TO THE GRADUATE SCHOOL AND RESEARCH

The members of the Committee approve the thesis of Gyongyi Plucer-Rosario presented March 24, 1983.

Charles Birkeland

Charles Birkeland, Chairman

Richard H. Randall

Richard H. Randall, Member

Lucius G. Eldredge

Lucius G. Eldredge, Member

Patty Jo Hoff

Patty Jo Hoff, Member

ACCEPTED:

Roy T. Tsuda
Acting Dean, Graduate School and Research

Date

EFFECT OF SUBSTRATE AND LIGHT ON GROWTH AND DISTRIBUTION OF *TERPIOS*, AN ENCRUSTING SPONGE WHICH KILLS CORALS

by

Gyongyi Plucer-Rosario

A thesis submitted in partial fulfillment of the
requirements for the degree of

MASTER OF SCIENCE
in
BIOLOGY

University of Guam

March 1983

AN ABSTRACT OF THE THESIS OF Gyongyi Plucer-Rosario for the Master of Science in Biology presented March 24, 1983.

Title: Effect of Substrate and Light on Growth and Distribution of _Terpios_, an Encrusting Sponge Which Kills Corals.

Approved: Charles Birkeland
Charles Birkeland, Chairman, Thesis Committee

The effects of light and substrate on the growth and distribution of _Terpios_ was demonstrated at three locations on Guam's reefs. _Terpios_ grows fastest on clean substrates followed by live coral, reef rock and red calcareous algae. Growth on these substrates is often intermittent as _Terpios_ typically exhibits periods of growth followed by long periods without growth. _Terpios_ encrusts _Montipora_ and _Porites_ colonies less frequently than would be expected by chance. This favors the relative abundance of these corals in comparison with abundances of corals which _Terpios_ encrusts more frequently. _Terpios_ is sometimes overgrown by _Montipora_, _Porites_, and red calcareous algae. Reef rock may harbor organisms which inhibit _Terpios_ growth.

Light does not affect _Terpios_ growth or distribution except in limiting it to illuminated areas of the photic zone on reefs. The growth of _Terpios_ does not vary with months between September and June. Senescence and death of _Terpios_ follows a distinct succession of conditions. _Terpios_ is able to form bridges of tissue from one coral

branch across open water to another coral branch and is also able to generate a new colony from a small fragment.

Terpios is probably a fast-growing competitor of corals for space rather than a predator of corals. *Terpios* overgrows most hard stable reef substrates, and the growth rate on all sample substrates is substantial. This demonstrates that *Terpios* has a great potential for covering a reef. *Terpios* may influence more of a reef over the long run than does *Acanthaster planci*, indicating that *Terpios* may be one of the most important causes of coral reef disturbances.

ACKNOWLEDGEMENTS

I would like to thank Dr. C. Wilkinson for sending pertinent literature, reviewing the manuscript, and ascertaining the presence of cyanobacteria in Terpios. I would also like to thank the following for assisting with field work: Gretchen Grimm, Susanne Wilkins, Tim Morton, Paul Gates, Jerry Davis, Frankie Cushing for constructing the air blaster, and Vaughan Tyndzik who always kept the boat's motor running long enough to get us home. I am also grateful to Gretchen Grimm and Henry G. Siegrist for reviewing the manuscript, Rob Myers for providing the slides, and Julie Santos and Lucy Lacsamana for typing the manuscript. I am especially indebted to Mitchell Colgan for moral and intellectual support at the beginning of the research, and Alicia Siegrist for assistance in using a computer in my data analysis. Finally, a special thanks to Frank Rosario, my husband, for his continued encouragement and help.

TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS	ii
LIST OF TABLES	iv
LIST OF FIGURES	v
INTRODUCTION	1
MATERIALS AND METHODS	6
Survey of Growth at Fafai Beach	6
Survey of Distribution at the Pugua Study Site	9
Experiments at Cocos Lagoon	10
RESULTS	14
Survey of Growth at Fafai Beach	14
Survey of Distribution at the Pugua Study Site	18
Experiments on Growth in Cocos Lagoon	22
DISCUSSION	27
The Influence of Substrate on Distribution and Growth	27
The Influence of Light on Distribution and Growth	32
Senescence and Death	34
CONCLUSIONS	35
LITERATURE CITED	37

LIST OF TABLES

Page

Table 1. Mean total growth of *Terpios* on different substrates, in the shade and exposed to light at Fafai Beach. 15

Table 2. Seven instances where *Terpios* was overgrown by another organism at Fafai Beach. 17

Table 3. Percent cover and total number of *Terpios* mesh points per depth and transect at the Pugua Study Site. 19

Table 4. Substrates covered by *Terpios* at the Pugua Study Site listed in order of their Electivity Index (E.I.). 20

Table 5. Mean growth rate of *Terpios* on four substrates in Experiment I in Cocos Lagoon. 23

Table 6. Mean growth rate of *Terpios* on two prongs of the *Acropora formosa* forks in Experiment II in Cocos Lagoon. 23

LIST OF FIGURES

Page

Figure 1. Map showing the locations of the three study sites on Guam. 7

Figure 2. Illustration showing how the amount of distal *Terpios* growth was measured on the dichotomous branch forks in Experiment II at Cocos Lagoon. 12

Figure 3. Bar diagram showing *Terpios* size-class frequency at Transects A-D at the Pugua Study Site. 21

Figure 4. Bar diagram showing *Terpios* growth on four different substrates in Experiment I at Cocos Lagoon. 24

Figure 5. Bar diagram showing the difference in growth of *Terpios* on the living and air-blasted prongs of *Acropora formosa* in Experiment II at Cocos Lagoon. 26

INTRODUCTION

A species of Terpios on Guam is an unidentified and possibly new species of Demospongiae, Order Hadromerida, Family Suberitidae (Bergquist, pers. comm.). Bergquist suggests that the local Terpios species may be a variety of *T. fugax*. Terpios is an encrusting sponge of 1 mm thickness (Bryan, 1973) which varies in color from gray in full sunlight to black in partial shade and deeper waters. Astrorhizae radiate from the oscules and are found throughout the surface, distinguishing the sponge from other dark encrusting organisms. The sponge surface lacerates easily and exposes a green inner tissue as well as the underlying substrate. The skeleton is composed of small hexactine-like spicules (Bryan, 1973).

Terpios has been found in Truk Lagoon, American Samoa (Birkeland, pers. comm.), Taiwan, Cebu Island in the Philippines, Saipan, Rota, Aguijan, and Pagan in the Northern Mariana Islands, and Belau and Yap in the Western Caroline Islands (Randall, pers. comm.). Auberson (1982) has described a "parasitic sponge which appeared as a thin layer of gray tissue extending over several square meters in different portions of the reef and gradually spreading over neighboring corals" occurring in his work site in the central Visayas, Philippines. Observations show that Terpios grows on most of the reefs of Guam and is most common on forereef slopes to at least 30 m. Bryan's (1973) survey of 37 reef locations on Guam shows that Terpios is abundant. Twenty-five sites contained Terpios with cover varying from a few small patches to areas 1000 m in length which were almost completely encrusted.

Terpios grows on most corals as well as on coral rubble, reef rock, red calcareous algae, shells, bottles, and on the sides of plastic aquaria in the laboratory. Although *Terpios* is found throughout Guam's reefs, little is known about the dynamics of its interactions with corals. Growth rates of *Terpios* recorded over 8 days showed growth to be four times faster on a *Porites lutea* than on reef rock (Bryan, 1973) and Bryan proposed that the sponge derives nutrients from the coral tissue. Although growth rates may be faster on living coral, Bryan's assumption that *Terpios* is deriving nutrients from the coral is not necessarily correct. It is possible that reef rock harbors organisms which inhibit the growth of *Terpios*, whereas living coral or newly killed coral (i.e., killed by *Terpios*) does not harbor these organisms.

Defining predation as one organism ingesting another and competition as two organisms contending for space, one may ask whether *Terpios* is a predator of corals or a competitor of corals for space (or both). Sponges are thought to be suspension feeders (Bergquist, 1978; Jorgensen, 1966; Stephens and Schinske, 1961). Reiswig (1971) studied the diets of three tropical Demospongiae: a *Mycale* sp., *Verongia gigantea*, and *Tethya crypta*. All three had similar diets consisting of material ranging in size from 0.3 μ to 50 μ. This material was composed of naked flagellates, fungi, diatoms, dinoflagellates, and bacteria. These species each showed a net production of detritus so the presence of detritus in their diets was difficult to determine. Although the hypothesis that Terpios is deriving nutrients from coral tissue cannot be discounted, it seems unlikely that sponges consume coral tissue.

