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LA THÈSE A ÉTÉ
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Ecological Studies of the Alga, Acanthophora spicifera (Vahl)
Børg. (Rhodophyta, Ceramiales): I. The Fragmentation
Strategy; II. Maintenance and Persistence in a community,
dominated by Laurencia papillosa (Forsk.) Grev.

By

© John A. Kilar

A thesis submitted to the Faculty
of Graduate Studies, Dalhousie University
in partial fulfillment of the requirements
for the Degree of Doctor of Philosophy

Biology Department
Dalhousie University
Halifax, Nova Scotia
Canada

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Abstract. Manipulative experiments were done and detailed descriptive data were gathered on a Panamanian fringing reef to elucidate the fragmentation strategy of Acanthophora spicifera.

From 1 February 1979 to 31 March 1980, more than 339 kg (d wt) of A. spicifera were broken off and removed from 1.32 ha of reef flat. A. spicifera was the major algal contributor to the drift biomass when the drift biomass of a species was standardized to a square meter of reef and expressed as wet weight.

Measurements of frond survivorship showed that A. spicifera constantly gave rise to fragments in the wave zone (Laurencia Zone) which were recruited into the more sheltered areas (Acanthophora and Thalassia Zones). Colonization rates were recorded as high as 15 fragments m⁻² d⁻¹ during the wet and dry seasons. Wave-action determined the number and size of fragments produced in the fore reef; however, the recruitment of fragments was also affected by the amounts and types of substrata, and the fore-reef biomass and growth form of A. spicifera.

More fragments of A. spicifera were recruited into the Acanthophora Zone than into the Thalassia Zone. Higher current velocities decreased the ability of free-floating fronds to snag, and increased their distance traveled before snagging in the back reef. In the Acanthophora Zone 25 % of the snagged fragments had greater than 3 days to attach to substrata. A. spicifera required less than 2 days to attach to L. papillosa or to another frond of A. spicifera and less than 4-5 days to attach to Porites-rubble or Thalassia testudinum. From the estimated size of the Acanthophora Zone, the distance used by a fragment to snag, and the time needed by a fragment to attach, it was found that fragments of A. spicifera that enter the Acanthophora Zone had between a 49 % and 93 % chance of successfully recruiting.

Aerial exposures of the reef flat were most frequent in May-June and September-October. In the Laurencia Zone, 38 consecutive days of daytime exposures were recorded. No exposure period lasted longer than 18 hours. Single fronds of L. papillosa tolerated longer periods of aerial exposure (30 min) than those of A. spicifera (15 min). Aggregates of L. papillosa fronds survived aerial exposures lasting five hours. By growing among fronds of L. papillosa, A. spicifera survived severe aerial exposures. Also, the spatial partitioning of photosynthetic activity in A. spicifera allowed the holdfast to function as a persistent stage during periods of aerial exposures when uprights were not maintained. At night, 12-hour aerial exposures injured A. spicifera, reducing the photosynthetic capacity of fronds as much as 82 % when return to light.

As wave exposure decreased, the abundance and spatial distribution of A. spicifera and L. papillosa increased. In areas of intermediate wave exposure, A. spicifera overgrew and reduced the growth of nearby L. papillosa, but the duration of Acanthophora overgrowth was short because of increased wave induced losses of fronds. L. papillosa then overgrew A. spicifera. A resistant holdfast prolonged the survivorship of A. spicifera when it was overgrown by L. papillosa until the overlying L. papillosa was removed by aerial exposures. In the sheltered areas, dense concentrations of A. spicifera developed with sufficient longevity to exclude L. papillosa from areas where A. spicifera was most abundant. A fine balance of adaptations between community disturbances and population interactions maintained the fragmentation strategy.

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List of Abbreviations

s		second
min		minute
h		hour
d		day
mo		month
mm		millimeter
cm		centimeter
m		meter
kg		kilogram
mg		milligram
g		gram
‰		parts per hundred or per cent
‰/oo		parts per thousand
°C		Centigrade
°		degree
d wt		dry weight
w wt		wet weight
Q		Savage(Mantel-Cox)Test
t		Student's t-test
F		ANOVA F-Ratio
ANOVA		Analysis of Variance
χ^2		Chi-Square Test
SE		Standard Error
SD		Standard Deviation
95 % CI		95% Confidence Interval
df		degree of freedom
n		number of samples
N		newton
p		probability
r^2		regression coefficient
ss		sum of squares
ms		mean squares
$\bar{x}$		mean
H ₀		Null Hypothesis
B		regression constants
LE/50		Lethal Wave Exposure 50%
j		joules
μE		micro-einstein
P _{max}		Maximum Photosynthesis
I _k		Saturation Constant.

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1.0 Introduction

Acanthophora spicifera (Vahl) Berg. is a rhodophycean alga widely distributed in subtropical and tropical seas (Doty, 1961; Russell, 1981; Taylor, 1967). Low seawater temperature limits the species to these warmer waters. The optimum temperature for growth is between 23° and 28°C (Russell, 1981; Trono, 1968). At high subtropical latitudes the alga is often present throughout the year, but may disappear during the colder winter months (Rao & Steeramalu, 1974; Taylor & Bernatowicz, 1969). Despite the wide distribution of A. spicifera, little is known about its ecology. Information has been generally limited to species lists (Dahl, 1973; Earle, 1972a; 1972b; Mathieson et al., 1975; Taylor, 1967; Trono, 1968) and relative abundances (Conner & Adey, 1977; Doty, 1969; Gilbert, 1976; Santelices, 1977), except for the study by Russell (1981) of the distribution of A. spicifera in Hawaii.

A. spicifera occurs in intertidal (Rao & Steeramalu, 1974; Tabb & Manning, 1961) and subtidal habitats (Dahl, 1974; Earle, 1972a; Mshigeni, 1978). As it is unable to withstand prolonged exposures in the air (Rao & Steeramalu, 1974), A. spicifera is restricted to the low intertidal or to the subtidal regions of the shore. Extensive stands of A. spicifera are found on shallow reef-flats (Conner & Adey, 1977; Doty, 1961; 1967; 1969; Meyer et al., 1974; 1975; Russell, 1981; Santelices, 1977), and the species occurs frequently at depths of 17 m in Puerto Rico (Dahl, 1973) and of 22 m in the Virgin Islands (Earle, 1972b; Mathieson et al., 1975). Hay (1981a) has shown that

herbivorous fishes can exclude the species from some subtidal habitats in Panama. Many herbivorous fishes, sea urchins, and crabs (Earle, 1972b; Hay, 1981b; Kilar & Lou, 1984; Randall, 1964; 1967; Vadas et al., 1982) are reported to readily consume or include A. spicifera as part of their diet. Russell (1981) considered water motion to be the limiting factor that determined the distribution of A. spicifera in Hawaii. The species occurs, however, both in sheltered bays (Almodovar & Pagan, 1971; Russell, 1974; Taylor & Bernatowicz, 1969) and on open coasts (Croley & Dawes, 1970; Kim, 1964; Russell, 1974; Taylor, 1967) in protected and exposed areas of wave action (Russell, 1981; Wormersley & Bailey, 1969).

