in roadcut areas on the main island, suggesting that all three may be favored by disturbance. Studies in sites with known histories could address this possibility. Host preference may arise from the mechanical or biochemical properties of the host (Kujit 1969). Certain species' vascular tissue may be more readily accessible, or alternatively may contain compounds that inhibit *Cassytha*. These possibilities could be addressed using bioassays similar to those performed on *Cuscuta* by Pennings and Callaway (1996).

Despite the existence of some degree of host preference, the overall generalist nature of *Cassytha* should not be overlooked. Out of 21 potential host species for which at least 10 individuals or ramets were observed, only two (the grass *Thuarea involuta* and an unidentified herb) were never infested. This is consistent with the expectation that a xylem parasite should be a generalist (Burch 1992). Kujit (1969) suggests host specificity can only evolve when a single host species is disproportionately abundant, most likely in species poor environments. A tropical species, and especially a pantropical species such as *Cassytha*, is unlikely to encounter such environments. Considering the wide variety of species *Cassytha* coexists with worldwide, it is obvious that the ability to infest multiple host species would be beneficial, and so *Cassytha*'s generalist nature may be an important factor in its success and widespread distribution.

**Conclusions**

*Cassytha filiformis* displayed a broad host range, infesting 19 of 21 potential host species examined. Within this range of hosts, certain preferences and patterns of infestation did emerge. *Cassytha* infestation rates were highest inside the broadleaf forest zone, possibly due to distributional patterns of preferred hosts. Infestation rates were higher on herbs, shrubs, and trees than on grasses and ferns, and higher on shrubs and trees than on herbs. Within groups of species sharing similar growth habits, limited preferences were found. The reasons for these preferences are not clear, and offer opportunities for further study. Other potential topics for further study of *Cassytha* include comparing densities of *Cassytha* infestation on various hosts or examining the effects of infestation on host plant fitness.

**Acknowledgments**

First and foremost, I extend my thanks to the faculty and station staff whose work over the years has assured that Gump Station remains an excellent site for research. The GSI's deserve tremendous gratitude for their constant efforts to help students learn and succeed while also managing day to day logistics. I thank Virginia Matzek in particular for help with the design, execution, and analysis of my study. I thank P. Vallejo, D. Firestone, and C. Nerney for their assistance and encouragement in the field, and the entire class for an enjoyable living and learning experience.

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**Appendix 1.** Guide to abbreviations used for species names.

| Abbreviation | Genus | Species | Family |
|---|---|---|---|
| **Grasses** | | | |
| Thu inv | *Thuarea* | *involuta* | Poaceae |
| Fim cym | *Fimbristylis* | *cymosa* | Cyperaceae |
| Cen ech | *Cenchrus* | *echinatus* | Poaceae |
| Lep rep | *Lepturus* | *repens* | Poaceae |
| **Herbs** | | | |
| Unk 1 | unknown | unknown | unknown |
| Cha pro | *Chamaesyce* | *prostrata* | Euphorbiaceae |
| Hib til | *Hibiscus* | *tiliaceus* | Malavaceae |
| Tac leo | *Tacca* | *leonteopetaloides* | Taccaceae |
| Pre ser | *Premna* | *serratifolia* | Verbenaceae |
| Pan tec | *Pandanus* | *tectorius* | Pandanaceae |
| Mor cit | *Morinda* | *citrifolia* | Rubiaceae |
| Unk 2 | unknown | unknown | unknown |
| Vig mar | *Vigna* | *marina* | Fabaceae |
| Pas foe | *Passiflora* | *foetida* | Passifloraceae |
| Emi fos | *Emilia* | *fosbergii* | Asteraceae |
| **Shrubs / Trees** | | | |
| Pan tec | *Pandanus* | *tectorius* | Pandanaceae |
| Hib til | *Hibiscus* | *tiliaceus* | Malavaceae |
| Coc nuc | *Cocos* | *nucifera* | Palmae |
| Unk 1 | unknown | unknown | unknown |
| Pre ser | *Premna* | *serratifolia* | Verbenaceae |
| Mor cit | *Morinda* | *citrifolia* | Rubiaceae |
| Lan cam | *Lantana* | *camara* | Verbenaceae |
| Sop tom | *Sophora* | *tomentosa* | Fabaceae |
| Sca tac | *Scaevola* | *taccada* | Goodeniaceae |

# The Distribution of Christmas Tree Worms on Coral Heads

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ABSTRACT. *Spirobranchus giganteus* (Annelida: Polychaeta) relies on water flow for food and gamete dispersal. The hypothesis of this experiment was that current speed and direction would have an influence on the distribution of *S. giganteus*. To test this hypothesis, current direction and velocity were measured around eight different *Porites sp.* coral heads. In Moorea, French Polynesia, velocity was characterized using a neutrally buoyant ping pong ball and the direction of the water flow was characterized using Plaster of Paris molds left to dissolve in the water over two days. The number of *S. giganteus* individuals was also counted on all coral heads.

Instantaneous velocities for low, medium, and high flow sites were characterized as having velocities of approximately .08 m/s, .11 m/s, and .16 m/s, respectively. A scattergram shows that there is a correlation between water flow and worm distribution. However, the results of the t-tests indicate that the flow at the coral surface cannot be characterized in simple section, such as front-versus-back and top-versus-bottom. An increase in worm density in medium flow regimes was also established. Future work could examine the possibility of a large variation within the medium flow range. The conclusion of this experiment is that there are many factors, including flow, that influence the distribution of Christmas tree worms.

**Introduction**

*Spirobranchus giganteus* is one of the few suspension feeding polychaetes found in Moorea, French Polynesia. *S. giganteus* is commonly called Christmas tree worm because it has a crown of feeding appendages that are in the shape of a christmas tree. They also come in a variety of colors such as red, blue, orange, yellow, and white. In Moorea, French Polynesia, *S. giganteus* is most often found on *Porites sp.* coral heads. *S. giganteus* is meroplanktonic and when its free swimming larvae settle out of the water column they secrete a calcium carbonate tube and remain sessile for the rest of their lives.

Because Christmas tree worms are sessile for their adult lives, water flow is crucial for bringing food and for gamete dispersal. For example, to obtain food particles, the Christmas tree worm sticks its feeding appendages into the water column and particles stick to the appendages as they flow by. Particle capture in suspension feeders has been shown to take place by "direct interception, inertial impaction, diffusional encounter, or gravitational deposition" (Shimeta 1997; Rubenstein and Koehl 1977). Capture of usable food items can be affected by many physical factors such as viscosity, temperature, flow speed, sediment in the water column, and the size of potential food particles (Podolsky 1994; Shimeta 1997). Past studies have focused on the method of particle capture, the desired size of a food particle, and the effects of particle capture on an organisms short term growth (Mayer, 1994; Shimeta, 1997; Eckman, 1993). However, the effects of location in flow on feeding ability has not been studied.

My hypothesis was that different flow velocities could directly affect the ability of a Christmas tree worm to capture a food particle. Suspension feeders located in fast flow environments select food particles of a smaller size than ones in slow flow environments (Shimeta, 1997). Furthermore, I hypothesized that feeding ability can be maximized if organisms distribute themselves in areas where larger food particles can be more easily obtained. In this case I predicted that the effects of shearing forces on the front side of coral heads in high flow environments would lead to a higher concentration of individuals on the back side. In addition to shearing forces, the amount of small scale upwelling on the back side of coral heads will be greater in high flow areas. The upwelling of bottom sediment may provide a food resource for *S. giganteus* individuals. In contrast, I hypothesized that coral heads in low flow environments would experience less shearing forces and upwelling and would therefore lead to higher concentrations of individuals on the front side of coral sites. I also predicted that small scale upwelling would lead to a larger number of worms on the bottom side of the coral heads in fast flow areas. The null hypothesis, or the

hypothesis that I would like to statistically reject, was that there would be a random distribution of *S. giganteus* individuals all over the coral head and the velocity of the water flow would have no effect on distribution.

To test my hypotheses I measured flow velocity and direction and I counted the number of worms on various sections of the coral head. My data were analyzed using a scattergram and a series of t-tests.

## Materials and Methods

*Site Selection*

All eight sites were located in the lagoon around Moorea, French Polynesia (Figure 2). Eight *Porites sp.* coral heads within the three different locations were chosen using flow velocity. Velocity was determined using a series of ping pong ball measurements (see below). Temae and the patch reefs to the northwest of Cook's Bay were characterized as high flow sites and the patch reefs to the northeast of Cook's Bay were characterized as either slow or medium flow sites. Individual coral heads were also chosen because of their spherical shape with few contours and a density of greater than 100 individuals per head.

*Velocity Measurement*

A neutrally buoyant ping pong ball was used to characterize instantaneous velocity at all eight sites. The ball was made neutrally buoyant by piercing with a syringe needle and filling with sea water. The ball's travel time between two fixed points was measured and its velocity calculated. Because flow velocity can vary throughout the day, a series of five ping pong velocity measurements were repeated during all points of tide (6am, 9am, noon, 1:30pm, 3pm, &6pm). The averages and standard deviations were calculated for 35 measurements, 5 replicas for each of 7 trials, for each site. The site was then characterized as either high, medium, or low. The velocity over the coral heads at Temae and the patch reefs to the northwest of Cook's Bay was approximately .16 m/s, three coral heads in the patch reefs to the northeast of Cook's Bay had velocities of .08 m/s, and the fourth had a velocity of .11 m/s. The standard deviation within flow groups was lower than the between-group variation.

*Current Direction*

To get the empirical data to make an accurate assessment of the direction of flow, Plaster of Paris molds were used. Six Plaster of Paris molds were made for each of the coral heads. The liquid was then poured into a cylindrical plastic container with a plastic zip-tie in the center. Molds were prepared and then left to dry for at least two days. Dry weight to the .01g of the plaster mold and the zip tie was recorded. The plaster cylinder was then labeled and attached to a 3 in. nail using the zip-tie and secured with duct tape.

The approximate direction of the current was judged using a neutrally buoyant ping pong ball. Molds were then placed at mid-elevation on the coral head at approximately even intervals around it. The plaster molds were collected and dry weight was measured to determine a net direction of water flow. I concluded that the mold with the greatest change in weight was the one that was experiencing the most force, and was therefore the front side of the coral head.

*Counting*

Using the nails from the Plaster of Paris cylinders, the coral heads were divided laterally into six approximately equal sections and longitudinally into top and bottom sections. Front and back was determined by combining the results of the Plaster of Paris and the circumference. The number of individuals was recorded for each section. An individual was indicated by either a worm crown or an obviously occupied tube with operculum intact. Each section was counted by two different people and the numbers were averaged. Because of the difficulty in determining what a worm hole was while floating upside down underwater, some of the data were inconsistent. Therefore, I would approximate the error in counting to be $\pm$10%.

## Results

To analyze the distributions of worms on the coral heads, I used a scattergram and a series of unpaired, one-tailed t-tests. The scattergram shows a trend between the density of worms and average velocity of the water flow (Figure 1). As the flow velocity increases, the density of worms also increases, but only to a certain point. The flow velocity then gets too high and density decreases. However, there is a large amount of scatter on the 1 medium flow site. This is also reflected in a t-test (Table 2). The mean is 70 individuals and there is a high standard deviation of 23 individuals.

T-tests comparing the percent of worms on the front versus the back and the top versus the bottom were performed to analyze the coral heads in high and low flow (Table 2). Although the means for front and back are approximately

50% and 50%, there is a large standard deviation of 8% and 14%, respectively. Similarly, there is a also a mean of approximately 50% and 50% for the top and bottom of the coral head, but again there is a large standard deviation, 17% and 14%, respectively.