An alternative hypothesis is that Terpios is in competition for space with corals. Some sponges are toxic to predators (Bakus, 1981; Bakus and Green, 1974; Bergquist, 1978; Wilkinson, 1978a), and there is extensive literature on competition for space between sessile marine organisms (Birkeland et al., 1981; Buss and Jackson, 1979; Gordon, 1972; Hildeman et al., 1977; Jackson, 1979; Karlson, 1978; Lang, 1973; Osman, 1977; Rutzler, 1970; Sara, 1970; Stebbing, 1973a, 1973b). There is also evidence that some sponges release chemicals toxic to competitors. Jackson and Buss (1975) state that many sponges and ascidians cause adverse reactions in ectoprocts. They claim that these reactions result from allelochemicals released by the sponges and ascidians and conclude that these allelotoxic interactions are examples of interference competition for space. Furthermore, Bergquist (1978) reports that many species of Tedania and Neofibularia sponges are toxic to competitors, thus affording protection by reducing fouling of their tissue and inhibiting overgrowth by other organisms. Bergquist also states that bare zones 1-3 mm wide of dead coral skeleton are commonly found adjacent to these sponges and that corals are more frequently overgrown by sponges than the reverse. In many cases these overgrown corals are killed by the sponges, whereas the overgrown sponges are never harmed. Neofibularia irata is a sponge which encrusts and kills corals (Wilkinson, 1978b).

Terpios, therefore, may be killing corals in competition for space rather than in the acquisition of nutrients. The possibility that Terpios does contain chemicals toxic to corals was tested by Bryan

(1973). When he placed a section of sponge on a _Fungia_, the coral immediately retracted its tentacles and the coral tissue adjacent to the sponge section died within 24 hours. In addition, bare zones of coral as described by Bergquist are found along boundaries with _Terpios_.

Terpios is usually found growing in areas fully or partially exposed to sunlight. It has never been observed growing deep in crevices or underneath explanate corals. Even when _Terpios_ has completely encrusted to the edge of a coral sheet, no _Terpios_ is ever found on its underside. Wilkinson has found that samples of _Terpios_ from Guam contain large amounts of extracellular cyanobacteria, possibly of the genus _Aphanocapsa_ (pers. comm.). Since cyanobacteria require light to photosynthesize, their presence may account for the fact that _Terpios_ is only found growing in areas exposed to some light. However, it is not known whether or not shade or depth affect the growth rate or distribution of _Terpios_. Wilkinson (1982) reports that sponges with symbiotic algae (cyanobacteria) comprise 81 percent of the sponge biomass to 20 m in depth on Davies Reef in Australia and proposes that some of these symbionts contribute a considerable amount of nutrients to their hosts. Wilkinson (1980) states that from 5-12 percent of the fixed carbon is translocated from the alga to the sponge. Wilkinson and Fay (1979) propose that some symbiotic algae recycle nitrogen to their sponge host. If _Terpios_ is provided with significant amounts of some nutrients by its algal symbiont, light should prove to be important in affecting _Terpios_ growth and distribution.

The purpose of this research was to examine some questions pertaining to the growth and death of *Terpios*. Does *Terpios* ingest coral tissue or is it merely a competitor of corals for space? What effect do light and different substrates have on *Terpios* growth? How long does a *Terpios* patch occupy an area? Is the death of a *Terpios* patch complete or does the patch shrink in size?

MATERIALS AND METHODS

The first phase was a field survey conducted at two locations. The survey at Fafai Beach was a survey in which growth of *Terpios* was measured on different substrates, depths, and in shade. In addition, observations were made on the death of *Terpios*. The survey at the Pugua Study Site was designed to acquire information on distribution and size classes of *Terpios* on different substrates and at different depths. The second phase was experimental. *Terpios* was transplanted onto different substrates and its growth rates measured. This further clarified the causal factors behind the differences in *Terpios* growth on different substrates.

Survey of Growth at Fafai Beach

Location. This survey took place at Fafai Beach (Gun Beach) at the northern end of Tumon Bay which is located on the northwestern coast of Guam (Figure 1). The area consists of an intertidal reef-flat platform, reef margin, a reef-front and submarine terrace to 10 m in depth, and a steep seaward slope to 35 m in depth. Above 10 m, only three 6 x 6 cm patches of *Terpios* were found encrusting an *Acropora* and reef rock. These patches were all within 900 cm^2. Also, coral cover above 10 m was greater than below 10 m, with much of the substrate covered by encrusting *Montipora* species. Below 10 m, an estimated 25-30 percent of the substrate was covered with large (1 x 1 m) patches of *Terpios*. Most of the remaining substrate was reef rock, with some

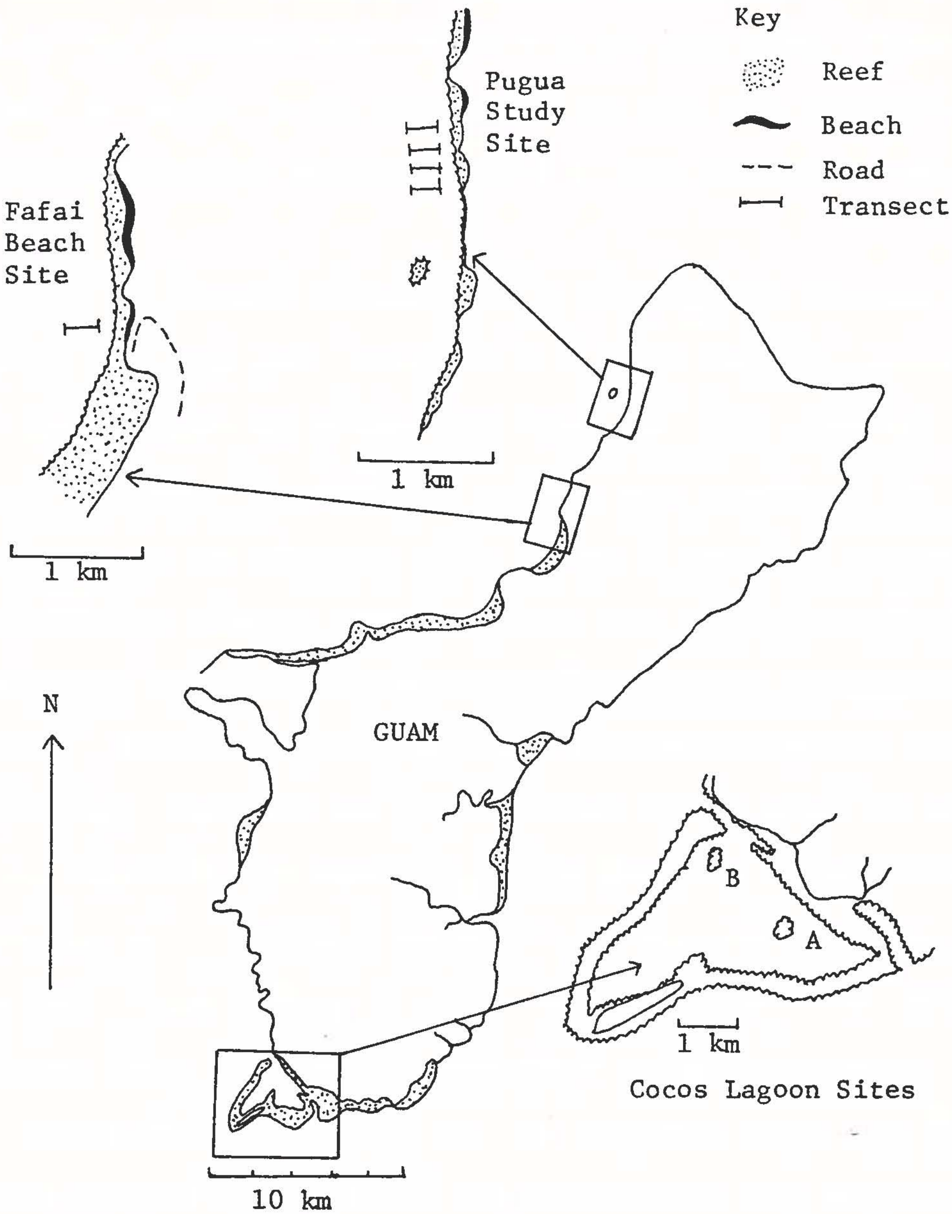

Figure 1. Map showing the locations of the three study sites on Guam.

colonies of live corals. _Porites_ (_Synaraea_) _iwayamaensis_ formed the largest and most abundant coral colonies in the study area. Since Fafai Beach is located on the northern end of Tumon Bay, it probably has a similar assemblage of coral species to that compiled by Randall (1971).