A. spicifera is found on a wide range of substrata. It grows on hard substrata (Almodovar & Pagan, 1971; Dawson, 1954; Mshigeni, 1978; Taylor & Bernatowicz, 1969; Varma, 1959), as an epiphyte on other algae (Mathieson et al., 1975; Russell, 1981), or as a stable, free-living population (Benz et al., 1979; Cowper, 1978; Doty, 1961; Eiseman & Benz, 1975; Russell, 1974; 1981). Benz et al. (1979) reported A. spicifera as one of the most common members of a free-living, macroalgal community near Ft. Pierce, Florida. Russell (1981) observed that A. spicifera was frequently associated with Laurencia spp. and Hypnea spp. and, in certain situations, competed with, displaced or replaced them.

Doty (1961) reported on the introduction to Hawaii of A. spicifera. In 1950, a fuel-oil barge, heavily fouled with marine organisms, was towed from Guam to Pearl Harbor, Hawaii. It was this barge that Doty (1961) suggests had A. spicifera on its hull. Subsequent studies by

Mshigeni (1978) and Russell (1981) have yielded conflicting results as how A. spicifera has been able to rapidly spread throughout Hawaii.

Mshigeni (1978), when investigating the colonization onto natural and artificial surfaces by benthic algae, concluded that A. spicifera was propagated by vegetative fragmentation. In contrast, Russell (1981) suggested that tetraspores were the principal agents of dispersal. He noted that mature tetrasporic plants were found throughout the year at several different localities. Similarly, Bergesen (1915-20), Feldmann (1937), and Joly (1957) had also noted the predominance of the sporophyte generation.

The first objective of my study was to consider the roles of vegetative fragments and spores of A. spicifera as means of propagation on the reef-flat at Galeta Point, Panama. At that site, Birkeland et al. (1973) reported that A. spicifera grew within the wave zone and in the back-reef. Closer observations revealed that: (i) water flowed in a unidirectional manner over the reef-flat; (ii) A. spicifera commonly occurred as drift; and (iii) A. spicifera grew primarily as an epiphyte in the back-reef. These observations led to my working hypothesis that, in the wave zone, A. spicifera gives rise to fragments that colonize the back-reef. By fragment, I mean an unspecialized, detached piece of thallus. Numerous approaches were undertaken to verify this hypothesis: (i) locating the principal fragment sources and areas of colonization; (ii) understanding the mechanics of thallus breakage; and (iii) examining the processes of fragment recruitment. To examine Russell's (1981) suggestion that tetraspores of A. spicifera were the principal

agents of dispersal, a phenological study was also done.

The second objective of my study was to demonstrate the persistence of the fragmentation process. To do so required an understanding of the community structure built around the effects of major community disturbances and of the interactions among the component populations.

The main factors involved were exposures of the reef-flat to air and wave action, and competition for space between A. spicifera and Laurencia papillosa (Forsk.) Grev. Predation, another form of community disturbance (Connell, 1970; Dayton, 1971; Paine, 1966; 1974), was examined and found not important (Appendix I).

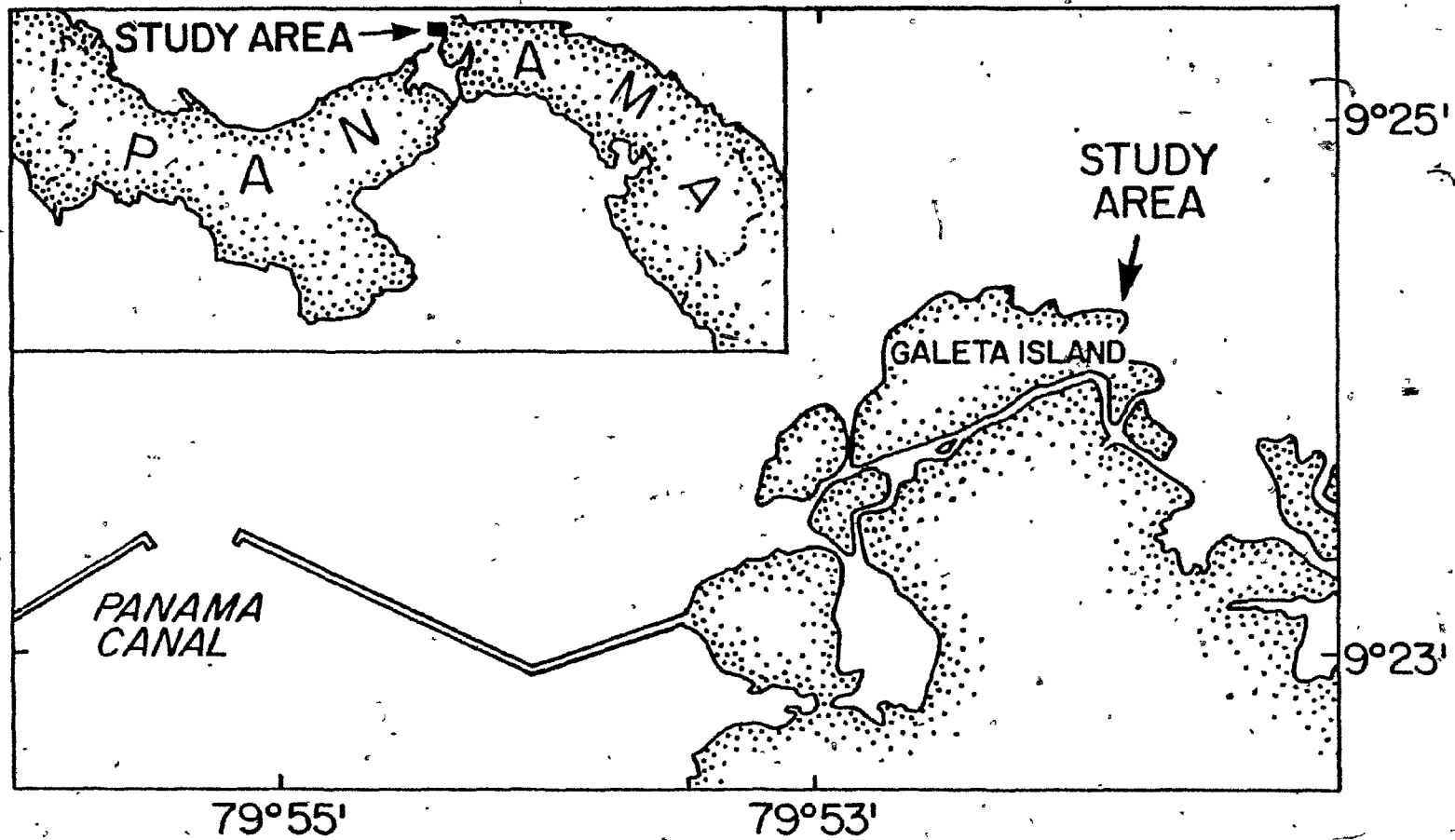
1.1 Study Area

Research was conducted on the reef-flat adjacent to the Smithsonian Tropical Research Institute (S.T.R.I.) Laboratory at Galeta Point, Panama ($9^{\circ} 24.3'N$, $79^{\circ} 51.8'W$). The reef is situated about 6 km northeast of Colon, Panama, the Caribbean entry into the Panama Canal (Fig. 1). Galeta Reef has been a biological preserve since 1965. Baseline monitoring surveys have been conducted there since 1969.