T-tests were also performed to compare front-back and top-bottom to a variety of other factors like location, size, and damage to coral; however, these results were also not significant.

## Discussion and Conclusions

The scattergram of density to average velocity shows that there is a trend between number of individuals and the water flow (Table 2). In low flow areas, water may be a limiting factor because enough food does not reach the organisms. Also, because the viscosity of the water is higher in low flow environments, it may be difficult for larvae to move through the water column to get to a coral head. Water velocity is also a limiting factor in high flow environments. The water in high flow areas is moving too quickly which increases the amount of shearing force. Too much shearing force may cause potential food items to be ripped out of the feeding tentacles. It can also make it difficult for larvae to settle and attach.

However, the increase in the mean density at the medium flow site is not completely conclusive because of the large amount of scatter (Figure 1). It is possible that the amount of scatter in the graph represents all the possible variation, and that further work including more medium flow sites might show that this trend does hold.

The results of the t-tests show that there is no significant correlation between the distribution of *Spirobranchus giganteus* on the major sections of the coral (front, back, top, bottom) and flow speed and direction. This leads me to the conclusion that there is too much occurring at the coral surface to break an individual *Porites* head into these large sections.

One possible explanation for not finding any significance is site selection. I chose to limit potential sites to those with greater than 100 worms because I hypothesized that patterns would be more obviously displayed with larger numbers. However, I may have chosen only successful sites and excluded sites that would have strengthened the correlation of distribution to velocity. A future study with a larger sample size might change the implications of this data.

This experiment has also led me to the conclusion that although flow may be a factor in determining distribution of Christmas tree worms, a variety of other factors should be considered. One possible influence on distribution is the amount of sediment in the water column. In areas where sediment concentration is high *S. giganteus* individuals need to dispose of sediment that falls on them and they must select usable food items from the water column. A possible future study could be to set out sediment traps on coral heads within different sections of the lagoon and determine their correlation with worm distribution.

In addition, because this study is only an assessment of the distributions of adult individuals, the settlement and survival of larvae cannot be accurately interpreted. It is possible that in low flow environments larvae do settle out on the front side of coral heads but that survival is also low. Therefore, by only measuring adult individuals settlement cannot be accurately assessed. A future study could use a larval trap to look at the amount of larvae that "settle out" within a given location.

Contrary to my hypothesis, I concluded that flow speed and direction are not the most important factors in determining Christmas tree worm distribution. This leads me to believe that factors like sedimentation, the location of a coral head within the lagoon, and other physical and biological factors may have a greater impact.

## Acknowledgements

I would like to thank my family for helping me get to Moorea. To professors David Lindberg, Jere Lipps, Vince Resh, David Stoddart; and teaching assistants Tegan Churcher, Amy Lesen, and Virginia Matzek for sharing their experience and wisdom. To Jessica Skinner and Rob Guralnick for helping me be loud and clear. Most especially to Virginia Rich for all her field assistance; her support and guidance; and for always being there. Finally, to the Moorea class of 1998 for the adventure.

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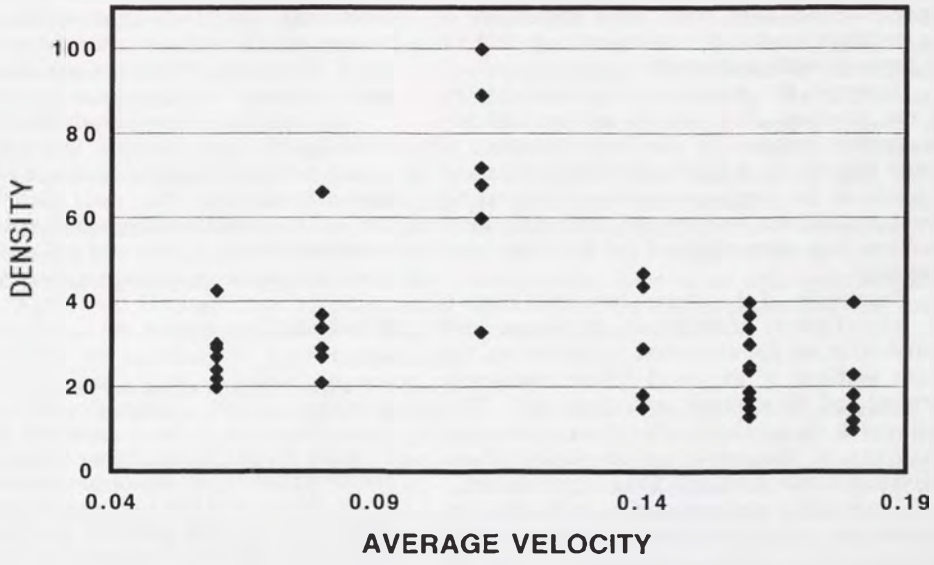


**Figure 1**: Scattergram of distribution of *S. giganteus*.

**Figure 2:** Study sites and locations with the lagoon surrounding the Northeast corner of Moorea.

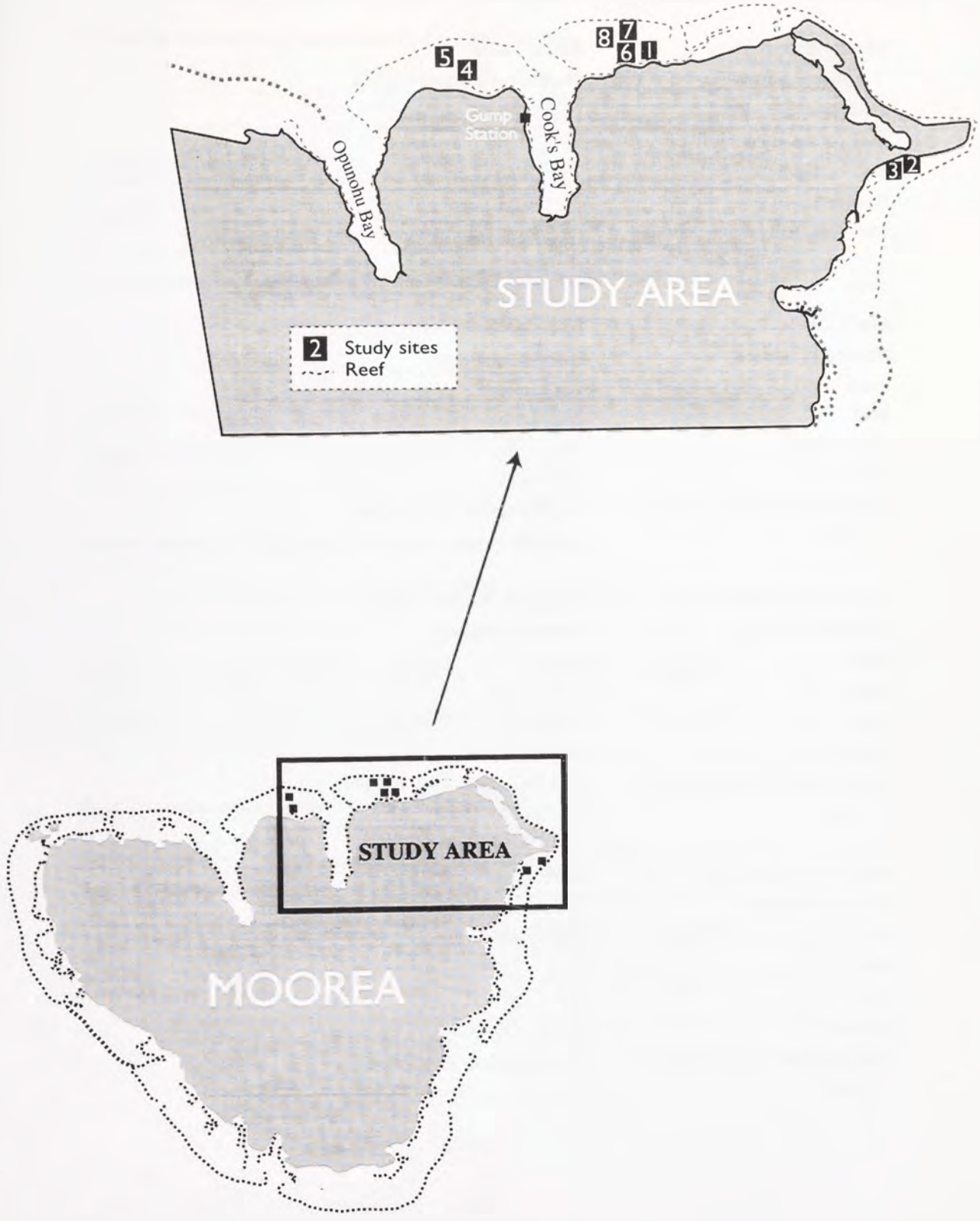

**Table 1**: List of the 8 sites, the total number of worms on the front, back, top, and bottom, and the average velocity over the coral head determined by ping pong ball measurements.

**Site 1**: NE Cook's Bay
Number of worms
Front (2-4.5) 105
Back (4.5-2) 109
Top 112
Bottom 125
Ping Pong Ball Avg vel (m/s)
0.08

**Site 2**: Temae
Number of worms
Front 71
Back 105
Top 48
Bottom 111
Ping Pong Ball Avg vel (m/s)
0.16

**Site 3**: Temae
Number of worms
Front 108
Back 63
Top 101
Bottom 61
Ping Pong Ball Avg vel (m/s)
0.14

**Site 4**: NW Cook's Bay
Number of worms
Front 78
Back 59
Top 81
Bottom 41
Ping Pong Ball Avg vel (m/s)
0.16

**Site 5**: NW of Cook's Bay
Number of worms
Front 39
Back 79
Top 75
Bottom 30
Ping Pong Ball Avg vel (m/s)
0.18

**Site 6**: NE of Cook's Bay
Number of worms
Front 79
Back 102
Top 86
Bottom 87
Ping Pong Ball Avg vel (m/s)
0.06

**Site 7**: NE of Cook's Bay
Number of worms
Front 68
Back 78
Top 134
Bottom 52
Ping Pong Ball Avg Velocity
0.06

**Site 8**: NE of Cook's Bay
Number of worms
Front 257
Back 165
Top 174
Bottom 273
Ping Pong Ball Avg Velocity
0.11

**Table 2:** Unpaired, one-tailed t-tests comparing the percent of worms on the front/back or top/bottom of coral heads to the speed of flow. Means are calculated as percent of total worms.