Methods. A transect perpendicular to the shoreline extended along a submerged telegraph cable from 10-26 m in depth along the seaward slope. This transect was divided into five equal depth intervals. In each depth interval, five permanent stations were selected within 15 m of either side of the telegraph cable. These 25 nonrandom stations were specifically selected because each had 3-10 boundary interactions between _Terpios_ and other substrates (_Terpios_-_Acropora_, _Terpios_-reef rock, etc.). A nail was driven into each interaction boundary selected for monitoring. Each nail was given a number and the nature of interaction was recorded. The amount of _Terpios_ growth or retrogression from each nail was recorded at one month intervals from September 1981 to June 1982. Where _Terpios_ was either being overgrown or was dying, the apparent reason was recorded (overgrowth by _Montipora_, death, etc.). Living corals, reef rock, and red calcareous algae were the substrates on which _Terpios_ growth and retrogression were monitored. Interactions occurring in the shade were also monitored. Reef rock includes smooth pavement, jagged rocky outcrops, and dead coral. A thin turf of blue-green algae and small (<5 x 5 mm) patches of calcareous algae were usually growing on reef rock substrates.

In all, 175 interactions were monitored over the nine months although only 91 remained at the conclusion of the research. Thirty-three nails disappeared, perhaps because of currents or curious divers, and 51 nails were no longer monitored because the Terpios died. Station 25 (26 m deep) was lost completely after the second month.

Analysis of variance tests (Sokal and Rohlf, 1969) were performed on the growth measurement data.

Survey of Distribution at the Pugua Study Site

Location. This survey took place just north of Pugua Patch Reef (Double Reef) on the northwest coast of Guam (Figure 1). This reef consists of a submarine reef terrace that dips gradually downward from the cliffline to a depth of 15 m. Numerous sand-filled depressions and large coral-covered patch-reefs and mounds are located throughout the shallow areas. This reef was selected because it sustains a healthy coral community as well as numerous Terpios encrustations.

Methods. Four transects 10-30 m apart were placed perpendicular to shore, beginning at the 5 m depth contour and extending to the 15 m depth contour. Below 15 m, no corals were found in two of the four transects. Each transect was divided into 2 m depth intervals. At each depth interval, 20 random quadrats were placed, and information was recorded as explained below. The first quadrat was randomly released at the appropriate depth. Each subsequent quadrat was flipped over along one side, moving along a somewhat circular route within the depth interval. The quadrat used was a 25 x 25 cm square made of thin metal pipe and divided with nylon fishing line into 5 x 5 cm sections (Sara, 1970). A record was kept of all coral genera, other substrates, and Terpios which were found beneath the cross points of the nylon line. Also recorded was identification of the substrate which Terpios was encrusting. These data supplied information from which substrate availability and frequency of cover by _Terpios_ could be calculated. These data also provided information on _Terpios_ density, frequency, and percent cover.

The _Terpios_ patch found closest to the upper right hand corner of each quadrat was measured; recording the greatest length and width in centimeters. If no patch was found within the quadrat, the closest patch outside it was measured. If none was found within 5 m of the quadrat, a measurement was not taken. These data supplied information on _Terpios_ size classes.

Each substrate was ranked according to an Electivity Index, and a chi-square value (Sokal and Rohlf, 1969) was calculated to determine the significance of _Terpios_ coverage on the different substrates. Electivity Index is calculated using the following equation: $EI = (Ai - Pi)/(Ai + Pi)$ where Pi = substrate covered with _Terpios_ and Ai = total substrate available.

Experiments at Cocos Lagoon

Location. Experiments I and II were conducted at Sites A and B in Cocos Lagoon, located at the southern end of Guam (Figure 1). Experiments were conducted on lagoon patch reefs ranging in depth from 7-10 m. Site A (Exp. I) was located in a depression in the center of a large patch reef composed mainly of _Porites_ (_Synaraea_) _iwayamaensis_, as well as colonies of _Montipora_, _Pocillopora_, _Acropora_, and other less abundant coral genera. The floor of the depression was strewn with algal-covered dead _Acropora_ rubble and living _Montipora_. _Terpios_ was encrusting much of the _Acropora_ rubble and some of the _Montipora_ and _P._

(S.) iwayamaensis. Site B (Exp. II) was located in a sandy depression in a large Acropora formosa patch reef where Terpios was found covering large areas.

Materials and Methods. Both experiments required the use of cleaned coral surface. A living piece of coral was air-blasted to remove as much of the living coral tissue as possible. This resulted in a clean, white coral skeleton, though some tissue may have remained in the interior of the skeleton. The air blaster was constructed of a scuba tank attached to a hose with a nozzle which directed a powerful concentrated stream of air when released.

Experiment I. Twenty-one samples each of four different substrates were tested over a two-week period. The four substrates were: (1) living Montipora, (2) reef rock, (3) plexiglass plate, and (4) cleaned Montipora. Each substrate sample was approximately 10 x 5 x 5 cm. A piece of Terpios-encrusted substrate called the transplant (5 x 7 cm), was attached to each sample substrate (using string or rubber band) and left in the field for 14 days. During this time, Terpios from the transplant grew onto the attached sample substrate. When collected, the growth of Terpios on the sample substrate was measured in millimeters. The Terpios transplants were not taken from a single colony because none was large enough to supply 44 transplants. Care was taken to choose only transplants with thick, healthy Terpios tissue.

Experiment II. In this experiment, Terpios growth rate and direction were monitored. Twenty-one forked-branches of Acropora formosa were prepared by air-blasting one of the two prongs (Figure 2). A Terpios transplant was attached with string to the base of the branch