Galeta Reef is typical of fringing reefs of the Caribbean coast of Panama (Glynn, 1972; MacIntyre & Glynn, 1976). It was formed about 7000 years B.P. from the coral Acropora palmata Lamarck. Subsequently, the growth of reef-building corals was restricted vertically by sea level and horizontally by unconsolidated sediments. MacIntyre & Glynn (1976) concluded that Galeta Reef is an example of a fully-developed fringing reef. They noted that the corals no longer contributed actively to the reef framework, that mangroves encroached onto the reef-flat, and that there was a thick talus cover on the fore-reef. The seaward side of the reef extends down to about 13 m depth, while on the landward side the reef is bordered by a lagoon or a mangrove swamp. The reef-flat is usually covered by 0.1 to 0.4 m of water and experiences tidal fluctuations of 0.7 m (MacIntyre & Glynn, 1976). Seawater temperature on the reef-flat is generally between 26° and $29^{\circ}C$ and the salinity is usually between 32 and 35 ‰ (Hendler, 1977).

During the dry-season (November through March), northern and northeasterly trade winds blow at a mean velocity of 24 to 27 $km\ h^{-1}$.

Figure 1. Study site at Galeta Point, Panama.



(Hendler, 1976), about three times the mean velocity occurring in the wet season. Waves that are generated by these strong winds cause considerable turbidity and remove weakly attached organisms throughout the reef-flat. The increased turbidity, occurring largely because of the resuspension of sediments, is believed to be a significant limiting condition for reef building at Galeta (Glynn, 1982; MacIntyre & Glynn, 1976).

Exposures of reef surfaces in the air are common in the Caribbean (Glynn, 1968) and occur with low spring tides or when calm seas coincide with a low pressure system (Hendler, 1977). Exposure periods of several weeks kill most non-swimming herbivores and reduce algal cover (Hendler, 1976; 1977; Glynn, 1968; Meyer *et al.*, 1974; 1975). At Galeta, such conditions are prevalent during the wet-season, April through October.

Unlike most tropical reefs, the reef-flat at Galeta has a luxuriant growth of algae and seagrasses. Birkland *et al.* (1973) identified five biotic communities or zones across the reef-platform. From seaward to landward these zones are: the Coralline Zone; the Laurencia Zone; the Zoanthus Zone; the Thalassia Zone; and the Acanthophora Zone (Figs. 2 and 3). The Coralline Zone represents a predominantly subtidal area where the reef-flat merges with the reef slope. This region is heavily grazed by fishes, mostly Scaridae and Acanthuridae, and by the sea urchins, Diadema antillarum Philippi, and Lytechinus variegatus Lamarck. In contrast, on the reef-flat, little to moderate predation occurs (Hay, 1981a; 1983; Appendix I). The principal inhabitants of the Coralline Zone are the corals, Millepora complanata Lamarck,

Figure 2. The reef flat at Galeta Point, Panama (from
Birkeland et al., 1973).

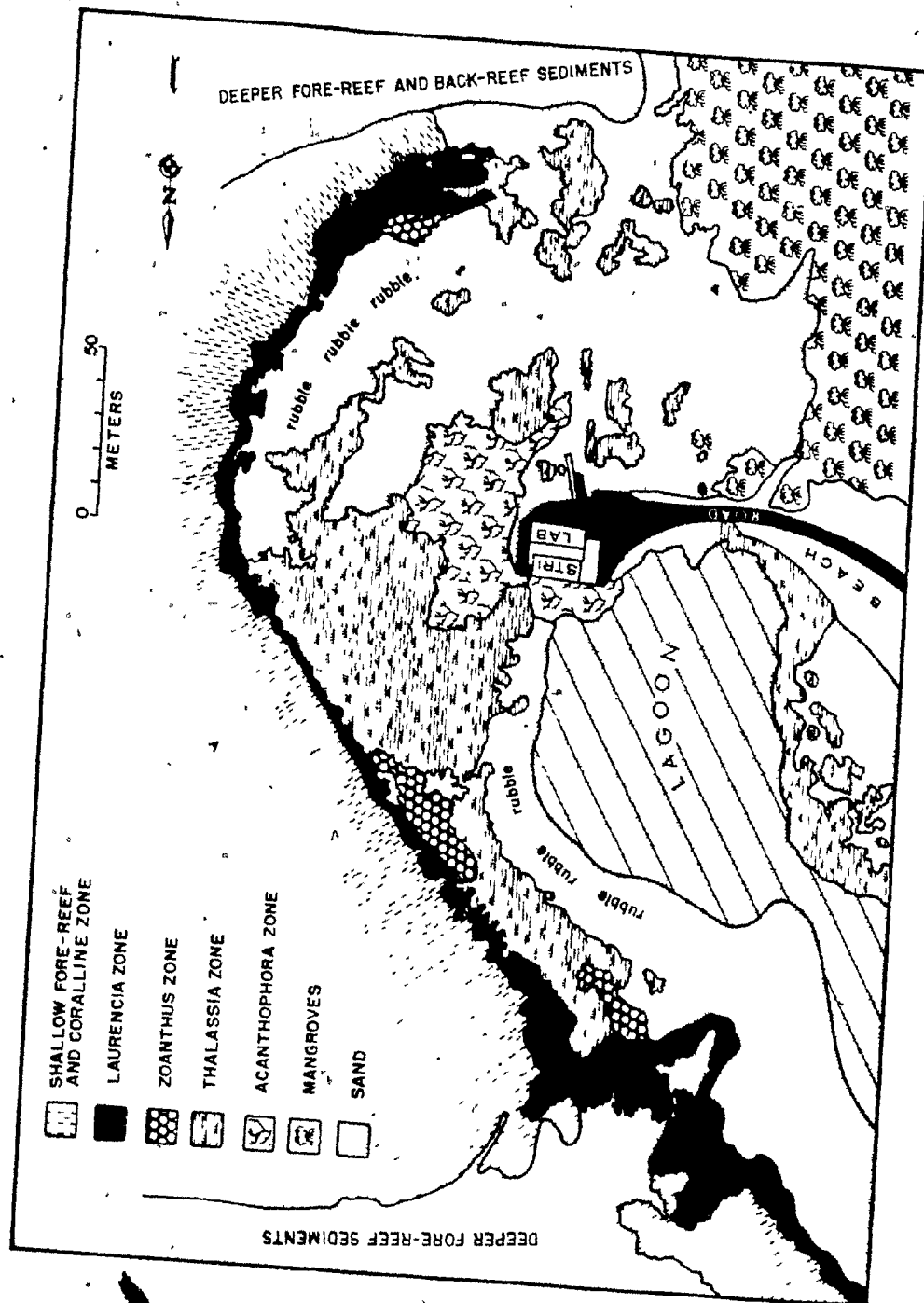
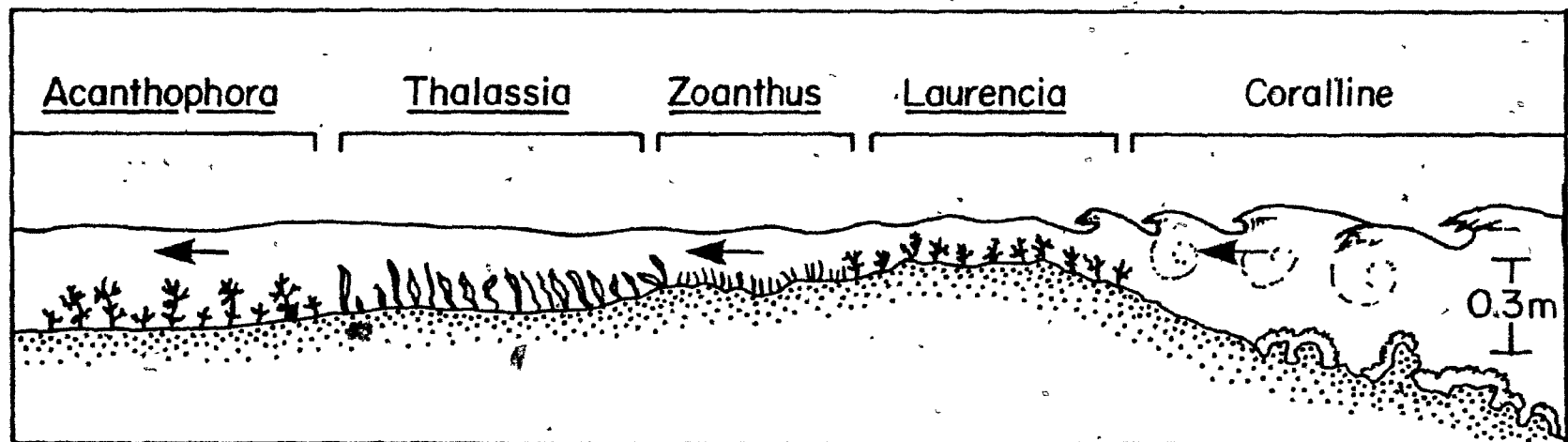