**Percent worms on Front/Back of the coral head in Fast flow**

| DF | Unpaired t Value | Prob. (1-tail) |
|---|---|---|
| 6 | -.337 | .3773 |

| Section | # Coral Heads | Mean % | Std. Dev. | Std. Error |
|---|---|---|---|---|
| Front | 4 | 48.383 | 14.03 | 7.01 |
| Back | 4 | 51.63 | 14.04 | 7.02 |

**Percent worms on Front/Back of the coral head in Slow flow**

| DF | Unpaired t Value | Prob. (1-tail) |
|---|---|---|
| 6 | .226 | .4143 |

| Section | # Coral Heads | Mean % | Std. Dev. | Std. Error |
|---|---|---|---|---|
| Front | 4 | 50.67 | 8.01 | 4.01 |
| Back | 4 | 49.37 | 8.24 | 4.12 |

**Percent worms on Top/Bottom of the coral head in Fast flow**

| DF | Unpaired t Value | Prob. (1-tail) |
|---|---|---|
| 6 | .969 | .185 |

| Section | # Coral Heads | Mean % | Std. Dev. | Std. Error |
|---|---|---|---|---|
| Top | 4 | 55.90 | 17.22 | 8.61 |
| Bottom | 4 | 44.10 | 17.22 | 8.61 |

**Percent worms on Top/Bottom of the coral head in Slow flow**

| DF | Unpaired t Value | Prob. (1-tail) |
|---|---|---|
| 6 | .397 | .3525 |

| Section | # Coral Heads | Mean % | Std. Dev. | Std. Error |
|---|---|---|---|---|
| Top | 4 | 51.99 | 14.14 | 7.07 |
| Bottom | 4 | 48.02 | 14.14 | 7.07 |

# Analysis of Coral Gradient along Vertical Coral Slopes on Fringing Reefs in Cook's Bay, Moorea, French Polynesia

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Cook's Bay, located on the northern coast of Moorea, French Polynesia reaches approximately 2 km into the island. Along the eastern coast of this bay, vertical walls of coral extend to a depth no greater than 10 m. Focusing on percent cover and generic diversity of corals, transects were conducted down the vertical slope to a depth no greater than 9 m at six sites. Environmental data, such as water clarity, nitrogen and salinity were also measured. Statistical analysis of the bay as a whole showed that mean percent coral cover increased from depth, from 8.46% at 9-7 m depth to 36.3% at 3-0 m depth. Generic diversity however, showed no relation to depth. Analysis by topographical categories showed that the sandy slope found on the bottom of the wall had the lowest mean genera (.875) and percent cover (4.75), with ranges of 0-3 genera and 0%-30%. Also, the category of wall slope was found to have the highest mean generic diversity with 4.44 genera, with a range of 3-6 genera found. Analysis of individual sites along the bay from the landward start to the mouth of the bay showed no significant gradient. Only by reducing the bays into two halves could a significant result found. Therefore, coral cover and generic diversity over depth along the coral walls moving through the bay are more likely affected by local anthropogenic impacts such as coastal development and tourism as opposed to large environmental gradients.

## Introduction

The effect of bays upon the distribution of corals is the focus of much research. Miyadi (1944) proposed a term, the "embayment degree" to provide a new understanding of the effects of the geography of a bay. He assigned a specific zonation for benthic organisms, such as corals, in a bay, based on the distance from the mouth of the bay. The main controlling factors were mixing of the water, and general wave energy of the site. Along with the change in species over the whole of the bay, coral cover and diversity would also change along the bay. Horikoshi (1988) recognized this phenomenon in the coastal region of Ryukyu and Palau.

On the island of Moorea, located in French Polynesia, Cook's Bay and Opunohu bay dominate the northern coast of the island. Both have been the subject of studies concerning spatial distribution of corals (Adjeroud 1997; Muto, 1997; Adjeroud and Salvat, 1996). All discovered increasing coral cover and diversity in a gradient moving from the landward head to the mouth of the bay in Cook's Bay.

The purpose of this study was to further examine the coral distribution along the coast of the bay, and to determine the presence and extent of such a gradient. The main focus of the study is the vertical slopes of coral found on the bays.

## Materials and Methods

The study site is located on Moorea, French Polynesia. Moorea is a high volcanic island with a circumference of 61 km, and an

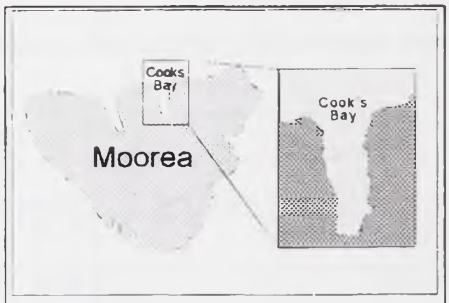


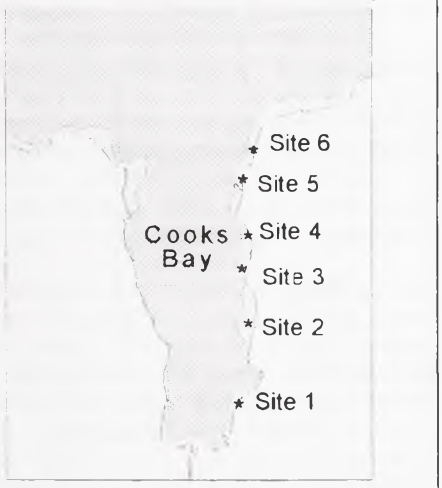

**Figure 1** - Moorea and Cook's Bay

area of approximately 134 km$^2$ (fig. 1). The island is found in the Society Island chain (17° 30' S; 149° 50' W), approximately 10 km northwest of the larger island of Tahiti. The

northern coast of this island is dominated by two bays. The primary site for this study was Cook's Bay.

In order to determine the extent of coral diversity and percent cover on the vertical slopes, I selected six sites along the eastern coast of Cook's Bay (Fig. 2). I chose the sites based primarily on the presence of a vertical slope running approximately 100 m and under 10 m in depth. My secondary consideration was the relative distance to the mouth of the bay. Along these sites, I ran a

**Figure 3** - Site locations in Cook's Bay




100 m transect line, and selected two points .

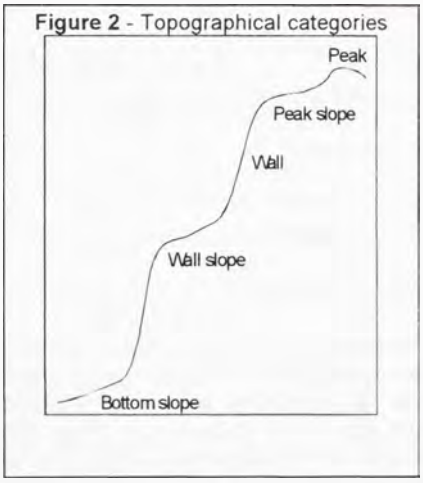
From these two points, a single transect line, 10 m in length and marked every meter, was placed heading downward along the wall. I began my transects at the deepest point on the line and worked my way upward, recording observations each meter. I used SCUBA to collect all my data. Coral percent cover, genera present, algae percent cover, algae genera present, substrate percent, substrate type were recorded using a 1x1 m quadrat to present a broad environmental picture.

I also assigned six topographical categories to the site in order to characterize the gradient of the slope (fig. 3). I recorded environmental data at each site, including nitrate, water clarity, and salinity of water at a depth of 9 m and at the surface in order to further characterize the environment of each site. The water was collected using a WILDCO Kemmerer Water Sampler bottle, while tests were performed with an AquaTest chemical kit (nitrate), a Leica refractometer (salinity) and a standard secchi disk (water clarity).

**Results**

To determine the relationship of coral cover and diversity to the combined factors of depth and site location, I used two-way ANOVA analysis. Tests considering both coral % cover and generic diversity resulted in significant variance between all sites and

**Figure 2** - Topographical categories




depths, as was predicted. Continued analysis using one-way ANOVA produced more varied results. While percent cover vs. depth, percent cover vs. site, and genera vs. site exhibited significant differences, analysis of genera with exact depth did not yield a significant result.

*i. Analysis of Geographic Location*

Analysis of the gradient along the bay showed no significant relationship to the two factors of coral cover or generic diversity. Concerning coral cover versus site location, site 1, located deep in the bay, had no similarity to any of the other sites. Therefore, the low mean of 3.15% cover was significant. Analysis of genera diversity of coral produced more balanced results. I found site 1 to be different from all other sites with a mean of 0.7 genera, and a range of 0-3 genera along the site.

Only by reducing the data to two distinct categories was I able to extract a significant result (table 1). T-testing of sites 1-3 vs sites 4-6 with respect to coral cover revealed a significant result.

**Table 1** - Result of Geographical Analysis with Consolidated Site Categories

| Site #'s | Range of Coral Cover (mean) | Range of Generic Diversity (mean) |
|---|---|---|
| 1-3 | 0%-80% (19.87) | 0-5 (1.55) |
| 4-6 | 0.5%-99% (32.33%) | 1-7 (3.02) |

| Depth Category | Depths included (m) |
|---|---|
| 3 | 9-7 |
| 2 | 6-4 |
| 1 | 3-0 |

**Table 3** - Depth Categories

*ii. Analysis of Depth*

Analyzing the data in ways other than simple geographic location along the bay proved to be more enlightening. Depth was much more of a determining factor in the distribution of corals. By assigning 3 depth categories, based on the recorded depth of the transects (table 3) I found a direct relationship. From analysis of both ANOVA and t-tests, I found a gradient, with coral cover increasing from bottom upward (table 4).

| Depth Category | Coral Cover Mean (range) |
|---|---|
| 3 (9-7 m) | 8.46 (0%-30%) |
| 2 (6-4 m) | 23.07 (0%-55%) |
| 1 (3-0 m) | 36.30 (5%-70) |

**Table 4** - Depth vs. Coral % cover gradient

*iii. Analysis of Topographical Categories*

T-testing on coral genera however, showed no significant differences amongst the depth categories. Topographic categories were analyzed in similar fashion. Following a significant result from ANOVA, t-testing of both factors produced the following results. For coral percent cover, the "bottom slope" category was found to be significantly different

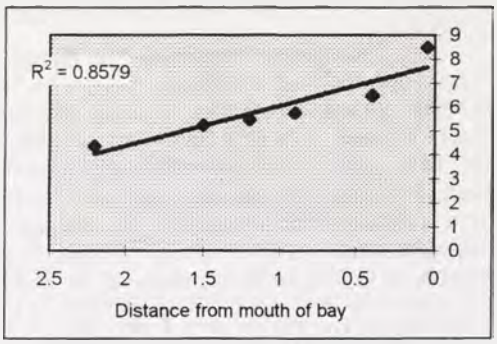



**Figure 4** - Water clarity in Cook's Bay

| Dist. From Mouth (km) | Surface | Depth (10m) |
|---|---|---|
| 2.2 | 10 | 15 |
| 1.5 | 10 | 10 |
| 1.2 | 10 | 10 |
| 0.9 | 10 | 10 |
| 0.4 | 10 | 10 |
| 0.05 | 10 | 10 |

**Table 5** - Nitrate data (ppm)

| Dist. From Mouth (km) | Surface | Depth (10m) |
|---|---|---|
| 2.2 | 36.33 | 36.75 |
| 1.5 | 36.83 | 37 |
| 1.2 | 36 | 37 |
| 0.9 | 36 | 38.5 |
| 0.4 | 38 | 37 |
| 0.05 | 36.33 | 37 |

**Table 6**- Salinity Data (0/00)

from the others, with the low mean of 4.75 percent. For coral genera, both "bottom slope" and "wall slope" categories were significantly different from the other categories. Means were 0.88 and 4.44 genera, respectively, while the range for the generic diversity was 0-4 along the bottom slope, and 3-6 genera found along the wall

slope. All other topographic categories were not significantly different.

*iv.. Environmental analysis*

Environmental data collected resulted in few significant patterns. Water clarity data revealed a gradient, increasing from the bayhead to the mouth (fig. 4). The other factors, including salinity and nitrate, did not reveal any gradient along the bay (tables 5 - 6).

**Discussion**

Analysis of the results among sites with depth supports the theory that light is a limiting factor for coral health; both depth and water clarity in Cook's Bay acted as controls upon the reefs. The endosymbionts within the corals require light in order to survive (Lobban & Schefter 1997). Table 4 showed the increasing diversity towards shallower water, where light is more available, thus supporting this idea.