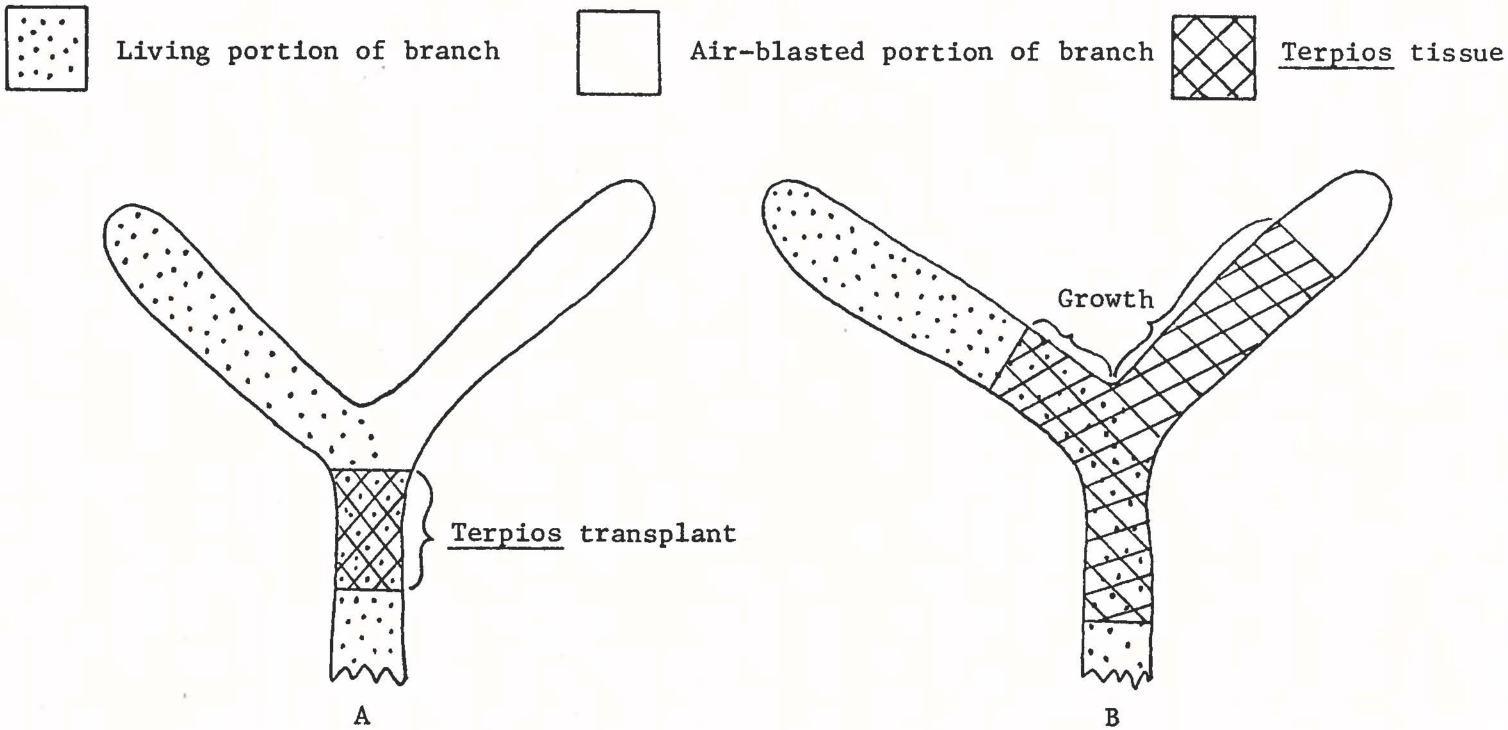

Figure 2. Illustration showing how the amount of distal _Terpios_ growth was measured on the dichotomous branch forks in Experiment II at Cocos Lagoon. A. Branch at time of _Terpios_ transplant attachment. B. Branch after 14 days of _Terpios_ growth.

and left for 14 days. During this time, *Terpios* grew onto the base, then past the junction from which the two prongs diverged. *Terpios* growth past the junction on each prong was measured in millimeters.

RESULTS

Survey of Growth at Fafai Beach

Although *Terpios* showed steady growth at many interaction sites over many months, *Terpios* exhibited short periods of growth followed by long periods without growth at 26 sites. At Site 12 (18 m depth), *Terpios* grew 5 mm in one month and then stopped growing for the next four months. Usually, when growth was evident, it was from 2-10 mm per month. The largest increment measured was 40 mm at a *Porites* (*Synaraea*) interaction site; the greatest retrogression measured was 17 mm at a reef-rock interaction site. No growth or retrogression was measured during the nine months of monitoring at eight interaction sites.

Growth of *Terpios* was significantly affected by substrate type (Table 1). Growth was greatest on living coral, followed by reef rock and red calcareous algae. Neither month ($Fs_{[4,341]} = 1.02$) nor depth (Table 1) significantly affected the growth of *Terpios*.

Because growth of *Terpios* was intermittent, mean growth rate was not calculated. Mean total growth on different substrates are presented in Table 1. The number of samples for each coral genus was: *Favia* (11), *Montipora* (4), *Porites* (53), *Goniopora* (2), *Leptastrea* (3), *Stylophora* (2), *Astreopora* (3), *Millepora* (1), and *Oulophyllia* (1). The number of samples of each coral genus was a general indication of the availability of that coral at the site. Mean total growth of *Terpios* was approximately four times that on reef rock (8 vs 2 mm).

Table 1. Mean total growth of *Terpios* on different substrates, in the shade, and exposed to light at Fafai Beach. Growth is in millimeters, and was measured over nine months. N = sample number, $\overline{Y}$ = mean growth, W = range, * indicates significant difference, ns = no significance difference. An anova table is given below the table of summarizing statistics.

A. Substrate	N	$\overline{Y}$	W
Red calcareous alage	31	-3.6	-20 to 30
Reef rock	52	1.8	-47 to 38
Corals	92	7.79	-20 to 120

Source	Degree of Freedom	Mean Square	F
Depth	4	37.69	.10ns
Substrate	3	1148.78	3.14*
Interaction	12	490.06	1.34ns
Error	155	365.51	

B. Light	N	$\overline{Y}$	W
Shade	26	-2.6	-47 to 10
Exposed to light	149	5.53	-20 to 120

Source	Degree of Freedom	Mean Square	F
Light	1	1468.79	3.89*
Error	173	377.09	

Terpios at red calcareous algae boundaries had a mean retrogression of 4 mm.

When measurements were combined according to light conditions, *Terpios* growth was shown to be significantly less in the shade (Table 1). However, of 26 *Terpios* interactions under shaded conditions, 17 were interactions with red calcareous algae (in which *Terpios* showed a mean retrogression), four were interactions with reef rock, and five with live corals. Few interactions were found in the shade, especially below 15 m, so it was not possible to select equal numbers of interactions in the shade for each substrate.

There were 126 measurements of *Terpios* retrogression (where measurements were negative). Of these, seven were interactions in which *Terpios* was being overgrown by *Montipora*, *Porites* (*Synaraea*), *Porites* (*Porites*), and red calcareous algae (Table 2). These overgrowth interactions were characterized by thick, uniform (healthy) sponge tissue and the presence of a raised ridge of coral or algal tissue at the boundary where *Terpios* was being overgrown. Overgrowth measurements were relatively uniform, averaging from 1-2 mm per month. These criteria distinguished these overgrowth measurements from the other 119 measurements of retrogression. In these interactions, *Terpios* tissue was thin, patchy, and disintegrating (dying). Measurements of *Terpios* retrogression in these dying patches were intermittent with 10-15 mm of tissue disintegrating at a site during one month.

The death of small patches of *Terpios* (up to 20 x 20 cm) took 2-3 months. The death of larger patches took longer than the nine month period of monitoring. Although a part of a large patch would die, another part would continue to live.

Table 2. Seven instances where *Terpios* was overgrown by another organism at Fafai Beach. Depth is in meters. Overgrowth was measured in millimeters and is the total amount measured over nine months.

Substrate	Depth	Amount Overgrown
Montipora	21.5	20
Porites (*Porites*)	21.5	8
Porites (*Synaraea*)	22.5	15
Porites (*Synaraea*)	25	10
Red calcareous algae	10	10
Red calcareous algae	11	15
Red calcareous algae	20	10

Survey of Distribution at the Pugua Study Site

Terpios was found encrusting 2.7 percent of the live corals and 4.1 percent of the reef rock, with a total cover of 3.1 percent. Substrates never found encrusted by *Terpios* were soft corals, sand, and fleshy and calcareous algae. *Terpios* was significantly clumped within quadrats ($X^2_{[399]} = 3104$) with a mean density of 0.57 points per quadrat. *Terpios* was found in 18.7 percent of the 400 quadrats recorded. The number of *Terpios* encrustations was significantly different between transects ($G_{[31]} = 521.84$). Transect C had the most *Terpios* (142) followed by D(39), B(12), and A(5). *Terpios* encrustations did not vary with depth (Table 3).

Table 4 contains a list of coral genera encountered within quadrats as well as relative frequencies of available substrates in comparison with frequencies of substrates occupied by *Terpios*. Although *Montipora* and *Porites* were the most abundant corals at the site, *Terpios* encrusted these corals significantly less than would be expected by chance. No significance was found in *Terpios* differentially occupying corals of different surface characteristics or colony forms such as smooth or irregular, and branched or encrusting.

Size class data for *Terpios* was available for all transects, but not for all depths of each transect. Measurements were available at Transect A only at the 7-9 m depth, Transects B and C had data available for all depths, and data were available only from the 9-15 m intervals at Transect D. There was a significant difference in size class distributions between transects ($Fs_{[3,269]} = 2.969$). A size class frequency bar diagram (Figure 3) shows that most patch sizes were less than 200 cm^2, and that between 200 and 900 cm^2, size class

Table 3. Percent cover and total number of <u>Terpios</u> mesh points per depth and transect at the Pugua Study Site. Parentheses enclose percent.