Figure 3. Biotic Zones of the Reef Flat at Galeta Point,
Panama (from Birkeland et al. 1973). Arrows indicate the direction of
water motion.



Siderastrea siderea Ellis & Solander, Porites furcata Lamarck, Porites astreoides Lesueur, the gorgonian, Gorgonia flabellum L., the crustose coralline algae, Neogoniolithon sp. and Porolithon sp., the green algae, Halimeda opuntia (L.) Lamour. and Caulerpa racemosa (Forsk.) J. Ag., and the fleshy red algae, Bryothamnion seaforthii (Turn.) Kütz. and Cryptonemia crenulata J. Ag. The Laurencia Zone marks the outer limits of the reef-flat on which the waves break. The topography of the reef-flat is such that the highest elevations occur in the Laurencia Zone and decrease moving in a landward direction (Fig. 3). On the seaward margin of the Laurencia Zone occurs the greatest diversity of algal species. The predominant algae are: L. papillosa, A. spicifera, H. opuntia, C. racemosa, and Gellidiella aceroa (Forsk.) Feldm. & Hamel. A broad band of L. papillosa occupies most of the calcareous substratum of the Laurencia Zone and provides an understorey habitat for many sessile invertebrates (i.e., anemones) and motile invertebrates (i.e., sea urchins and polychaetes). Landward to the Laurencia Zone is the only animal-dominated community, the Zoanthus Zone. Dense colonies of the small green zoanthid, Zoanthus sociatus Ellis, and the large brown zoanthid, Polythoa variabilis Verrill, are very prominent in some locations (Seben, 1977) while in others they are obscured by a Laurencia canopy. The Thalassia Zone, which is dominated by Thalassia testudinum König, is the most extensive. Sand restricts the algae in the Thalassia meadow to psammophilic species (i.e., sand loving), as Penicillus capitatus Lamarck and Caulerpa cupressoides (West) C. Ag., or to facultative epiphytes, as A. spicifera, Centrocerus

clavulatum (C. Ag.) Mont. and Spyridia filamentosa (Wulfen) Harv. Some areas of the Thalassia Zone have large amounts of coral rubble, while other areas have mostly fine sediments and sand as substratum. Next is the Acanthophora Zone, a zone sheltered from wave exposure. The Acanthophora Zone substratum consists of patches of coral rubble dispersed in a sand plain. A. spicifera, the predominant alga, grows in dense mats on an understorey of L. papillosa, which occupies most of the coral substratum. The landward edges of the Acanthophora and Thalassia Zones abut a lagoon or spillway from which water is channeled back to sea. More detailed information about Galeta Reef and its species assemblages is available in Birkeland et al. (1973), Earle (1972a), and MacIntyre & Glynn (1976).

1.2 Morphology, and Terminology

A. spicifera is attached to the substratum by a large, irregularly lobed disc, from which many erect branches may arise (Børgesen, 1915-1920). Plants are sparingly branched to bushy, growing to 0.23 m tall. Main branches are beset with short, determinate branchlets which are markedly spinose and arranged spirally with a $1/4$ divergency (Børgesen, 1915-1920; Taylor, 1967 [Fig. 4a]). The main axis has a diameter of 2 to 3 mm from which branches emerge occasionally. Plants are fragile and break easily upon handling.

Tetrasporangia develop in stichidial ramuli on short determinate

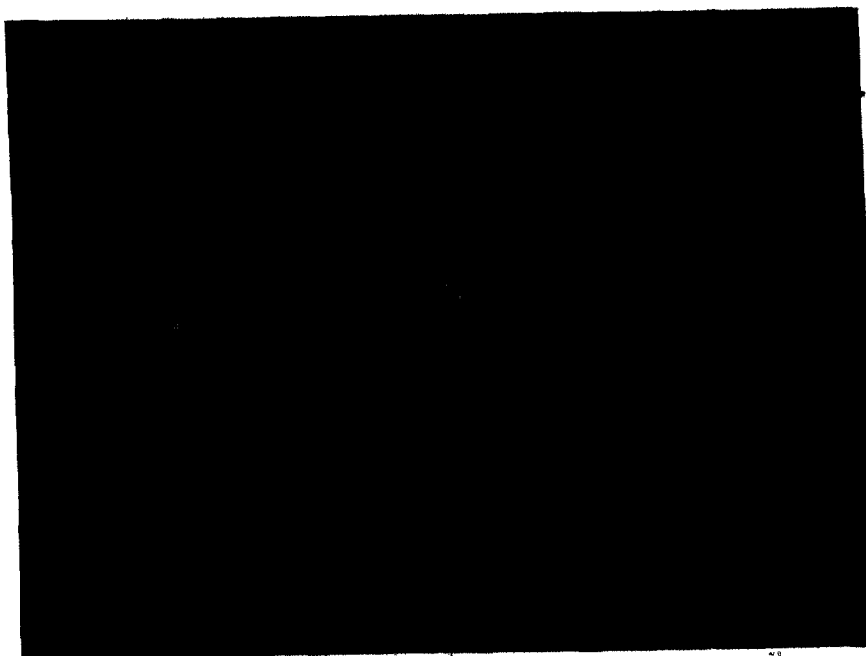
Figure 4. Morphology of A. spicifera and L. papillosa.