Analysis of topographical categories also provided evidence for known limiting factors of coral reefs. The lack of stable substrate along the sandy bottom (pers. obs.) prevents any corals from settling out and establishing a colony upon the shifting sands (Brown & Howard 1985). In addition, the constant fall of sediment from the wall above would smother any corals that did manage to establish themselves in the sand. In contrast, the wall slope may have the highest genera due to the available light to all corals. The near horizontal orientation of the slope along the wall would permit more radiant energy to reach organisms in comparison to a wall orientation. The wall topography was often times dominated by a single species, such as *Porites rus* (pers. obs.); the large plates built by *P. rus* may serve as large solar collectors; they may also block out light beneath them on the walls, preventing establishment of new colonies.

Analysis for the existence of a gradient in coral growth along the bay was inconclusive, despite encouraging environmental data. Only by reducing the data to the broadest categories (i.e. the 1$^{st}$ half vs. the 2$^{nd}$ half) was an applicable result found. While significant, it is nonetheless a gradient existing on a much larger scale than any previously recorded. I believe it to be too broad to be practical. Numerous studies suggest the opposite, however.

The "embayment degree" apparently had little effect upon the distribution of corals within Cook's Bay. According to Horikoshi , the "embayment degree", as found by Miyadi, is not an analytical concept. Instead, he proposes that it is the sum total of the location factors. He clarifies himself, stating, "it is the sum total of all the factors affecting the structure and function of the biotic communities at that site". In the case of Cook's Bay, this would certainly include the coral along the walls as one of the communities. The data I collected therefore, should have followed a specific gradient.

As the sites moved from inside the bay to the mouth, coral cover and generic diversity should have increased. Ample evidence exists that supports this hypothesis. Adjeroud (1997), working in Cook's Bay, studied several aspects of the coral, including species richness and coverage. Working on three distinct areas, the reef walls, reef crest, and reef flat, he observed that coral coverage increased from the bayhead to the mouth of the bay. He found that species richness increased along the same gradient. The cause for this pattern in distribution was mostly attributed to the effects of depth and substrate.

Muto (1997) also examined coral distribution, focusing solely upon the reef flat. His analysis of the coral coverage along the eastern coast of the bay, documented a similar gradient as found by Adjeroud. Total coral cover increased along the eastern coast gradually, with the highest coverage occurring at the mouth of the bay. However, total coral coverage never exceeded 30%. Causes for the spatial distribution of coral was attributed to the presence of the Pao Pao river at the head of the bay. He found it to be the most influential factor within the bay, the impact stemming from sediment plumes discharged into the bay during the months of September through November. No other environmental data was collected.

These two experiments may have produced contrary results due to differences in experimental method. Adjeroud chose only four sites in Cook's Bay, and did not run vertical transects. Instead, he chose a large area quadrats, 10 $m^2$ in area along three depths. Muto picked 37 sites; however, he focused upon the reef flat exclusively,

performing belt transects every 50 meters. These factors may account for the difference in data.

However, my data follow no pattern that suggests the presence of a large scale limiting factor in the bay. Neither environmental data nor coral data provided conclusive evidence towards the existence of a single bay gradient. Instead, I believe that more localized factors, around each site are responsible for the coral distribution. Determinants such as positive or negative fish impacts, coastal construction, and tourism may play a major role along Cook's Bay.

The damselfish *Stegastes nigricans* has already been documented to have a positive effect upon coral diversity. The algal mat territories maintained by the damselfish were found to be the sites of increased coral diversity over time in the Society Islands (Gleason 1994). Further experiments found the high mortality of juvenile corals outside of the *S. nigricans* territories was due to predation by small grazing herbivores (*Anthuridae* and *Scaridae*) and urchins as well. Done et al. (1991) postulate that, "the mechanism protecting coral survival may be the *S. nigricans*' defense of its territories against herbivorous organisms...". The presence of *S. nigricans* was found throughout my sites, in scattered distributions throughout sites 2-6. Therefore, their effects upon coral distribution occurred with little regard for any environmental constraints.

In the absence of *S. nigricans,* and its territorial nature, coral grazing may dictate the spread of corals along the walls. The effects of predation upon vertical coral distribution have been documented (Grottoli-Everett & Wellington 1997). When corals were moved from depths of 26 m to less than 15 m, predation increased by 50%. The key aspect was the absence of the coral grazer at depths greater than 15 m. A similar organism may consume corals within Cook's Bay, preying on specific depth ranges of coral along the walls.

The shoreline inhabitants of Cook's Bay may play a more direct impact as well, as the eastern coast is moderately developed with three major hotels, and numerous small homes and businesses, including a gas station and fish cooperative. The effects of coastal development on coral reefs has been the focus of many studies, most negative. The short term effects of coastal construction include increased sedimentation and nutrient levels in the water (Johannes 1972). Analysis of corals over depth in the Netherlands Antilles found the influence of coastal construction to be "the most likely cause of degradation of the shallow part of the reef (Bak & Nieuwland 1995). While increased sedimentation would kill most corals, some corals, such as certain species of *Acropora, Porites,* and *Pavona*, are most certainly more adaptable to such an altered habitat. Large polyped species, such as some *Turbinaria* and *Leptastrea* are also more successful at coping with increased suspended and accumulating sediments (Maragos 1972). Other research documented the interspecific differences in tolerance to sedimentation (Stafford-Smith 1993), showing the ability of certain species to readily handle increased sediment loads.

However, effects need not always be negative. In one case, analysis of increased sedimentation found a positive correlation between sedimentation and species diversity (Huston 1985). While conducted at a deeper depth, the suggestion that sedimentation may actually have a diversifying effect much like predation is a provoking thought. So the changes in the environment caused by coastal construction may influence both generic diversity and coral cover both positively and negatively.

In a final, irrefutable note on direct impact, the tourism industry may cause quite tangible damage to the reef. In late September, 1998, the cruise ship Paul Gauguin drifted from her anchorage in the middle of Cook's Bay. She struck the reefs near site three, and on-site documentation showed severe impacts. Large sections of coral were flattened, while paint from the hull was photographed on large coral heads and tiny rubble alike. Both fresh scars and aged scars were observed, suggesting that this was not an isolated occurrence.

These are but a few of the factors that may influence coral distribution in any developed bay on a tropical island. In different bays, these factors may have differing effects; without a doubt, even more exist. However, the discussion of these few gives an idea as to presence of many determinants in coral health.

## Conclusion

The purpose of this project was to examine the distribution of corals along the

vertical walls in Cook's Bay. However, I found that the corals along the walls were not limited by a gradient enforced by any factor extending throughout the bay. While a gradient was discovered, the fact that the data had to be placed into two categories that encompassed over 2 km questions the usefulness of such an assessment. While I do not doubt that the "embayment degree" exists in other bays around the world, within Cook's Bay, and other bays similarly developed, the overriding elements of coastal construction, small, localized organismal impacts (predation, etc.), and tourism are likely to have a much greater impact. In addition to the great number of factors present in a developed bay, the fact that any of those factors may affect corals positively or negatively increases the difficulty in assessing the true relationships.

Much more research can be done concerning the topic of coral distribution. Studies of similar methods, but extending to depths over 10 m would be most helpful, to help assess the extent of the relationships discovered in this paper. A study of similar nature completed in Opunohu Bay would using the same methods could help to provide further insight into a) differences in the bays, and b) more evidence into the effect of bay gradients. Finally, long-term studies, examining the effects over depth of localized impacts, such as the construction of new hotel, would be extremely useful, as they may provide valuable insight into the true impacts of shore-based factors.

**Acknowledgments**

I would like to thank Dr. Jere Lipps, Dr. David Stoddart, and Dr. Vince Resh for their assistance and suggestions throughout this study. I would also like to thank John and Debbie of the Gump Station for all their help and support. To Tegan Churcher, Amy Lesen, and Virginia Matzek, my eternal gratitude for teaching me innumerable life lessons. And special thanks to Audrey Bowers, my SCUBA buddy and faithful assistant. And finally, to my parents, for giving me this opportunity.

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# Comparison of damselfish (*Stegastes nigricans)* defensive behavior in reef lagoon and motu ponds on Moorea, French Polynesia

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ABSTRACT. The damselfish *Stegastes nigricans* (Pomacentridae), live in colonies and defend individual territories from both conspecifics and heterospecifics on shallow-water reefs in tropical waters. Observations on the behavior of *S. nigricans* were made in two shallow lagoon sites and three permanent tidal pools on Motu Tiahura in Moorea, French Polynesia (17°30'S, 149°50'W). There were three foci of this study: 1) to compare the relationship of territorial defense in colonies of the shallow lagoon and colonies within ponds by comparing the number of chases on territory intruders, 2) to test relationships between the number of defensive fish chases and other behavioral and physical conditions, and 3) compare conspecific aggression before and after an increase in the number of *S. nigricans* in two ponds. Data on fish length, territory area, algal bites, algal quality, colony population, colony area, pond population and pond area were collected to test for relationships with the number of chases. Performing a one way ANOVA followed by paired t-tests on the number of chases at each site revealed that the sites cannot be grouped into two significantly different categories of lagoon versus pond, inconsistent with the hypothesis that fish defense is related to the two habitat categories. The number of chases was not found to be significantly related to the other behavioral and physical parameters studied. The introduction of conspecifics into two of the ponds resulted in an increase in the number of conspecific chases ($p<0.05$).

## Introduction

Damselfish (family Pomacentridae) are among the most conspicuous territorial fish on coral reefs (Harrington and Losey 1990; Wilson and Bellwood 1997). They guard individual territories for both food resources and reproduction (Robertson et al. 1981; Harrington and Losey 1990). Within their territories, damselfish tend algal turfs which they defend from both conspecifics and heterospecifics (Low 1971; Myberg and Thresher 1974). Territorial damselfish appear to feed on almost exclusively on the epilithic algal community within their territories (Wilson and Bellwood 1997). Territories are aggregated in colonies to provide group defense from roving herbivores and egg predators (Meadows 1995). Damselfish defend territories from intruders by aggressive displays and chases.

The Dusky Gregory (*Stegastes nigricans*) is a widespread damselfish which ranges from Australia northwards to the Ryukyu islands, and from eastern Africa to the islands of Oceania as far east as the Tuamotus. They inhabit lagoons and inshore coral reefs from one to twelve meters in depth and reach a maximum standard length of 115mm (Allen 1991). The Dusky Gregory is common on the island of Moorea, French Polynesia.

Colonies of *S. nigricans* were found in permanent marine ponds on Motu Tiahura in the northwest corner of Moorea. A motu is a low coralline islet formed from coral rubble which is deposited by storms on the inside of a barrier reef. The ponds studied are located on the northern, or ocean side of Motu Tiahura on the conglomerate platform. A conglomerate platform is formed by the cementing of coral rubble into a coarsely level coastline on the oceanside of the motu. The conglomerate platform erodes irregularly to form depressions which hold water thus creating ponds (Murphy 1991). The ponds studied were permanent and were connected to the reef lagoon through the porous conglomerate platform. These ponds were also subject to occasional spill over from the lagoon during the highest tides.

Pomacentrid fishes are highly aggressive when defending their territories from both conspecific and heterospecific intruders. In this study, the defensive behavior of *S. nigricans* was studied in confined ponds and compared to the behavior in lagoon sites. The occurrence of these damselfish in ponds provided a unique opportunity to study the relationship of defense to clearly defined areas and populations of fish.