	Depth					
	5-7 m	7-9 m	9-11 m	11-13 m	13-15 m	Total
Transect						
A	(0)0	(1.25)4	(31)1	(0)0	(0)0	(.31)5
B	(0)0	(.31)1	(2.18)7	(1.25)4	(0)0	(.75)12
C	(27)87	(6.25)20	(5.62)18	(2.18)7	(3.12)10	(8.87)142
D	(0)0	(0)0	(.62)2	(1.56)5	(10)32	(2.43)39
Total	(6.79)87	(1.95)25	(2.18)16	(1.25)16	(3.28)42	(3.09)198

Table 4. Substrates covered by *Terpios* at the Pugua Study Site listed in order of their Electivity Index (E.I.). n = the number of mesh points counted per substrate, f(obs) = number of points covered by *Terpios*, f(exp) = number of points expected to be covered by *Terpios* given a 3.33 percent cover. Where a genus has f(exp) <5, it is combined in groups. When p is significant, the substrate is covered by *Terpios* out of proportion to the availability of the substrate. Where the E.I. is negative, the substrate is covered by *Terpios* less frequently than would be expected by chance, while a positive E.I. indicates a substrate covered more frequently than expected by chance. Where p is not significant (ns), the substrate is covered in proportion to its availability. Groupings A, B, and C include the following genera: (A) *Psammocora*, *Stylocoeniella*, *Astreopora*, *Pavona*, *Goniopora*, *Galaxea*, *Merulina*, *Acanthastrea*, *Lobophyllia*, *Millepora*, *Heliopora*, (B) *Stylophora*, *Pocillopora*, (C) *Favia*, *Oulophyllia*, *Goniastrea*, *Echinopora*, *Platygyra*, *Hydnophora*, *Montastrea*, *Cyphastrea*.

Substrate	n	f(obs)	f(exp)	Probability by X^2	E.I.
Acropora	220	7	7.3	ns	.937
Leptastrea	160	4	5.3	ns	.950
(A) 10 remaining families	383	20	12.7	ns	.950
Montipora	1261	27	42.0	$p<.025$	-.953
(B) Pocilloporidae	224	7	7.4	ns	.969
(C) Faviidae	495	13	16.5	ns	.974
Porites	374	5	12.4	$p<.025$	-.983
All corals	3117	83	103.8	$p<.05$	-.974
Reef rock	2828	115	94.2	$p<.05$	+.960

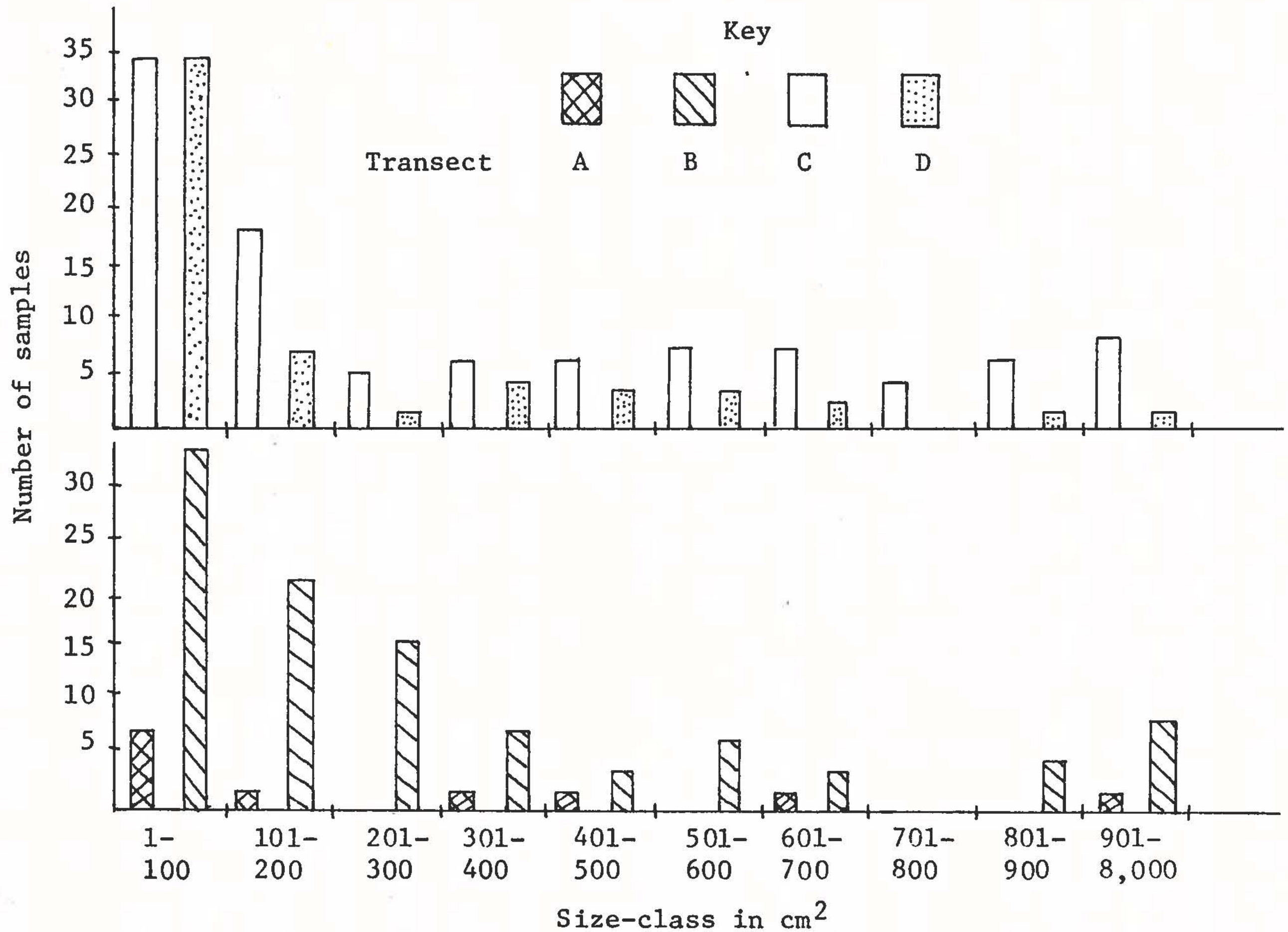

Figure 3. Bar diagram showing _Terpios_ size-class frequency at Transects A-D at the Pugua Study Site.

frequency was relatively constant. Transect C had the largest mean patch size (491 cm^2), followed by B(346 cm^2), A(277 cm^2), and D(178 cm^2). The largest patch was found at Transect C(7,252 cm^2), and the smallest was found at Transect D(1 cm^2). Size class frequency and mean patch size were not related to the number of Terpios patches found in different transects.

Experiments on Growth in Cocos Lagoon

Experiment I. Growth of Terpios on the four substrates tested was significantly different (Table 5). The mean growth rate of Terpios growing on cleaned Montipora (3 mm/day) was more than twice that on living Montipora (1 mm/day), followed by reef rock (0.89 mm/day) and plexiglass plate (0.55 mm/day).

Although the mean growth rate of Terpios on the plates was slow, once Terpios established itself on a plate, growth was rapid (2.19 mm/day). This was shown by Terpios growth on plates when not including zero growth measurements (Table 5). Zero-growth indicates that although the sample substrate was found attached to the Terpios transplant, no Terpios had grown onto the sample. Figure 4 shows that the largest growth on a plate (40 mm) was almost twice that on a reef rock (24 mm).

Experiment II. Table 6 gives the mean growth rate of Terpios in the fork experiment. In ten out of 21 forks, Terpios grew on both prongs of the fork, whereas on the other 11, it grew only on the cleaned prong. The amount of growth on the cleaned prong was over three times that on the living prong. Total growth of Terpios on a single cleaned prong reached 60 mm, whereas the largest total growth on

Table 5. Mean growth rate of *Terpios* on four substrates in Experiment I in Cocos Lagoon. Column A gives mean growth rates when including zero growth measurements, B gives mean rates when not including zero measurements. An anova table (using data from column A) is given below. *** indicates significance.

Substrate	Growth in mm/day A	B
Plexiglass plate	.55	2.19
Reef rock	.89	1.09
Live coral	1.42	1.53
Clean coral	2.88	2.88

Source	Degree of Freedom	Mean Square	F
Substrate	3	1087	18.81***
Error	67	57.8	

Table 6. Mean growth rate of *Terpios* on two prongs of the *Acropora formosa* forks in Experiment II in Cocos Lagoon. An anova table is listed below the data. *** indicates significance.