Determinate branches = branches of a smaller, more uniform size. (A)

A. spicifera, bar length = 3.8 mm; (B) L. papillosa, bar
length = 2.8 mm.



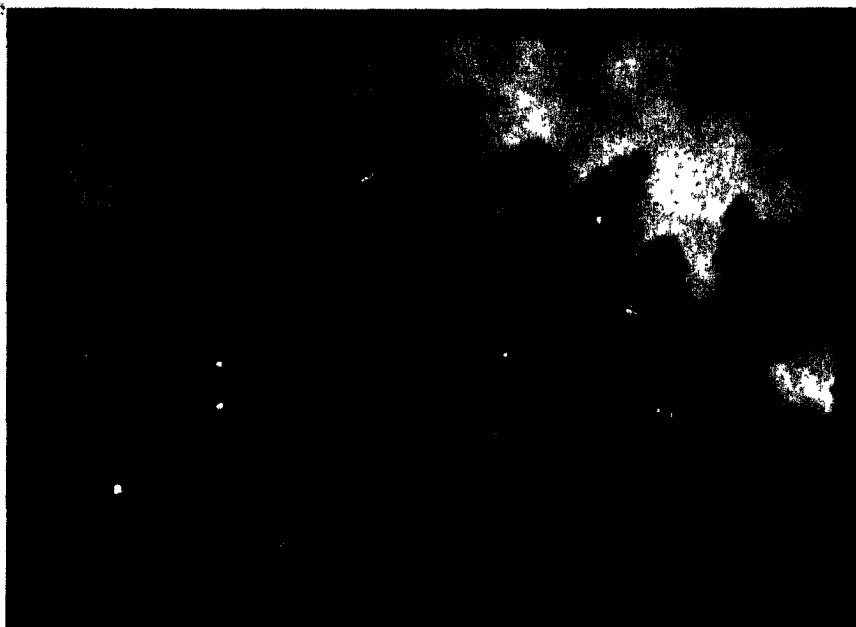
(B)



(A)

Figure 4. (cont'd) (C) Spineless branches of A. spicifera, bar
length = 2 mm.

(C)



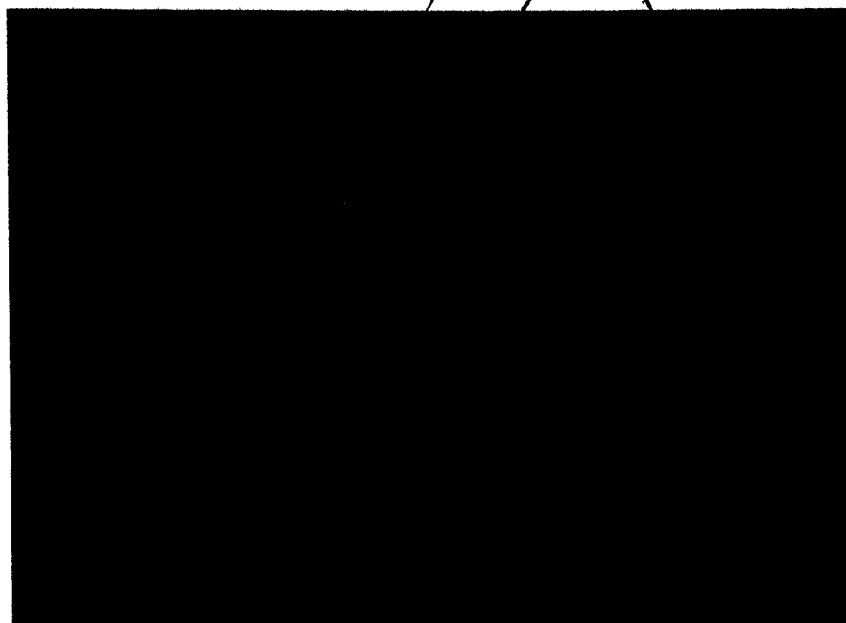
branchlets (Fig. 5); tetrasporangia sometimes occur within the branchlet itself. Spermatangial clusters are platelike, each developing from a trichoblast of which the basal cell persists as the stalk of the disc (Taylor, 1967). Pericarps are stout-stalked and urceolate, and are subtended by a small spine (Taylor, 1967 [Fig. 5]).

The recruitment of fragments into the back reef depends upon the chances of the fragments snagging and becoming attached to a variety of substrata. A "snagged plant" is any fragment that is mechanically interlocked with its substratum, as opposed to an "attached plant" that is bonded to its substratum. A combination of the branches and spines mechanically snag A. spicifera to different substrata and then the branchlets of A. spicifera attach to the substrata directly or produce one-to-several spineless branches (Fig. 4c). These spineless branches can either surround the contacted substratum or adhere to it by forming a secondary holdfast.

Four different growth forms of algae are recognized in this study: "individuals", "mats", "aggregates", and "turfs". An "individual" is a plant that produces one to several uprights (i.e., any part of the plant above the holdfast) from a single holdfast (i.e., area of thallus designed to act as an organ of attachment). In this study, I also consider the basal 5 to 20 mm of the thallus to be part of the holdfast because of its darker pigmentation and greater thickness. Ideally, two adjacent "individuals" of the same species rarely have overlapping fronds. In contrast, a "mat" is a group of closely arranged "individuals" of the same species whose uprights form a loose matrix



Figure 5. Fertile cystocarpic and tetrasporic plants of A. spicifera. (A) cystocarpic plants, bar length = 13 mm; (B) tetrasporic plants, bar length = 17 mm.



(B)



(A)

with little organization. "Mats" may form when uprights that lack a ridged structure entangle and sometimes attach to each other. "Mats" may also form from the accumulation of fronds in sheltered habitats. Many filamentous reds, greens, and browns that have been previously referred to in the phycological literature as "filamentous turfs" or "caespitose species" comprise this category. The third growth form, an "aggregate", is made up of a group of closely arranged "individuals" whose uprights are slightly ridged or cartilaginous. Aggregate-forming species produce a carpet of uprights of almost uniform size.

"Aggregates" are consolidated by their interwoven branches or by specialized branches that grow horizontally into neighboring fronds. For example, L. papillosa (Fig. 4b) has branches that grow among adjacent fronds and, when contact is made with hard substrata, are capable of forming a secondary holdfast. Secondary attachment between fronds within an "aggregate" is rare, because of the typically slow growth of these fronds. The last growth form, the "turf", is a specialized form of "aggregate". With the removal or death of the apical cell, the upright branches are modified (i.e., using apical dominance release) to produce a dense cluster of terminal branches. In the absence of disturbance, such species revert to the "aggregate" growth form. It has been suggested by Hay (1981a) that the turf growth form is better adapted to tolerating desiccation and herbivory.

2.0 Materials and Methods

2.1 Study Sites and Sampling Periods

Studies were done at Galeta Reef from February 1979 to July 1980 and from September 1981 to January 1982. The initial fieldwork documented: (i) the abundance and distribution of reef-flat species; (ii) the abundance of drift biomass; (iii) the growth of A. spicifera in the Acanthophora and Laurencia Zones; and (iv) the reproductive phenology of A. spicifera in the Acanthophora and Laurencia Zones.