Three hypotheses were tested in this study. The first hypothesis was that the defensive behavior of *S. nigricans*, both conspecifically and heterospecifically, would be greater in pond sites than in the lagoon sites. The greater defense in ponds would be due to the confinement of fishes within a reduced area and the limited food and space resources available. The alternate hypothesis to this study was that confinement

seven fish previously observed for each pond was observed four days after the introduction.

## Results

*Site Comparisons*

The total number of chases per site ranged from 36 to 165, and the average number of chases ranged from 5 to 24 (table 1). The two lagoon sites had the greatest difference in total and average number of chases. Pond site 1 and pond site 2 had the closest total number of chases with 136 and 131 respectively (<4% difference) and the same average number of chases per fish.

A single factor ANOVA was used to determine whether a difference existed among sites. A significant difference was found among sites ($p<0.05$). Paired t-tests were then used to determine the pair-wise grouping of sites. All possible combinations of sites were tested. Of all comparisons made, three comparisons had significant results ($p<0.05$). Pond sites 2 and 3, pond site 2 and lagoon site 4, and pond site 11 and lagoon site 5 were significantly different.

*Chase Comparisons to Behavioral and Physical Factors*

The criteria in assigning relative values to algal quality is presented in table 2. The data collected on algal bites, fish size, territory area, and algal quality are summarized in table 3. The total number of algal bites ranged from 531 in pond site1 to 928 in lagoon site 5. Average fish size ranged from 5.9cm in pond site 3 to 9.0cm in lagoon site 4. Average territory area ranged from 3850cm$^2$ in pond site 2 to 8679cm$^2$ in pond site 3. Average algal quality ranged from 1.7 in pond site 3 to 4.0 in pond site 1 and lagoon site 4.

Data collected on colony and pond area, fish population, and fish density are summarized in tables 4 and 5. Pond site 3 had the largest colony population of 41 *S. nigricans* whereas the rest of the sites had between 7 and 9 individuals per colony. Pond site 1 had the highest density, with 1.82 damselfish per square meter and pond site 3 had the lowest density of 0.74 damselfish per square meter. Pond site 1 had the largest population of both conspecifics and heterospecifics with a total of 207 fish, and pond site 3 had the smallest total of 28 fish. Pond density (total fish per pond area) was highest in pond site 2 with 4.6 fish per square meter, and pond site 3 had the lowest density of 1.87 fish per square meter.

Paired linear regressions and a multiple regression with parameter removal were used to analyze the effect of behavioral and physical factors on the number of chases. All paired and multiple regressions resulted in insignificant results.

*Introduction of Conspecifics*

A paired t-test was used to test for a difference between the number of pre and post introduction chases. There was a significant increase in the number of chases after the introduction of the conspecifics ($p<0.05$). The average number of conspecific chases increased from 1.3 to 3.5 chases per fish.

## Discussion

*Site Comparisons*

The number of chases did not appear to differ by habitat type. Although the single factor ANOVA demonstrated a statistically significant difference among all the sites, the paired t-tests failed to support the hypothesis that chases were associated with the habitats in which the individuals lived. Of all the paired comparisons made, only three of the site comparisons had significantly different results ($p<0.05$).

The low number of replicates per site and the variation in the number of chases per individual at each site is perhaps responsible for the lack of statistically significant results. Only seven replicates per site were observed due to the small colony populations in all sites except pond site 1. Pond sites 1 and 2 have total number of chases of 136 and 131 respectively. These values are relatively close (<4% difference), yet the variation in the number of chases recorded by individuals within the ponds show a greater difference. Pond 1 has a minimum value of 3 chases, pond 2 a minimum of 7. Pond 1 has a maximum of 47 chases, whereas pond 2 has a maximum of 32. Repeated observations for individuals may reduce the variation seen at each site and give a more accurate portrayal of the overall behavior of fish at each site. The suite of characteristics used to characterize the sites was variable, with no two sites having the same behavioral or physical characteristics. These data are discussed in the following section.

*Chase Comparisons to Behavioral and Physical Factors*

There are many other factors which may have contributed to differences in the number of chases by individuals. All sites had different values for all the observations and data collected, thus resulting in a different suite of characteristics which

does not dictate defense, and that other behavioral and environmental factors are what alter territorial defense. The third hypothesis tested was that the introduction of conspecifics into ponds would result in the increase in chases on conspecific fish. This could be attributed to an increase in the density of fish with a limited amount of suitable territory space within each pond resulting in an increase in conspecific agonistic behavior.

**Materials and Methods**

*Site*

The study was conducted on Motu Tiahura on the northwest corner of Moorea, French Polynesia (17°30'S, 149°50'W) during the months of October and November of 1998. Behavioral and physical data were collected on colonies of *S. nigricans* in three saltwater pond sites (sites 1, 2 and 3) and two shallow lagoon sites (sites 4 and 5) on the northwest corner of Motu Tiahura.

*Behavioral Observations*

The defensive and feeding behavior of *S. nigricans* was observed between 10:00 and 14:00 hours on seven randomly chosen territory holding individuals within colonial aggregations at each site. All observations were conducted from above water at positions which allowed for the best viewing of the behavioral activities of each fish. The defensive behavior of *S. nigricans* within their territories was characterized by the number of conspecific and heterospecific chases performed in a ten minute time interval. A chase was counted for each time an intruder was pursued at normal swimming speed for at least two fish lengths, and/or if the individual accelerated at the intruder for a distance less than two fish lengths. The feeding behavior was quantified by the number of bites on the algal substrate taken within an individual's territory per ten minute time interval.

*Physical Data and Observations*

Data on fish size, territory area, and algal quality were collected on each individual of *S. nigricans* observed. Fish size was quantified by total length (TL) in centimeters. Size was estimated by observing the fish in front of reference objects within their territories, which were then measured. Territory surface area was estimated by observing the area within which individuals would chase other fish, take algal bites, and patrol without confrontation with fish in adjacent territories within the colony.

Algal quality within an individual's territory was given a categorical value from one to five, with one representing the lowest quality and five representing the highest quality. Two parameters were used to determine these values: substrate texture (three-dimensionality) and algal height.

Data on colony population and area were collected at each site. The population numbers of *S. nigricans* were estimated by observing smaller areas within the colony and counting the number of territory holding individuals, then obtaining a grand total for the entire colony. The surface area of the colony was obtained by measuring the extent of continuous adjacent territories.

Pond total fish population –conspecifics and heterospecifics- was determined by two visual estimations and then averaged. Pond area was calculated using measurement of axes.

*Site Comparisons*

The number of chases per site was compared to test for the hypothesis that pond sites have more chases than lagoon sites. A one way ANOVA was used to test for a significant difference among sites. Paired t-tests were then performed between all combinations of pond and lagoon sites to test which sites were significantly the same or different.

*Chase Comparisons to Behavioral and Physical Factors*

Comparisons of number of chases to the other behavioral and physical factors listed above were conducted to test for significant relationships. A multiple regression with parameter removal was used to determine the importance of these factors in determining the number of chases by individuals. Paired regressions were performed between all factors to test for significant relationships with the number of bites.

*Introduction of Conspecifics*

Pond sites two and three were selected to perform a conspecific fish introduction. A comparison was made between the number of chases before and after the introduction of conspecifics to test the hypothesis that an increase in the population density would result in an increase in conspecific chases. These two ponds were chosen for their small and similar population sizes. Six *S. nigricans* were caught from the shallow lagoon with aquarium nets, measured with calipers (TL), and fin clipped on the dorsal lobe of the caudal fin for easy identification. Three fish were then introduced into each of pond sites 2 and 3. The defensive behavior of the same

Table 1. Site total and Average Chases

| Site | Number of Chases | |
|---|---|---|
| | Total | Average |
| 1 | 136 | 19 |
| 2 | 131 | 19 |
| 3 | 52 | 7 |
| 4 | 36 | 5 |
| 5 | 165 | 24 |

Table 2. Algal Quality Ranking

| Value | Quality | Parameter Characterization (relative) | |
|---|---|---|---|
| | | Substrate texture | Algal height |
| 1 | Lowest | low | algal coloration of substrate |
| 2 | | low | low |
| | | medium | low |
| 3 | | low | tall |
| | | medium | medium |
| | | high | low |
| 4 | | medium | tall |
| | | high | medium |
| 5 | Highest | high | tall |

Table 3. Site Behavioral and Physical Data

| Site | Average Fish Size (cm) | Average Territory Area ($cm^2$) | Algal Bites | | Average Algal Quality |
|---|---|---|---|---|---|
| | | | Total | Average | |
| 1 | 8.4 | 5,395 | 531 | 76 | 4.0 |
| 2 | 6.6 | 3,850 | 644 | 92 | 2.4 |
| 3 | 5.9 | 8,679 | 559 | 80 | 1.7 |
| 4 | 9.0 | 5,421 | 626 | 89 | 4.0 |
| 5 | 8.3 | 7,536 | 928 | 133 | 3.4 |

Table 4. Colony Area and *Stegastes nigricans* Population Sizes

| Site | Site Classification | Colony Area ($m^2$) | Colony Population | Colony Density (fish/$m^2$) |
|---|---|---|---|---|
| 1 | pond | 22.5 | 41 | 1.82 |
| 2 | pond | 7.56 | 9 | 1.19 |
| 3 | pond | 10.85 | 8 | 0.74 |
| 4 | lagoon | 4.14 | 7 | 1.69 |
| 5 | lagoon | 6.15 | 9 | 1.46 |

Table 5. Pond Area and Fish Population Sizes

| Site | Site Classification | Pond Area ($m^2$) | Heterospecific Population | Total Population (con and hetero) | Pond Density (fish/$m^2$) |
|---|---|---|---|---|---|
| 1 | pond | 56 | 157 | 207 | 3.68 |
| 2 | pond | 13 | 49 | 58 | 4.64 |
| 3 | pond | 15 | 20 | 28 | 1.87 |

describe each pond. For example, pond 1 had the largest colony population, with a total of 50 *S. nigricans*, whereas ponds 2 and 3 had populations of 9 and 8 respectively.

Colony geometry plays an important role in the number of individuals with edge versus interior positions in the colony. A study by Meadows (1995) demonstrated the impact of the relative position of an individual within a colony. Fish on the edge of colonies show more territorial defense than those in the interior of the colony. Central territories are buffered from herbivorous intruders by peripheral territories. All ponds had different ratios of edge to interior individuals, which may have affected the number of chases counted for each individual. A random sample of fish in pond 1 was observed due to the large colony population of 50, and no distinction was made between edge and interior individuals. The low number of individuals per colony at all other cites did not allow for the consideration of edge versus interior positions.

Different species of fish elicit different responses from territorial damselfish, depending on the threat that the intruder poses (Harrington and Losey 1990). A herbivore may elicit an attack by the damselfish because it threatens algal resources, whereas a small planktivore would be ignored because it does not pose a threat to the food resources of *S. nigricans*. The composition of the heterospecific community present differed for each site. The relative percent and population sizes of each species of fish was different for each pond site. The pond populations are most likely a result of stochastic occurrences, such as a storm creating a tidal surge which strands fish in the ponds, and thus were not representative subpopulations of the lagoon. Although some populations of heterospecifics may occupy areas near the lagoon sites, the open nature of the lagoon can allow for fluctuations in the species of the intruders present. Thus, the higher incidence of herbivorous fish in one site would result in an increase in the number of chases.