Substrate	Growth in mm/day A
Living prong	.56
Cleaned prong	1.88

Source	Degree of Freedom	Mean Square	F
Substrate	1	3621.40	27.14***
Error	40	133.39	

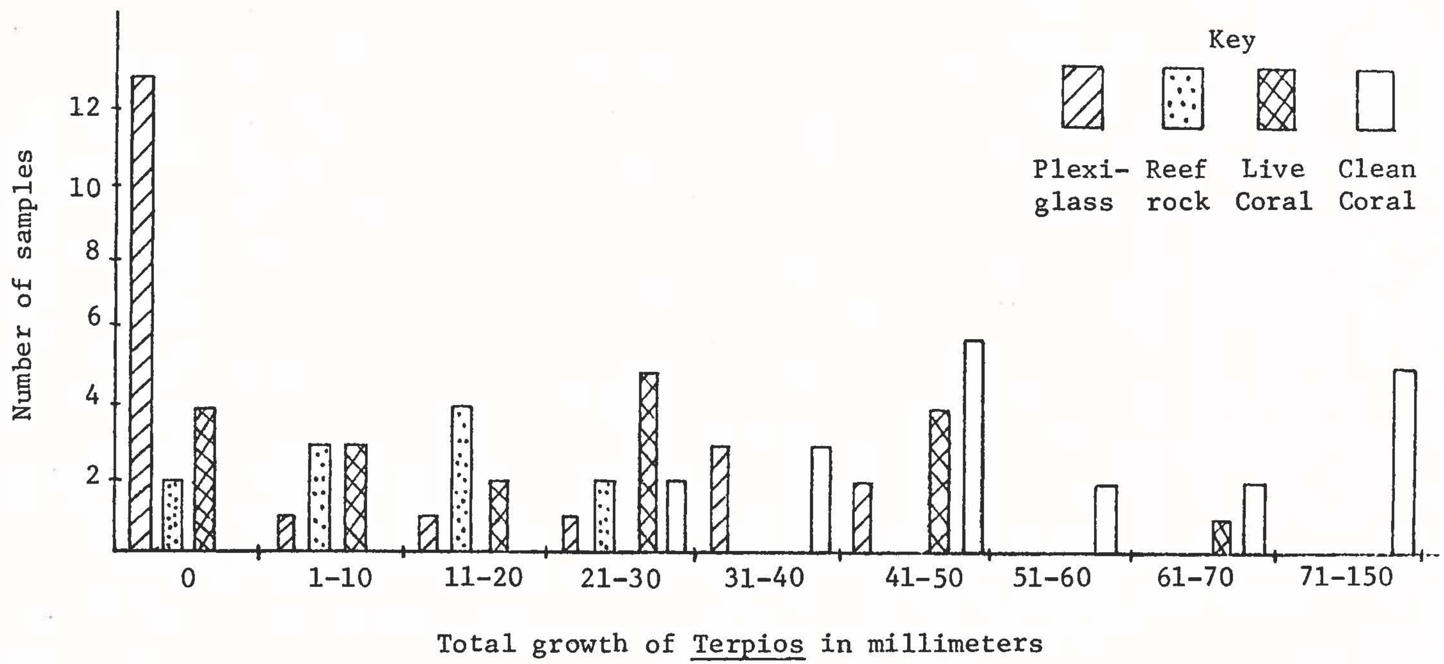

Figure 4. Bar diagram showing <u>Terpios</u> growth on four different substrates in Experiment I at Cocos Lagoon.

the living prong was only 40 mm (Figure 5). The modal growth (Sokal and Rohlf, 1969) of Terpios on cleaned prongs was 30 mm, whereas the modal growth on the living prong was zero.

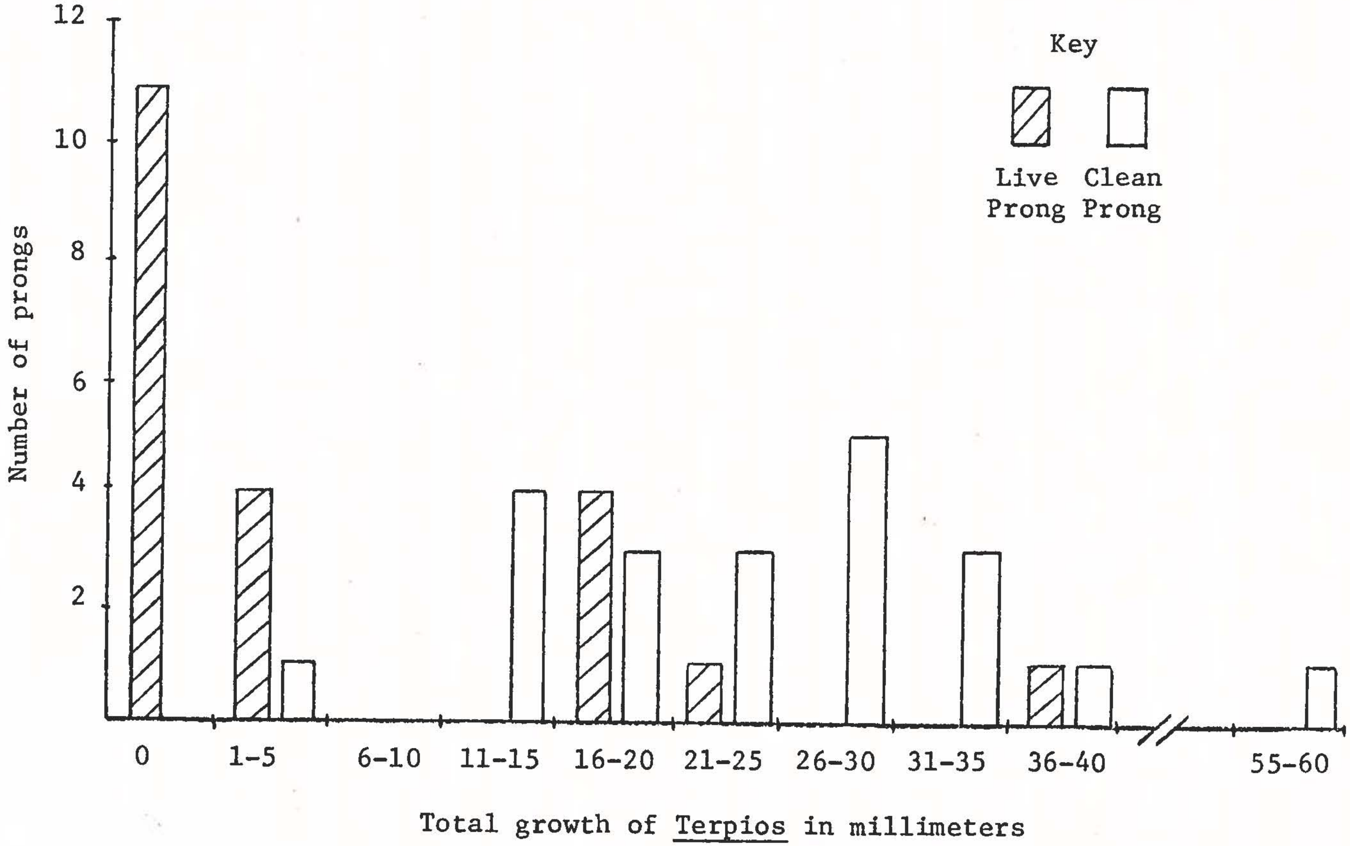

Figure 5. Bar diagram showing the difference in growth of _Terpios_ on the living and air-blasted prongs of _Acropora formosa_ in Experiment II at Cocos Lagoon.

DISCUSSION

The Influence of Substrate on Distribution and Growth

Terpios grows on a great variety of substrates. It grows on all scleractinian corals on Guam that live in areas exposed to light. It also grows on *Tubipora musica* (Randall, pers. comm.) and *Heliopora coerulea* (two species in subclass Octocorallia), *Millepora* species (Class Hydrozoa), up the base of *Halimeda gigas*, and on branching crustose algae (Randall, pers. comm.). Although it usually grows on stable substrates, it also grows on unattached rocks or corals at least as small as 7 x 5 x 5 cm. It does not grow on sand or articulated algae.

No evidence was found to support Bryan's (1973) suggestion that *Terpios* grows faster on living corals than on other substrates because of nutrient utilization from coral tissue. The growth of *Terpios* was significantly faster on corals that have had their living tissue removed by air-blasting than on live corals. In addition, when growth took place on a plexiglass plate, *Terpios* again grew faster than on living coral. Furthermore, when given a choice between a living coral prong and an air-blasted prong, *Terpios* did not grow on the living prong in 11 out of 21 cases.