Biomass sampling was concentrated in two reef-flat zones, Acanthophora and Laurencia Zones (Fig. 6). The study site in the Laurencia Zone consisted of a 20-m X 50-m plot that was located away from the major study area so as not to interfere with ongoing S.T.R.I. studies. The site in the Acanthophora Zone (30-m X 50-m plot) was established outside the channel of water that abuts the laboratory, seawall, so as to minimize any influences that the construction of the laboratory or the causeway may have had on adjacent reef assemblages. Commencing in February 1979 and continuing until March 1980, biomass sampling was also done throughout the reef-flat to document the spatial distributions of A. spicifera, L. papillosa, and T. testudinum.

The channeling of drift biomass into the mangrove and the subtidal regions was measured from locations on the downstream edge of the reef-flat. The unidirectional flow of water over the reef enabled permanently fixed nets to be used. The sampling period began in January

Figure 6. Station locations on Galeta Reef, Panama

(N-no. = Drift Net; ⊗ = Tide Gauges; C-no. = Colonization Station

(Thalassia Zone); Bm = Biomechanic Study Area; Ph = Phenology

Transects; [] = Border to Laurencia or Acanthophora Zone Biomass

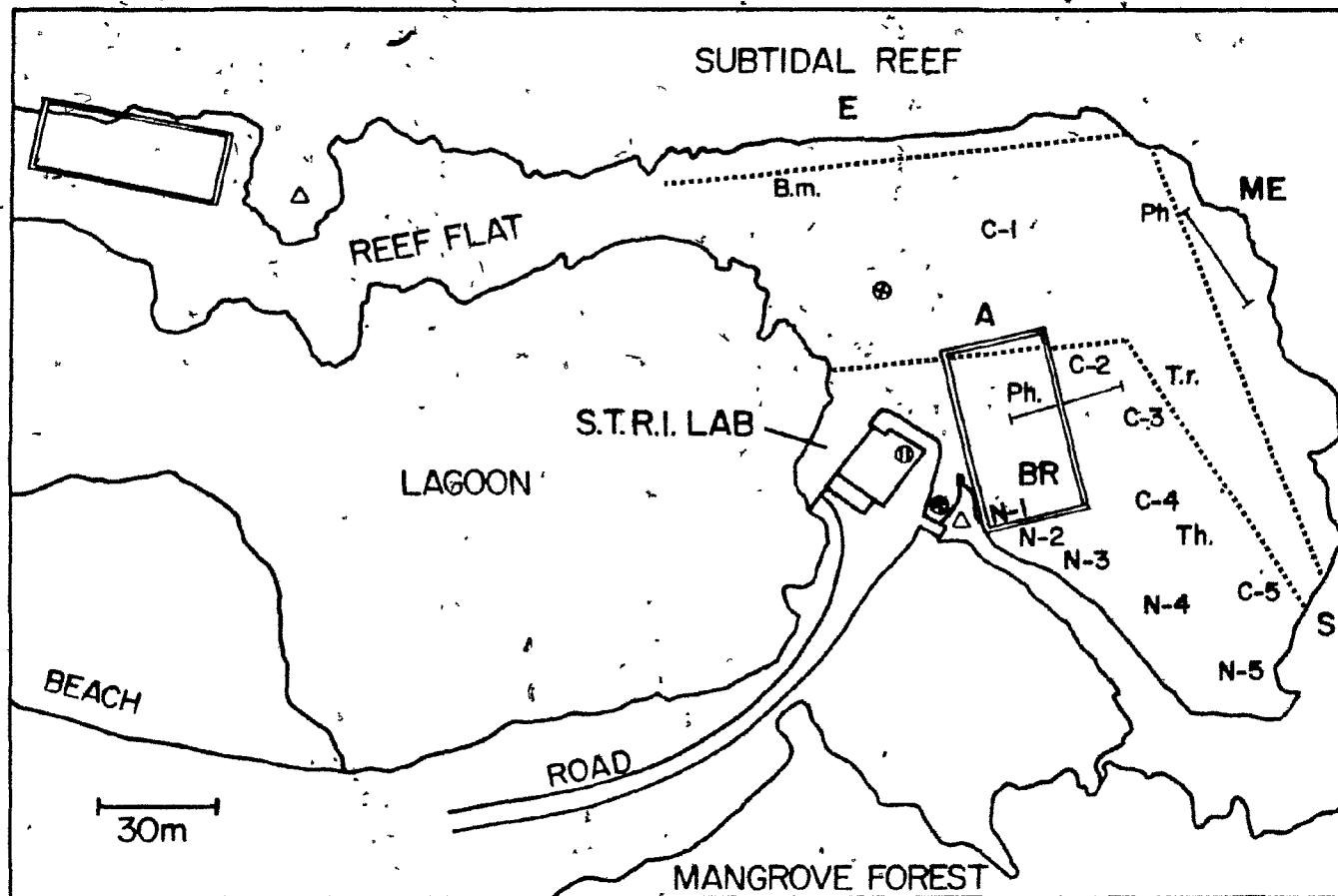
Stations; ----- = Drift Biomass Transects; Δ = Temperature and

Growth Stations; ⊙ = Solarimetry Sensor; E = Exposed Station;

ME = Moderately-Exposed Station; S = Sheltered Station; BR = Back-Reef

Station; A = Acanthophora Zone Station; Tr = Thalassia-rubble Station;

and Th = Thalassia Zone Station.



1979 and was terminated in March 1980.

From January 1979 to February 1980, the growth rate of A. spicifera was measured in the Acanthophora and Laurencia Zones (Fig. 6). At the same time, plants were collected for phenological studies along permanent transects, one transect in each of the Acanthophora and Laurencia Zones (Fig. 6).

Coinciding with the above studies, numerous short-term experiments and manipulations (i.e., less than three months) were done throughout the reef-flat to elucidate the fragmentation strategy of A. spicifera. From August 1979 to July 1980, rates of fragmentation and colonization of A. spicifera were measured under varied sea conditions and within different reef-flat habitats (Fig. 6).

From September to December 1981, the emphasis of the study shifted to an evaluation of the response of A. spicifera to wave action and aerial reef exposures, and to examine the possibility of competitive interactions between A. spicifera and L. papillosa. Sampling was confined to four reef-flat stations which were located in a wave exposure gradient. They were labelled as: (i) the Exposed Station; (ii) the Moderately-Exposed Station; (iii) the Sheltered Station; and (iv) the Back-Reef Station (Fig. 6).

2.2 Measurements of Environmental Variables

Water Temperature (Maximum-Minimum)

From June 1979 to June 1980, maximum and minimum water temperatures were measured once monthly in the Acanthophora and Laurencia Zones.

Taylor U-shaped maximum-minimum thermometers, coated with an epoxy resin and covered with dark plastic to reduce fouling and corrosion in salt water, were used. The thermometers were calibrated in the field against a certified laboratory-grade thermometer and secured by metal stakes into pools (0.5-m deep) which were never without water.

Solarimetry

Measurements of solar irradiance ($\text{g cal cm}^{-2} \text{ h}^{-1}$) from January 1979 to March 1980 were made available from the Smithsonian Institute's Environmental Science Program at Galeta Point, Panama, and were collected continuously from over the reef-flat (Fig. 6). These data were converted to $\text{J cm}^{-2} \text{ d}^{-1}$, according to Wetzel (1975).