Other physical parameters at each site may have played a role in the behavior of the damselfish at the different sites. Further site characterization may provide insight into the differences between sites which could explain the variation in chases. For example, average depth, pond volume, and algal species present may play a role in fish behavior.

*Introduction of Conspecifics*

The introduction of conspecifics into two ponds resulted in a statistically significant increase in the number of chases by individuals. This supports the hypothesis that an increase in conspecific fish density results in an increase in agonistic conspecific interactions. While conducting observations on the seven previously examined fish in both ponds, the introduced fish were yet to establish territories. The introduced fish would generally stay at the periphery of the colony and make periodic ventures into the colony. Each time the fish roamed through the colony, chases were elicited by the established territory holding individuals. Thus the increase in the number of conspecific chases may not simply be a result of increased density. Once territorial boundaries have been established within a colony, a neighbor poses little threat to an individual's territory, and confrontations with neighbors would be waste of the individual's time budget (Jaeger 1980). Thus the majority of the post introduction chases may have been directed towards the introduced individuals and not the established neighbors.

**Acknowledgments**

I would like to thank my parents Carol and Gerardo Vallejo for making my college education possible, with this course being the culmination of my college experience. Rosa Isela Rodriguez provided unlimited encouragement and support for me to be confident in my studies and work. I would also like to thank the GSIs, Amy Lesen, Tegan Churcher and Virginia Matzek, and Professors Jere Lipps and Vince Resh for making this field experience run smoothly. The members of the class helped make this course an unforgettable experience.

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# Spatial distribution of the epiphytic coralline red alga *Jania* within populations of the brown alga *Turbinaria ornata*

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ABSTRACT. The distribution of an unknown species of the red coralline alga *Jania* within a population of the brown alga *Turbinaria ornata* was studied. Four 100 meter transects were demarcated on the NW protected barrier reef at the mouth of Cook's Bay in Moorea (Society Islands, French Polynesia). The transects were divided into four zones based on depth and flora: fore reef, algal ridge, reef flat, and lagoon. *T. ornata* along the transect was collected, dried, weighed, and an epiphyte load was calculated (mass *Jania*/mass *T. ornata*). A scatter plot of distance vs. epiphyte load was constructed and linear trendlines inserted. The mean epiphyte load on fore reef samples was 10 times higher than reef flat and lagoon samples. Wave action meters were placed along the transect for a 24 hour period to determine if wave energy was responsible for the observed distribution of *Jania*. High wave action was correlated with high epiphyte load. A caged/uncaged transplant experiment was conducted to determine if herbivory was responsible for the *Jania* distribution. Both caged and uncaged *T. ornata* with *Jania* epiphyte transplanted from the fore reef to the lagoon lost their epiphyte rapidly within the first week of a one month period. This suggests that herbivory by fish is not responsible for *Jania* distribution. An alternate hypothesis that *Jania* epiphyte load is inversely proportional to sediment load was tested. Plastic sediment plates were placed across a transect for a 24 hour period and sediment load recorded. A wave action blocker was placed around a stalk of *T. ornata* on the fore reef for a period of two days to simulate the low wave action environment of the reef flat and lagoon. During this test period, *Jania* epiphyte on the *T. ornata* collected an increased amount of sediment relative to surrounding, unmodified stalks. Further replication is required to verify these results, but the present data suggest that *Jania* is restricted by high sediment load in the lagoon and proliferates on sediment free *T. ornata* on the fore reef.

## Introduction

Much research has been done to determine the physical and biological factors that determine the distribution of algae and their faunal communities in environments subjected to wave energy stress (e.g. Whorff et. al. 1995; Adjeroud & Salvat 1996; Adjeroud 1997). Whorff and colleagues found that the epifaunal community varies significantly with respect to both wave height and substratum slope. In addition, they found that algal mats trap more sediment on horizontal slopes with lower mean wave height. Numerous studies involving terrestrial epiphyte spatial distribution within host populations have been undertaken (e.g. Campbell & Darwyn 1997; Freiberg 1996; Freiberg 1997; McCune 1993). These studies reveal that different microclimates surrounding a host can influence the type and amount of epiphyte species present. In the terrestrial environment, these factors can include wind, light, and humidity. A simple assumption is that local environmental factors would shape the distribution of aquatic epiphytes as well.

Indeed, there has been a considerable amount of research done on seagrass communities, including one study that examined seagrass epiphyte loads along a nutrient gradient (Frankovich & Fourqurean 1997). Frankovich and Fourqurean found that a large, localized increase in nutrients (especially phosphorous) could increase epiphyte load within adjacent seagrass beds. The authors also reported that epiphyte load can be modified by light availability and quality.

However, little research has been conducted on the spatial arrangement of macroalgal epiphytes within the coral reef community. It was the goal of this study to examine the distribution of a single epiphyte species across an algal bed in the context of wave action and sediment load. Based on the work of Whorff and colleagues, it was expected that sediment load would vary inversely with wave action. Frankovich and Fourqurean's finding that light availibility can modify seagrass epiphyte load suggested that sediment load (which can block out light) would have an effect on macroalgal epiphytes as well.

The brown alga *Turbinaria ornata* is a common member of the algal ridge community on coral reefs throughout the Indo-Pacific (Dawes 1998). Red coralline algae of the genus *Jania* are common in southern Australia and other tropical regions and are sometimes epiphytic (Johansen & Womersley 1994). This project examined the spatial distribution of an epiphytic *Jania* species (voucher specimen deposited at UC Berkeley herbarium) within a population of *T. ornata* on a coral reef in Moorea, French Polynesia (Fig. 1). Moorea is a high Pacific island in the Societies at 149°W longitude 17°S latitude. My study consisted of five different experiments to investigate three distinct questions: 1) Is there a difference in *Jania* epiphyte load between *T. ornata* on the fore reef and *T. ornata* on the reef flat and in the lagoon? 2) If so, is difference in epiphyte load caused by wave action? and finally, 3) Through what secondary mechanism does wave action alter the epiphyte load in the two different zones—herbivory, or sediment load?

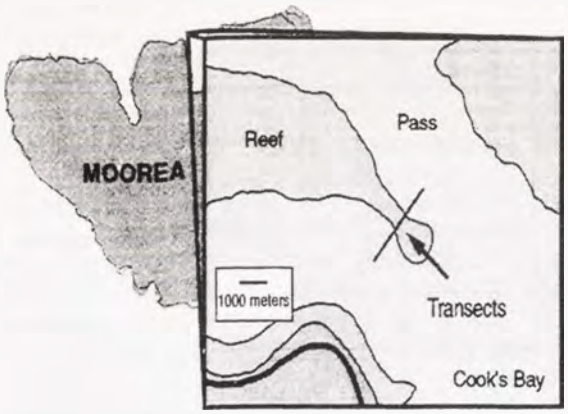


**Figure 1.** Study Site and Transects

## Materials and Methods

My study site is located on the NW protected barrier reef at the mouth of Cook's Bay. *Turbinaria ornata* is the dominant alga on the ridge, and the zone is interspersed with *Sargassum* and other less common algae. I used five experimental procedures to answer the questions presented above. I ran transects across the reef and calculated the epiphyte load on *T. ornata* along the transects to determine a distribution gradient of *Jania* across the reef. I constructed wave meters to measure the amount of wave action on the fore reef, the reef flat, and in the lagoon. I performed three experiments (two sedimentation assays and caged/uncaged transplants) to determine whether herbivory or sediment load was responsible for the epiphyte load gradient.

*Transects*

I randomly marked four 100 m transects within a region where *T. ornata* was observed to be prevalent (Fig. 1). I divided the transects into four biological zones based on depth and flora: fore reef, algal ridge, reef flat, and lagoon. The fore reef (-20 to 0 m) extends from the transect start to the wave break and the start of the algal ridge. The algal ridge (0 to 5 m) is the highest point on the reef and is dominated by *Sargassum* and *T. ornata*. The reef flat (5 to 40 m) is shallow (0 to 0.5 m) and spans from the rear of the algal ridge to the start of the lagoon. The lagoon (40 to 80 m) is deep (0.8 to 2.0 m) and begins where the hard substrate of the reef flat is replaced by a sandy bottom interspersed with large coral heads (Fig. 2).

I collected five leaflets from each piece of *T. ornata* that touched the transect line and recorded distance from the ridge. The *T. ornata* leaflets were cleaned of sediment, small invertebrates, and epiphytes other than *Jania* and dried for 48 h at approximately 30° C. After drying, I removed *Jania* with forceps and weighed epiphyte and bare leaflets. The epiphyte was identified to genus level by Dr. Debbie Woodward, UC Berkeley.

*Wave Action Meters (WAM's)*

Wave height can be used to quantify wave action, since a wave's energy is proportional to the square of its height (Denny 1988). However, waves do not reach the reef flat and lagoon; these zones receive force in the form of a steady current that flows over the ridge from the break zone. To compare these different zones, I constructed devices to measure both wave and current force. Each WAM consists of a quick-tie fastener, rubber band, fishing line swivel, nail, and steel paddle (Fig. 3). I hammered seven WAM's each into the fore reef and the reef flat/lagoon, and collected them after 24 hours. When a wave or strong swell pushes against the paddle, the quick-tie

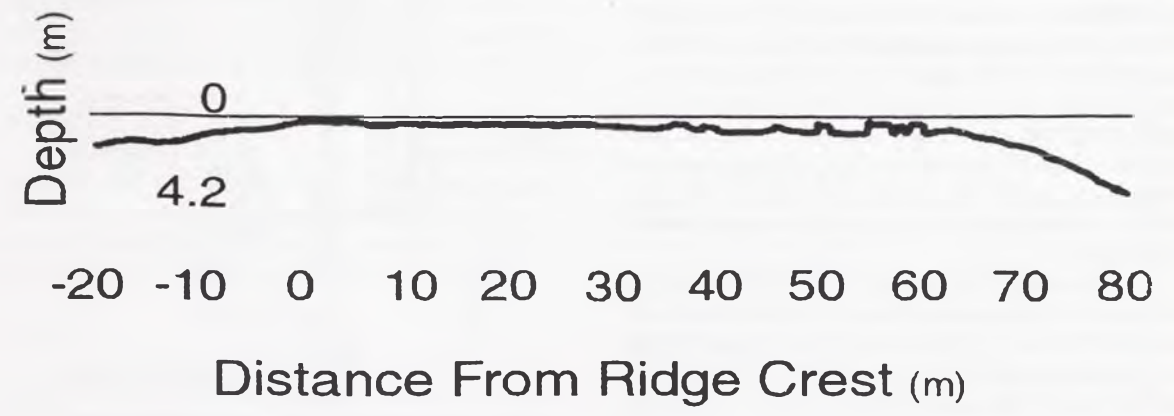


**Figure 2.** Cross Section of a Typical Transect

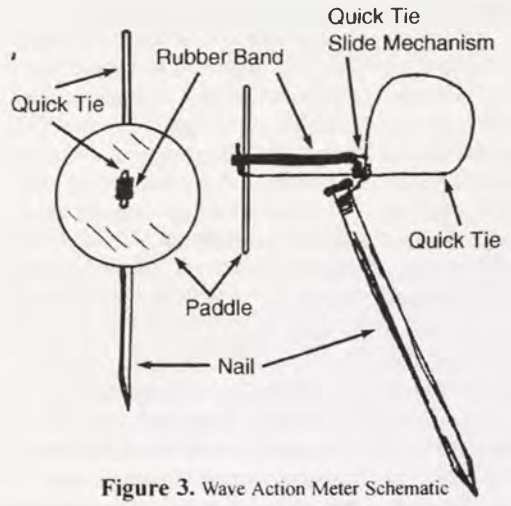


**Figure 3.** Wave Action Meter Schematic

slides against the force of the rubber band. A stronger wave will push harder against the paddle and the quick-tie will slide further against the force of the rubber band. The quick-tie cannot slide backwards. Therefore, a weaker wave will not produce enough pressure on the paddle to cause the quick-tie to slide further than the maximal force it has thus far encountered. In this way the pressure of the strongest wave (up to the limit of the wave meter) within the 24 hour period can be indirectly determined by measuring the amount the quick-tie has moved from its starting position.