It is likely that corals are merely one of many hard substrates on which *Terpios* grows, and that *Terpios* is frequently found on live corals because they do not harbor organisms which inhibit *Terpios* growth. These organisms may be microscopic bacteria or blue-green algae. Growth may also be inhibited by the presence of newly settled encrusting red calcareous algae, which has been shown to retard the growth of Terpios. Coral surfaces are kept clean by polyp and cilia movements, so organisms which inhibit the growth of Terpios would be unable to settle and grow. However, a small patch of Terpios is often found completely surrounded by living coral, indicating that Terpios is able to settle on live corals.

Corals cleaned by air-blasting are similar to corals eaten by Acanthaster planci. Although Bryan (1973) noted that the greatest abundances of Terpios did not always coincide with the areas with the largest A. planci outbreaks, it is possible that Terpios growth is at least encouraged by the presence of corals cleaned by A. planci. This possibility is supported by the fast growth rate of Terpios on cleaned corals.

Terpios may be one of the most important sources of disturbance affecting coral reefs. Connell (1978) and Colgan (1981) reviewed many of the known physical and biological disturbances on reefs. Acanthaster planci, which reached epidemic proportions in 1968-1969 (Randall, 1971), was felt to be one of the major coral reef disturbances, and its impact was studied throughout the Pacific. However, A. planci may have less long term impact on coral reefs than Terpios. Acanthaster planci kills only corals, causing no disturbance to other substrates, whereas Terpios kills corals as well as other living organisms, and encrusts reef rock. Furthermore, A. planci kills a coral quickly, leaving a clean skeleton which is immediately ready for recolonization. Terpios, however, occupies substrates for many months. In addition, A. planci is limited in distribution to calm water habitats because of its inability to hold onto substrates in strong currents or in wave assaulted areas. *Terpios* thrives at all depths to at least 35 m, as well as on shallow reef platforms, and is unaffected by wave assault or currents.

The 1968-1969 *A. planci* epidemic decreased percent coral cover to 0.5 percent on the seaward slope, but recovery was essentially complete by 1981 (Colgan, 1981). Colgan suggested that recovery was attributable to the presence of living coral in areas barely touched by *A. planci* (reef-flat platform and reef margin), as well as living remnants of corals fed upon by the starfish. However, recolonization was only possible because of the short duration of the epidemic. If *A. planci* had continued to inhabit the area in epidemic proportions for many more years, recovery could not have been complete by 1981.

If disturbance levels remain high at a location for long periods of time, coral recolonization may not be possible, at least until the disturbance decreases (Connell, 1978). At Fafai Beach, *Terpios* encrusts an estimated 30 percent of the substrate and has been present in large quantities at least since 1970 (Randall, pers. comm.). Corals are present in small patches with only *Porites* (*Synaraea*) *iwayamaensis* still abundant in large colonies. The level of disturbance has remained high for at least 13 years and shows no indication of decreasing. Recovery cannot occur until *Terpios* levels decrease, allowing juvenile corals to grow without being killed. Where *Terpios* levels decrease following an epidemic, coral recovery can begin. The reef surrounding Anae Island in Guam was almost completely covered by *Terpios* in 1973 (Bryan, 1973). By 1981, only five *Terpios* patches were found during a 20-minute search, and much of the substrate was covered with living corals.

The rapid growth and longevity illustrated by *Terpios* indicates that it has a great potential for covering a reef area. When extrapolated over a year, a *Terpios* growth of 1 mm per day could reach 365 mm per patch. Although this potential is not usually reached, its reported growth surrounding Anae Island and outside Cocos Lagoon in 1973 (Bryan, 1973) indicates that it could occur.

The impact of *Terpios* on coral reefs may be even greater than estimated because of its relatively infrequent occurrence on *Montipora* and *Porites* species. By infrequently encrusting these corals, *Terpios* may be increasing their proportion on these reefs, while decreasing the prevalence of other species. At Fafai Beach where *Terpios* encrusts a large percentage of the reef, *Porites* (*S.*) *iwayamaensis* is the most abundant species, and the only coral which forms large colonies. Where *Terpios* is present in lower levels, such as at the Pugua Study Site, *Terpios* has a less intense impact on the coral community, though again, *Montipora* and *Porites* are the most abundant at the site.

When surveying a reef, *Terpios* patches are generally found in close proximity. At the Pugua Study Site, the majority of patches were found in one place. Surrounding this small area were large areas where no patches were found, although no other differences were noticeable in the surrounding community. It is possible that this phenomenon is caused by short-lived larvae or eggs, an attraction for settling near adults, or some method of asexual reproduction.

Terpios sexual reproduction is not documented, and details of sexual reproduction in sponges varies from group to group. Many demosponges are hermaphroditic and release larvae which swim from 3-48 hours before settling. Others release larvae which sink to the substrate and creep until settlement, taking from 20-60 hours. Larval release is not universal among demosponges, as some species release tiny fully-formed sponges, and others release eggs which are fertilized externally (Bergquist, 1978).

Once _Terpios_ settles in an area (probably as a result of sexual reproduction) and establishes a colony, it is likely that asexual reproduction plays an important role in dispersing the sponge in the area. Some mechanism for asexual reproduction is probably found in all sponges. Some marine sponges produce gemmules which allow for extreme environmental conditions, while others produce buds. Most sponges are able to regenerate a new sponge from a small fragment, providing a useful mechanism for dispersal as well as for reproduction (Bergquist, 1978). Bergquist et al. (1970) suggest that intertidal demosponges are commonly able to produce larvae asexually.

Terpios is able to generate a new sponge from a small fragment. Transplanting _Terpios_ onto different substrates requires little manipulation, as found in the Cocos Lagoon experiments. Although the fragments were all encrusting a substrate, these _Terpios_ encrusted pieces had been broken from larger colonies but were still able to grow. _Terpios_ is also able to form bridges of tissue across open water, from the tip of a completely encrusted coral branch across to the tip of a new branch. Growth from the bridge then extends down the new coral branch. This illustrates that a substrate is not necessary for _Terpios_ growth, as the bridges extended from 2 cm in the field to 6 cm in the laboratory. These bridges were observed at Fafai Beach on a *Stylophora mordax*, in Cocos Lagoon on a *Pocillopora damicornis*, and in the laboratory on another *S. mordax*. These bridges were formed in less than two weeks. If a tissue bridge is broken off, it is possible that it could grow onto a new subtrate as long as it lodged into a small illuminated crevice in coral or rock.

A problem encountered during the distribution survey at the Pugua Study Site was the identification of *Terpios* encrusted corals. When *Terpios* encrusted a coral that still had living tissue, the coral identity was recorded. However, where no living coral patch survived, the substrate had to be categorized as reef rock, since there was no way of knowing whether the coral had been alive or already dead prior to being encrusted by *Terpios*. It is probable that this caused a bias in the data, resulting in recording a higher number of *Terpios* encrustations on reef rock than on live corals (Table 6).

The Influence of Light on Distribution and Growth

If translocation of nutrients from cyanobacteria to some sponges occurs as shown by Wilkinson (1980), autotrophy may be more important to tropical sponges than to temperate sponges because of the low availability of nitrogen and carbon compounds in tropical waters (Wilkinson and Fay, 1979). It is therefore not surprising that most sponges with cyanobacteria are found in the tropics. Vogel (1977) has shown that erect sponges use less energy filtering water than do thin encrusting sponges. Their erect structure combined with the ambient water current sets up a passive current which aids them in filtering water. It is therefore possible that flat, encrusting sponges (such as *Terpios*) which must expend more energy to filter water, would be especially aided by symbiotic association with cyanobacteria (Wilkinson, 1982).

Although cyanobacteria may be important in limiting the distribution of *Terpios* to the photic zone, other than limiting it to illuminated areas, it does not play a significant role in affecting *Terpios* growth or distribution within that zone. *Terpios* is not affected by differences in depth between 10 and 26 m, and is present in significant quantities to at least 35 m at Fafai Beach. Although *Terpios* is rare above 10 m at Fafai Beach, it is unlikely that light is the limiting factor, since it is present in large quantities in other areas as shallow as 3 m.

Small amounts of shade do not significantly affect *Terpios* growth. However, *Terpios* does not grow in completely shaded areas. Even when *Terpios* grows to the margin of an explanate coral sheet, it never grows over the edge onto the coral's underside. When Wilkinson (1982) surveyed nine predominant species of sponges containing cyanobacteria, he found that there was no decrease in proportions when surveying from 1-20 m in depth. The greatest proportion of these sponges was found at 20 m (94 percent), even though light at this depth was 16 percent of that available at the surface. Therefore, the cyanobacteria in *Terpios* (and possibly other sponges) shows an ability to photosynthesize efficiently even in reduced light conditions. If the cyanobacteria aid in filtering harmful sun rays from sponges (Sara, 1964), they may also make it possible for these sponges to survive in areas too shallow for survival without their presence.