Tidal Elevation and Aerial Exposure

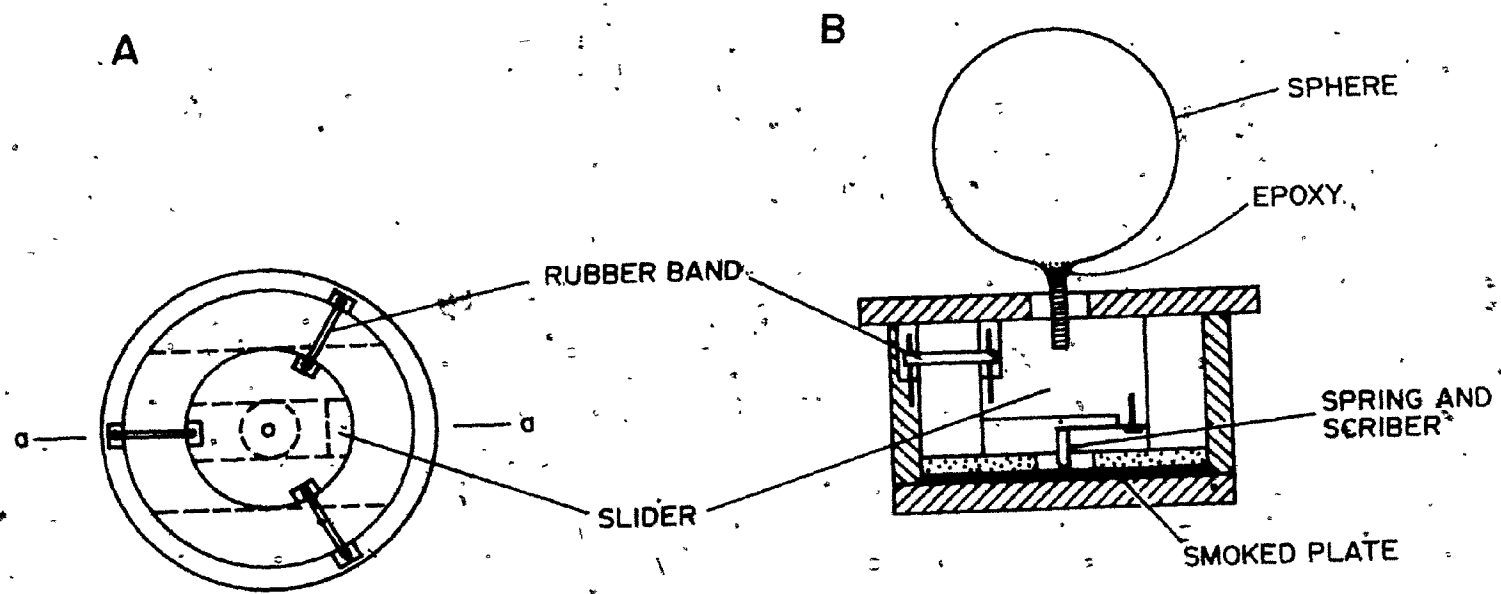
Measurements of tidal elevation from January 1979 to December 1980 were supplied by the Smithsonian Institute Environmental Science Program at Galeta Point, Panama. These data were used to show seasonal variations

in tidal elevation and to quantify the frequency and periodicity of exposures in the air of the reef-flat. Variations in reef-flat elevation, tidal amplitude, wave exposure, and wind velocity make it difficult to predict the precise tidal elevation that would result in an aerial exposure of the reef-flat (Druehl & Green, 1982; Hendler, 1976). As conservative estimates, Hendler (1976), using the tide gauges at Galeta, determined a tidal elevation of 0.30 m to be the critical exposure level of a Laurencia Zone and 0.25 m to be that for the middle of the reef-flat. Several spot readings of the tidal gauges were taken at the time of reef exposures and found to concur with Hendler's (1976) estimates. For the Acanthophora Zone, 0.24 m was determined from spot readings as the critical exposure elevation.

Wave Exposure and Current Velocity.

Wave exposure was measured from four stations on the reef-flat: the Exposed; Moderately-Exposed; Sheltered; and Back-Reef Stations (Fig. 6). Two methods were employed. The first method employed a dynamometer developed by Denny (1983), which was modified to measure the force exerted on a 2.54-cm diameter sphere (Fig. 7). Measurements were taken daily over a fortnight at the seaward edge of the Laurencia Zone, beginning on 28 November 1981. The second procedure made use of a Marsh-McBirney Multidirectional Electromagnetic Water Current Meter (Model 511) coupled to a portable chart recorder. At each station, water velocity was noted at one-minute intervals for a 15-minute period

Figure 7. A construction diagram of the wave force dynamometer, modified from Denney (1983). (A) Top view with the top plate removed to show the slider and rubber bands. Dashed circle shows the position of the holes cut in the lower plate through which the scriber extends; dotted lines show the position of the grooves in the base of the slider and in the housing base. (B) Side view of the section made through the line a---a in panel A.



and then averaged. Water velocities were taken during moderate sea conditions and were displayed relative to incoming waves by vector diagrams. On 5 December 1981, current velocities were measured at numerous locations on the reef-flat to describe the flow of water over the reef platform.

Fore Reef Topography

The elevation of the Laurencia Zone was measured relative to tide gauges at Galeta Reef, using standard levelling procedures. Reef elevations were recorded along transects perpendicular to incoming waves at the Exposed, Moderately-Exposed, and Sheltered Stations.

Substrate rugosity, described by Luckhurst & Luckhurst (1978) as a measure of actual distance relative to linear distance (similar to "fractal dimension"; see Willison, 1982), was measured to demonstrate subtle differences in the surface topography in the Laurencia and Acanthophora Zones. Substrate rugosity measurements were made using a 2-cm linked, 13-m long brass chain. The chain held taut measured linear distance, while the brass chain, conforming to the terrain beneath, measured actual distance. In this instance, substrate rugosity was defined as:

$$\text{S.R.} = \frac{1}{13 \text{ m}} \times \frac{\text{Chain Length Over Substratum}}{13 \text{ m}}$$