*Cages*

To test whether the difference in epiphyte load between *T. ornata* in the lagoon and fore reef could be attributed to herbivory, I conducted caged/uncaged transplants. I constructed cylindrical cages with 3 cm nylon mesh netting, wire supporting rings, and plastic floats. These cages excluded fish >3 cm but did not eliminate potential herbivory of small fish, nudibranchs, or invertebrates. I transplanted two clumps of *T. ornata* (with holdfast and attached substrate) from the fore reef to the lagoon (45 m from the algal ridge). One was placed in a cage and one was simply anchored to the substrate. An additional clump was left on the fore reef and placed in a cage as a control. I also transplanted one caged and one uncaged clump of *T. ornata* from the lagoon to the fore reef (15 m from the algal ridge), and left a caged control in the lagoon.

I monitored the cages for a period of three weeks, and recorded any apparent change in epiphyte load. At the end of three weeks, I brought the caged/uncaged clumps of *T. ornata* and samples of *T. ornata* from the fore reef and the lagoon back to the laboratory. Since it was not possible to calculate a change in epiphyte load over the experiment's duration (obtaining a dry mass is destructive), a post-manipulation, blind ranking protocol was used. The samples were randomized by a third party and I classified each clump as "Fore Reef" or "Lagoon" based on the amount of epiphyte present.

*Wave Action Blockers (WAB's)*

I also hypothesized that the difference in epiphyte load between *T. ornata* in the lagoon and the fore reef could be explained by the differential amount of sediment that settles on *T. ornata* stalks in the two zones. To test this hypothesis I constructed a device to block wave action on the fore reef and thereby mimic fluid flow conditions in the lagoon. The WAB consists of a cylindrical plastic bottle open on both ends. The bottle slides around a stalk of *T. ornata* on the fore reef and is firmly anchored to the ground with nails and fishing line (Fig. 4). The bottle allows some water to exchange between the inside and the ocean (this way oxygen is replenished and the water is not allowed to stagnate), but the rigid cylinder blocks waves and the stalk of *T. ornata* does not sway in the current. WAB's were placed around one stalk of *T. ornata* on the fore reef (15 m from the algal ridge) and one stalk in the lagoon (45 m from the algal ridge) for a period of one week. The amount and physical characteristics of epiphyte on the stalks was monitored and recorded during the experiment.

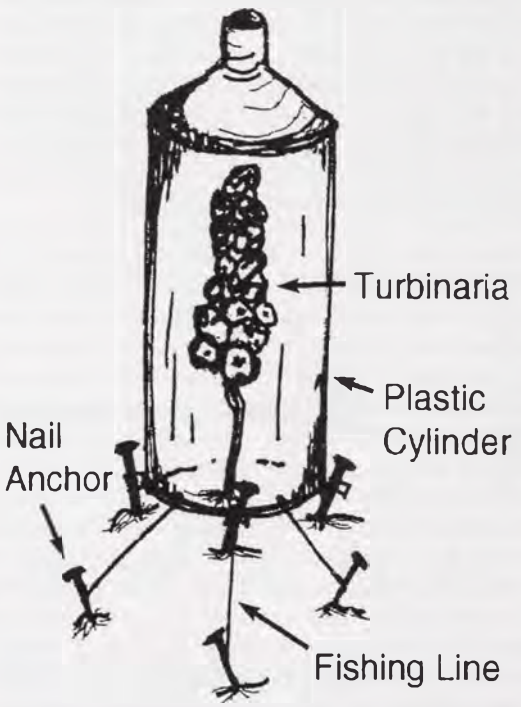


**Figure 4.** Wave Action Blocker Schematic

*Sediment Measurements*

I attached plastic petri dishes next to clumps of *T. ornata* within different zones of the reef for a period of 24 hours to qualitatively measure the amount of sediment that could accumulate on the algae. I recorded whether or not sediment covered the plate and the location of the plate with respect to the algal ridge.

*Morphological Assessment*

I collected approximately 100 stalks of *T. ornata* from the fore reef and 100 from the lagoon and then randomly selected 20 from each population for measurement. I measured the stem length, total length, and stem diameter of each stalk. I then calculated a ratio of stem length to total length and stem diameter to total length. I used confidence intervals and a t-test to determine significance.

**Results**

*Transects*

The epiphyte load for each 5 leaflet sample was calculated by dividing the mass of epiphyte by the mass of bare leaflets (Frankovich & Fourqurean 1997). I combined data from all four transects and constructed a scatter plot of epiphyte load vs. distance (Fig. 5). The plot is divided into the four biological zones discussed earlier for the purpose of data analysis. I inserted linear trendlines for each of the four zones and calculated R-squared values of 0.327, 0.2617, 0.0039, and 0.0671 for the fore reef, algal ridge, reef flat, and lagoon respectively.

The scatter plot did not suggest any clear linear trends, however it did show a large difference between epiphyte load on fore reef samples and load on reef flat/ lagoon samples. To quantify this difference, I calculated mean epiphyte load on samples collected from the fore reef and samples collected from the reef flat/lagoon. The fore reef mean is 65.33 and the reef flat/lagoon 6.23 with a calculated 95% confidence interval of ±9.09 and ±1.25 respectively (Fig. 6). A two-sample t-test assuming unequal variance produced a p value of $2.13 \times 10^{-16}$.

*Wave Action Meters (WAM's)*

The WAM's produced inconsistent measurements, and only two broad results can be stated. The WAM's from the reef flat/lagoon recorded a $\Delta x$ of 0 mm and those from the fore reef an average $\Delta x$ of 76.12 mm with a 95% confidence interval of ±23.98.

*Cages*

The transplants from the lagoon to fore reef could not be recovered. Despite multiple transplant attempts, the *T. ornata* stalks would break after two to four days. The transplants from the fore reef to the lagoon were collected and ranked as discussed in the Materials and Methods section (Table 1). Both the caged and uncaged fore reef → lagoon transplants were classified as having epiphyte loads characteristic of *T. ornata* from the lagoon. This implies that the transplants lost a sufficient amount of epiphyte to more closely resemble *T. ornata* from the lagoon than *T. ornata* from the fore reef. The other blind classifications matched the actual recorded locations of the *T. ornata* stalks.

*Wave Action Blockers (WAB's)*

Despite repeated attempts, the WAB's could not be anchored firmly enough onto the reef to withstand wave action for more than two to three days. I observed that after two days, epiphyte on the stalk of the protected *T. ornata* on the fore reef was covered in sediment and appeared less dense than epiphyte on neighboring stalks of *T. ornata*. *T. ornata* within the lagoon WAB appeared normal compared to surrounding stalks.

*Sediment Measurements*

The two sediment plates recovered from the reef flat/lagoon were partially covered with some white sediment. The three plates recovered from the fore reef were bare.

*Morphological Assessment*

I calculated an average fore reef stem length/total length of 0.282 with a 95% confidence interval of ±0.0297, and an average lagoon stem length/total length of 0.514 ±0.0480 (Fig. 7). A two-sample t-test assuming equal variance produced a p value of $9.93 \times 10^{-10}$. I calculated an average fore reef stem diameter/ total length of 0.0233 ±0.0022, and an average lagoon stem diameter/ total length of 0.0142 ±0.0157 (Fig. 8). A two-sample t-test assuming equal variance produced a p value of $9.05 \times 10^{-4}$.

**Table 1.** Classification of Transplants

| Transplant Location | Blind Classification |
|---|---|
| Fore → Lagoon Caged | Lagoon |
| Fore → Lagoon Uncaged | Lagoon |
| Fore Reef Caged Control | Fore Reef |
| Fore Reef | Fore Reef |
| Lagoon Caged Control | Lagoon |
| Lagoon | Lagoon |