Senescence and Death

Terpios undergoes a distinct succession of conditions during senescence and death. Young, healthy *Terpios* specimens have thick, uniform tissue with distinct growing edges. As senescence commences, the tissue thins, exposing small patches of underlying substrate. The *Terpios* edges bordering on these patches of substrate are thin, indistinct, and often partially detached from the substrate below. Disintegration of the tissue continues exposing larger areas of the underlying substrate until finally a large area or a whole patch of *Terpios* has disappeared. When a patch is small, the process usually takes 2-3 months from the onset of thinning to its death.

On large *Terpios* patches, only a part of it may be dying, while another part remains thick and healthy. However, once thinning of tissue commences in an area, it continues. A previously thinning area never regenerates thick, healthy tissue, even when another side of the *Terpios* patch is healthy. Death to a large patch may take considerably longer than nine months from the onset of thinning.

The underlying substrate exposed by disintegrating *Terpios* is indistinguishable from the surrounding reef rock. Since senescence often takes many months (depending on patch size), the exposed substrate is quickly colonized with a thin veneer of blue-green algae, tiny patches of encrusting algae, and other encrusting organisms.

CONCLUSIONS

Terpios is an encrusting sponge which overgrows most hard stable substrates in the photic marine environment. Its killing of corals and other marine organisms makes it an important organism to study. Although the presence of cyanobacteria in its tissue may not affect its growth between depths of 5 and 26 m, it clearly restricts it to areas where it receives direct or at least strong indirect sunlight. Methods of dispersal include its ability to generate new colonies from fragments and the formation of tissue bridges.

Since *Terpios* grows fastest when living coral tissue is removed, it is not likely that *Terpios* ingests coral tissue. Instead, *Terpios* is probably an efficient competitor of corals for space. Encrusting organisms are often killed by other encrusting organisms which are growing over the same space. Many have evolved characteristics which aid in the acquisition of available space such as fast growth rate or the ability to live in areas without sunlight. *Terpios* competes by killing organisms and using their surface for growth.

Growth on all substrates is intermittent as *Terpios* typically exhibits periods of growth followed by long periods without growth. The growth of *Terpios* does not vary from September to June, but the substrate on which it is found substantially affects its growth rate and distribution. *Terpios* grows fastest on clean substrates, followed by living corals, reef rock, and red calcareous algae. It grows less frequently on _Montipora_ and _Porites_ than would be expcted on the basis of the relative availability of these corals.

Although _Terpios_ encrusts a wide variety of substrates, some organisms are able to inhibit _Terpios_ growth. _Montipora_, _Porites_, and red calcareous algae are sometimes able to overgrow _Terpios_, and reef rock may harbor organisms which inhibit _Terpios_ growth.

Terpios may be one of the most important sources of disturbance on a coral reef, and may disturb more substrate over the long term than _Acanthaster planci_. By not encrusting _Montipora_ and _Porites_ species as frequently as would be expected by chance, _Terpios_ may be favoring their prevalence on reefs, while decreasing the abundance of species which they more frequently encrust.

LITERATURE CITED

Auberson, B. 1982. Coral transplantation: an approach to reestablishment of damaged reefs. Kalikasan, Phil. J. Biol. 11(1):158-172.

Bakus, G. J. 1981. Chemical defense mechanisms on the Great Barrier Reef, Australia. Science 211:497-499.

Bakus, G. J., and G. Green. 1974. Toxicity in sponges and holothurians: a geographic pattern. Science 185:951-953.

Bergquist, P. R. 1978. Sponges. Univ. of Calif., Berkeley. 261 p.

Bergquist, P. R., M. E. Sinclaire, and J. J. Hogg. 1970. Adaptation to intertidal existence: reproductive cycles and larval behavior in Demospongiae. Symp. Zool. Soc. London 25:247-271.

Birkeland, C., L. Cheng, and R. Lewin. 1981. Motility of didemnid ascidian colonies. Bull. Mar. Sci. 3(1):170-173.

Bryan, P. G. 1973. Growth rate, toxicity and distribution of the encrusting sponge Terpios sp. (Hadromerida:Suberitidae) in Guam, Mariana Islands. Micronesica 2:237-242.

Buss, L. W., and J. B. C. Jackson. 1979. Competitive networks: non-transitive competitive relations in cryptic coral reef environments. Am. Nat. 113:223-234.

Colgan, M. W. 1981. Long term recovery processes of a coral community after a catastrophic disturbance. M.S. Thesis, Univ. of Guam. 69 p.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302-1310.

Gordon, D. P. 1972. Biological relations of an intertidal bryozoan population. J. Nat. Hist. 6:503-514.

Hildeman, W. D., R. L. Raison, C. J. Hull, L. K. Akaka, J. Okamoto, and G. P. Cheung. 1977. Tissue transplantation immunity in corals. Proc. 3rd Int'l Coral Reef Symp. 1:537-543.

Jackson, J. B. C. 1979. Overgrowth competition between encrusting cheilostome ectoprocts in a Jamaican cryptic reef environment. J. Anim. Ecol. 48:805-823.

Jackson, J. B. C., and L. Buss. 1975. Allelopathy and spatial competition among coral reef invertebrates. Proc. Nat. Acad. Sci. 72(12):5160-5163.

Jorgensen, C. B. 1966. Biology of suspension feeding. Pergamon Press, London. 375 p.

Karlson, R. 1978. Predation and space utilization patterns in a marine epifaunal community. J. Exp. Mar. Biol. Ecol. 31:225-239.

Lang, J. C. 1973. Interspecific aggression by scleractinian corals. II. Why the race is not only to the swift. Bull. Mar. Sci. 23:260-279.

Osman, R. W. 1977. The establishment and development of a marine epifaunal community. Ecol. Monogr. 47:37-63.

Randall, R. H. 1971. Tanguisson-Tumon, Guam, reef corals before, during and after the crown-of-thorns starfish (*Acanthaster planci*) predation. M.S. Thesis, Univ. of Guam. 119 p.

Reiswig, H. 1971. Particle feeding in natural populations of three marine demosponges. Biol. Bull. 141:586-591.

Rutzler, K. 1970. Spatial competition among Porifera: solution by epizoism. Oecologia 5:85-95.

Sara, M. 1964. Association di demospongie con zooxanthelle e cianelle. Bull. Zool. 11:214-221.

_______________. 1970. Competition and cooperation in sponge populations. p. 273-284. *In* W. G. Fry (ed.), The biology of the Porifera. Symp. Zool. Soc. Lond. Academic Press, London.

Sokal, R. S., and F. J. Rohlf. 1969. Biometry. W. H. Freeman and Co., San Francisco. 776 p.

Stebbing, A. R. D. 1973a. Competition for space between the epiphytes of *Fucus serratus* L. J. Mar. Biol. Assoc. United Kingdom 53:247-261.

_______________. 1973b. Observations on colony overgrowth and spatial competition. p. 173-183. *In* G. P. Larwood (ed.), Living and fossil Bryozoa. Academic Press, London.

Stephens, G. C., and R. A. Schinske. 1961. Uptake of amino acids by marine invertebrates. Limnol. Oceanog. 6:175-181.

Vogel, S. 1977. Current induced flow through living sponges in nature. Proc. Nat. Acad. Sci. 74:2069-2071.

Wilkinson, C. R. 1978a. Description of two Demospongiae, one being toxic, from the Great Barrier Reef. Tethys 8(3):267-270.

_______________. 1978b. Microbial associations in sponges. I. ecology, physiology, and microbial populations of coral reef sponges. Mar. Biol. 49:161-167.

_______________. 1980. Nutrient translocation from symbiotic cyanobacteria to coral reef sponges. p. 425-447. In C. Levi and N. Boury-Esnault (eds.), Biologie des spongaires. Coll. Int. CNRS. No. 291.

_______________. 1982. Significance of sponges with cyanobacterial symbionts on Davies Reef, Great Barrier Reef. Proc. 4th Int'l. Coral Reef Symp. 2:705-712.

Wilkinson, C. R., and P. Fay. 1979. Nitrogen fixation in coral reef sponges with symbiotic cyanobacteria. Nature 279:527-529.