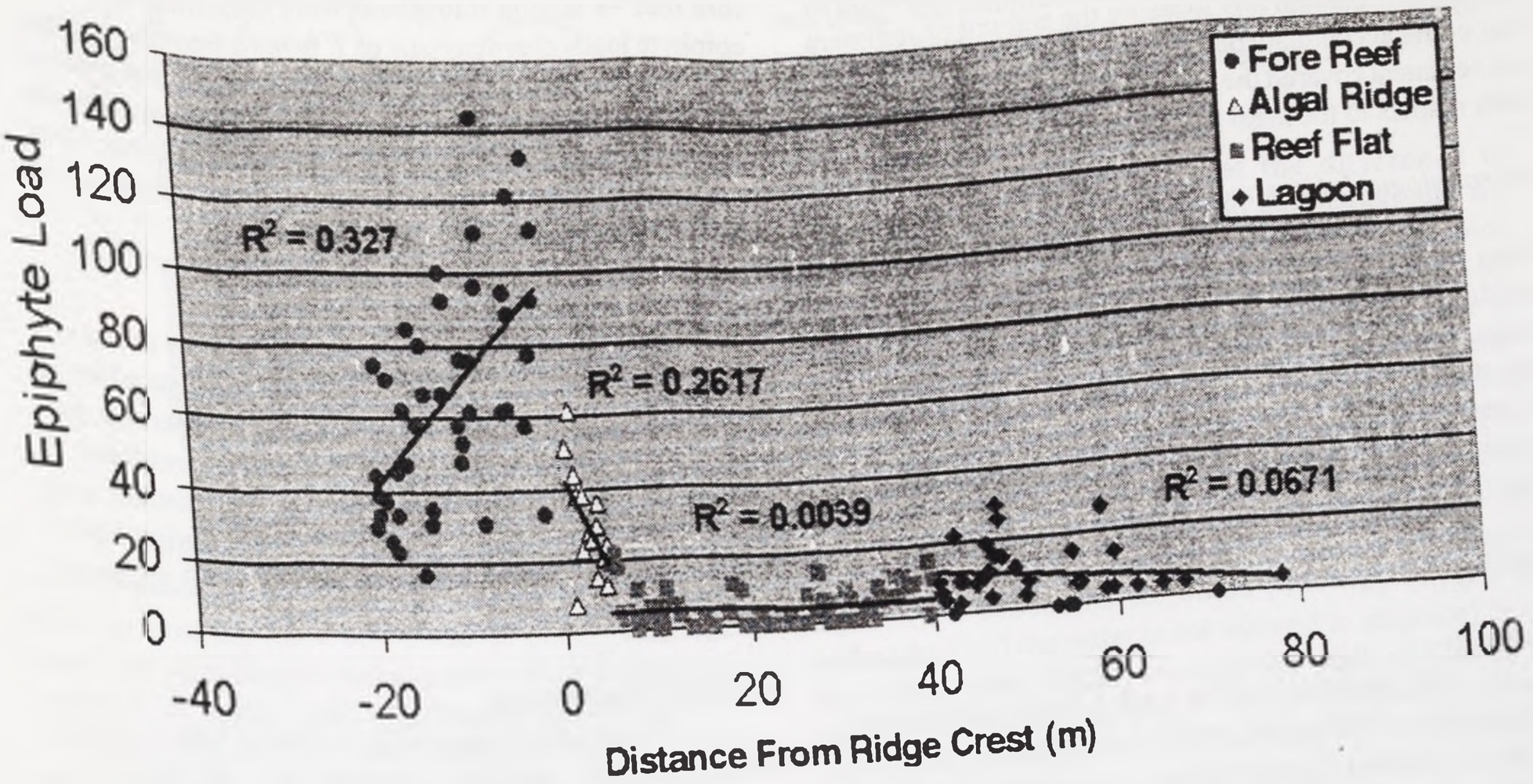


**Figure 5.** Scatter Plot of Combined Transects

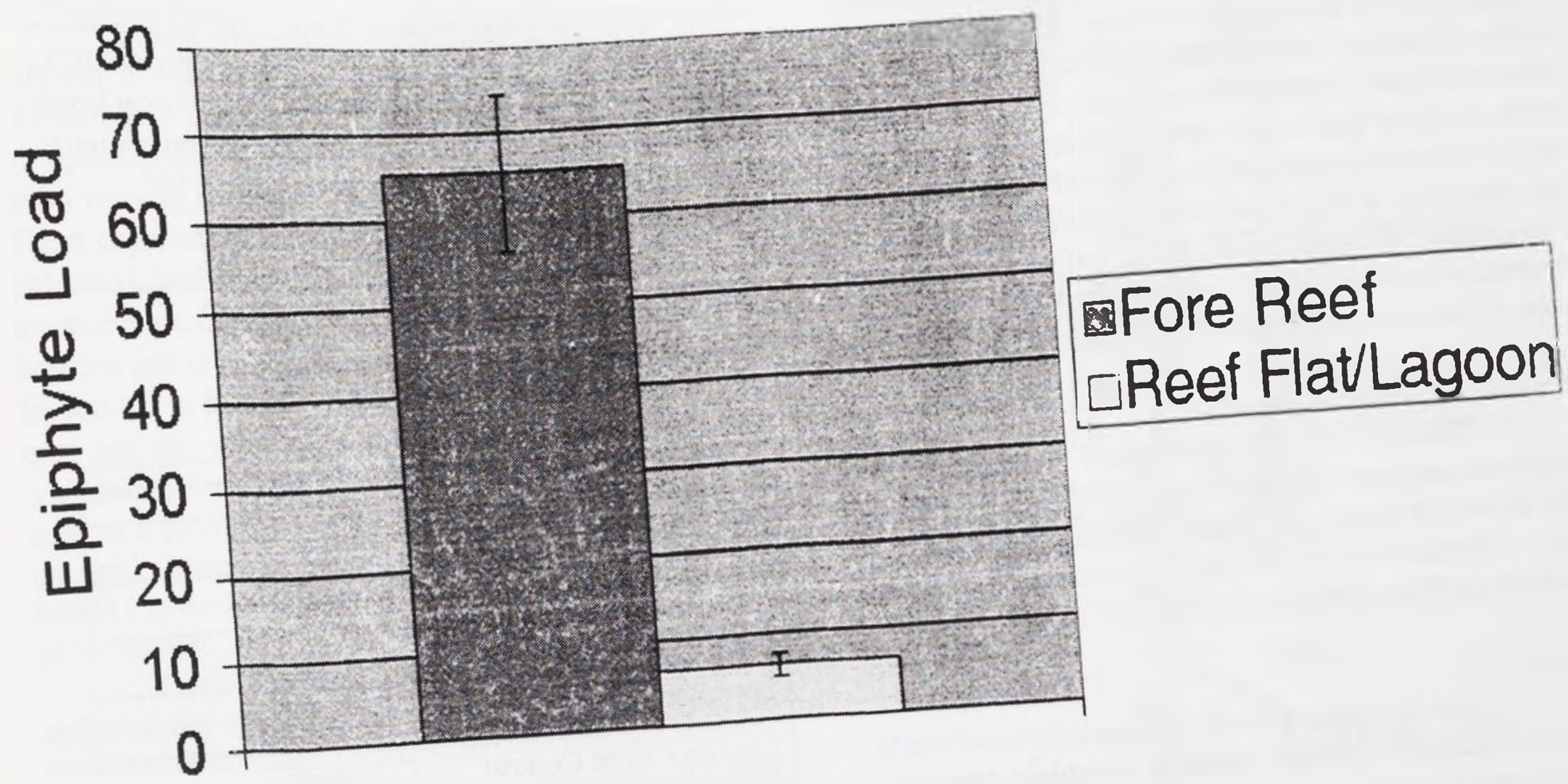


**Figure 6.** Mean Epiphyte Load

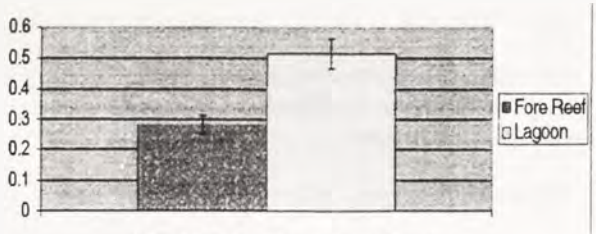


**Figure 7.** Stem Length/Total Length

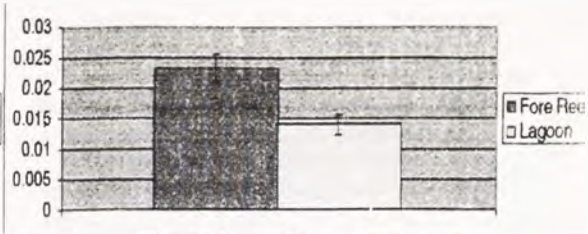


**Figure 8.** Stem Diameter/Total Length

## Discussion

*Jania* epiphyte load is highest on *T. ornata* individuals from the fore reef and significantly lower on individuals sampled from the reef flat and the lagoon (Fig. 6). Biota on the fore reef are subjected to the high wave action present in that zone, and the algal ridge serves as a transition from that environment to the calmer, zero wave action habitat within the lagoon zone. The R-squared values for the linear trendlines are all quite low, and only two trends can be suggested. First, there is a linear trend of increasing epiphyte load from the deep fore reef (-20 m) up to the edge of the algal ridge (0 m) where epiphyte load then rapidly decreases (Fig. 5). Although the WAM's were not sensitive enough to record a difference in wave action between the deep fore reef and the edge of the algal ridge, visual and tactile observations suggest that wave force is stronger at the break zone on the edge of the ridge than it is in the deep fore reef. Further wave action measurements and finer sampling of epiphyte load may show that epiphyte load increases linearly with wave energy. Second, epiphyte load drops on the reef flat and proceeds almost unchanged across the flat and into the lagoon. A perfectly horizontal line will produce an R-squared of zero and this explains the low value reported for the linear trendlines across the reef flat and lagoon.

It is more difficult to determine conclusively what physical or biological factors are responsible for this extreme distribution of *Jania* epiphyte across the reef. The WAM data suggests that high wave action is correlated with high epiphyte load. In addition, it is only possible to make suggestions for the mechanism through which wave action may be acting. Herbivory by fish >3 cm can be tentatively ruled out as a mechanism since both caged and uncaged fore reef → lagoon transplants (high initial epiphyte load) lost their epiphyte over a one month period. In fact, the process appears to be quite rapid. Within two days, the *Jania* epiphyte on both transplants became covered in sediment, less dense, wilted, and the strength of their attachment to *T. ornata* leaflets greatly reduced. It is possible that the herbivore is smaller than the 3 cm mesh size used, therefore herbivory cannot be definitively ruled out as a mechanism. In addition no replicates were used and more experiments are needed to verify these results.

Unfortunately, the inverse transplant of *T. ornata* from the lagoon to the fore reef was unsuccessful. The stems of transplanted *T. ornata* repeatedly broke when exposed to the high wave action present on the fore reef. The stems of lagoon *T. ornata* are longer and thinner with respect to the length of the whole stalk (Fig. 7 and 8). Stems of fore reef *T. ornata* are shorter and thicker relative to the entire stalk (Fig. 7 and 8). For the purpose of these estimates, the *T. ornata* stem can be modeled as a solid cylinder. Given that the bending strength of a solid cylinder is directly proportional to $r^4$ and inversely proportional to l, it can be concluded that the stems of lagoon *T. ornata* are much weaker than those of *T. ornata* growing on the fore reef (Stemheim & Kane 1991). This explains why lagoon → fore reef transplantation was unsuccessful, and suggests that in the future measures must be taken to artificially strengthen lagoon *T. ornata* stems before the transplant.

High sediment load is most likely responsible for restricting *Jania* epiphyte growth on *T. ornata* in the lagoon and reef flat. The sediment plate data shows that high epiphyte load is correlated with low sediment load and low epiphyte load with high sediment load. In addition, the limited WAB observational data showed a decrease in epiphyte load and increase in sediment on fore reef *T. ornata* stalks within the artificially created low wave action environment of the WAB. Finally, the observational data collected during the transplants and discussed above also suggests that high sediment load is responsible for low *Jania* epiphyte load. The transplant and WAB experiments are singular; no replicates were performed. As such, these conclusions must be considered speculation until additional experiments are conducted to causally link sediment load and epiphyte load.

## Conclusions

The factors responsible for creating an epiphyte gradient within a host population are difficult to determine. Other studies have noted the importance of environmental factors, but cautioned that these factors are often hopelessly entangled (McCune 1993). Despite these problems, I believe there are five conclusions that can be taken away from this study:

(1) *Jania* epiphyte load is high on *T. ornata* on the fore reef and low on *T. ornata* in the reef flat and lagoon.
(2) The stems of *T. ornata* in the lagoon are twice as long and ½ the diameter of fore reef *T. ornata* stems.
(3) High wave action is correlated with high epiphyte load and low wave action with low epiphyte load.
(4) High sediment load is correlated with low epiphyte load and and low sediment load with high epiphyte load.
(5) Sediment load appears to restrict *Jania* epiphyte growth in the reef flat and lagoon.

The final three conclusions are not definitive and are based on preliminary studies conducted without the use of replicates. Further research is required to verify or disprove these results. Further caged/uncaged transplants using cages with different mesh sizes would be useful to definitively rule out herbivory. Experiments with more precisely constructed WAM's (e.g. using springs instead of rubber bands, metal swivels instead of fishing line, and quick ties with less resistance to allow measurement of very small forces) will provide refined wave/current data that could be used to construct a scatter plot of epiphyte load vs. wave force. Finally, laboratory and field testing of the effect of sediment load on *Jania* epiphyte load could be used to determine if sediment is indeed responsble for reducing epiphyte load.

**Acknowledgements**

First, I would like to thank the professors and graduate students who made this class possible. Living with a large group of undergraduates is difficult (even for us sometimes), but you were able to provide help and support despite the close quarters. Thanks to Debbie Woodward for identifying my epiphyte. Thanks to Amy Lesen for suggesting the project, Tegan Churcher for helping me formulate hypotheses and run experiments, and Virginia Matzek for guiding my statistics and providing critical analysis of my procedures. Anyone who ever helped me on the fore reef (Cat, Laura, and Sarah especially) deserve a special thanks for risking their life as my buddy. Thanks Dr. Lindberg for providing the intial spark that became my wave meter. I'll give you a cut of the profits when the big bucks start rolling in. Thanks to all the students for making this the truly memorable experience that it was.

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