Values approaching zero show the greatest surface relief. Surface

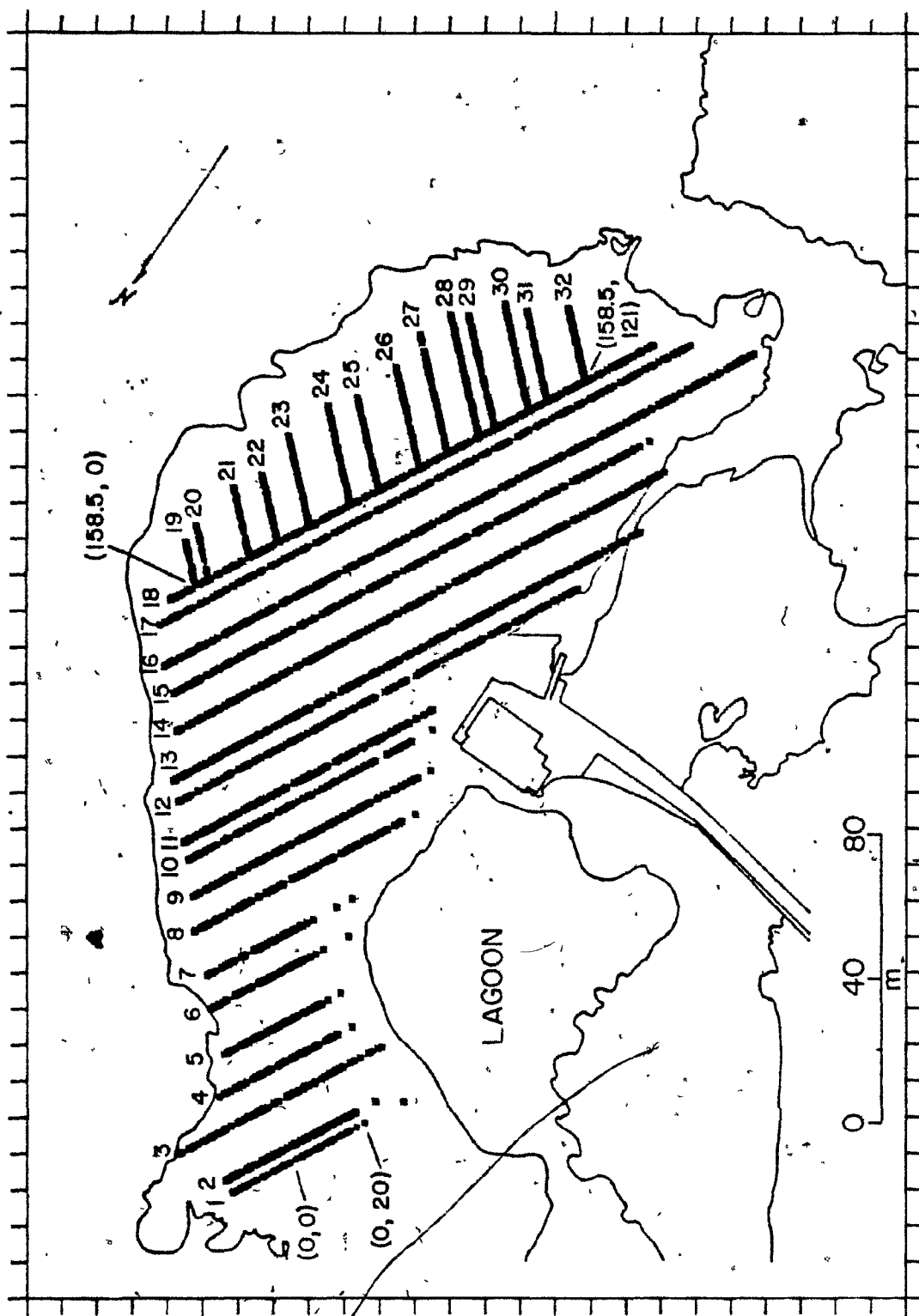
profiles were measured in the Acanthophora and Laurencia Zones, with 15 transects in each zone.

2.3. The Fragmentation of A. spicifera

Spatial and Seasonal Distribution and Abundance

Seasonal variations in algal and seagrass abundance were sampled along 32 stratified random transects that were located in X,Y coordinate space (Fig. 8). This permitted an accurate record of the abundance and distribution of major reef-flat assemblages. Every 10 m of transect was divided initially into 20 potential sampling locations that were assigned numbers randomly from 1 to 20. In increasing order of occurrence, each number was then designated as the location for a monthly sample, beginning in February 1979. This insured a random sampling design with no overlap in location. One sample, consisting of the contents of a 3.81-cm diameter core, was taken monthly from each 10 m of transect, sorted to species, washed in fresh water, and dried at 90°C to constant weight. About 200 cores were sampled each month for a 14-month period. Hereafter, I will refer to this study as the Reef Biomass Study. In addition, 100 samples collected from a 30-m X 50-m plot in the Acanthophora Zone, and 50 samples collected from a 20-m X 50-m plot in the Laurencia Zone were similarly sampled. Here, 20

Figure 8: Transect numbers and X,Y coordinates used in the Reef-Biomass Study. Each mark indicates a location of a biomass sample (February 1979 to March 1980).



potential sampling locations were assigned randomly for every 5 m of transect along 10 Acanthophora Zone and 25 Laurencia Zone transects.

In September 1979, dry-weight to wet-weight conversions were obtained for A. spicifera and L. papillosa from 15 samples collected in the Acanthophora Zone. Specimens were held in seawater tanks, removed and blotted dry with absorbent towelling, and weighed on an analytical balance. This procedure was repeated five times, each time returning the alga to seawater. The plants were then dried to constant weight at 90°C after a fresh water rinse.

Drift Sampling

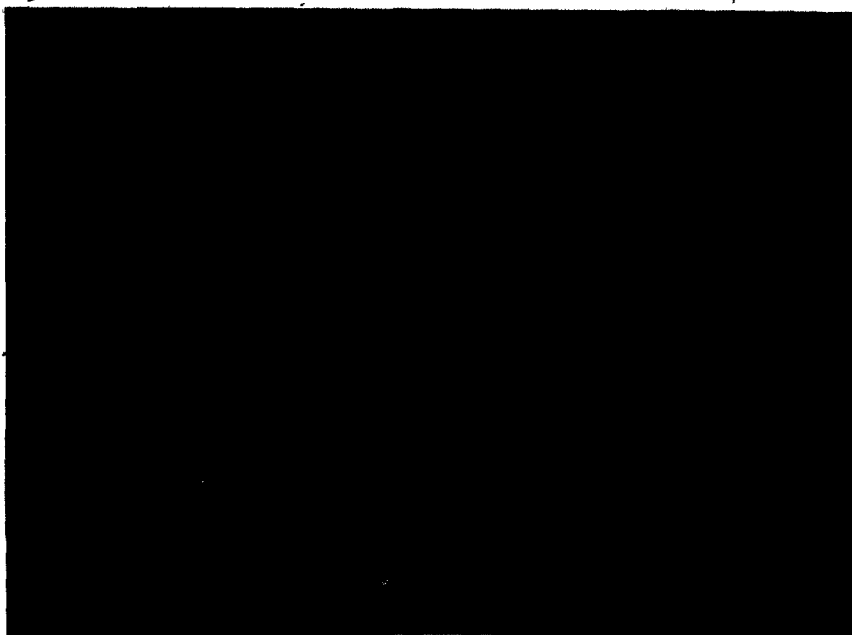
Drift materials leaving the reef were collected continuously in five nets. Permanent nets consisted of an upstream, 0.91-m high X 0.46-m wide, P.V.C. framed opening and a downstream, 0.25-m diameter opening, joined by 2-mm Vexar Netting (Fig. 9). A removable 0.75-m X 1.25-m nylon bag (2-mm mesh) was attached to the downstream end and emptied weekly or more often if full.

Materials from each net were subsampled. The contents of a net were first mixed before being emptied into 30 to 60 (0.13-m X 0.13-m X 0.20-m tall) containers. Four containers were randomly selected and sorted to species. All remaining materials and sorted aliquots were rinsed in tap water and dried to constant weight at 90°C.

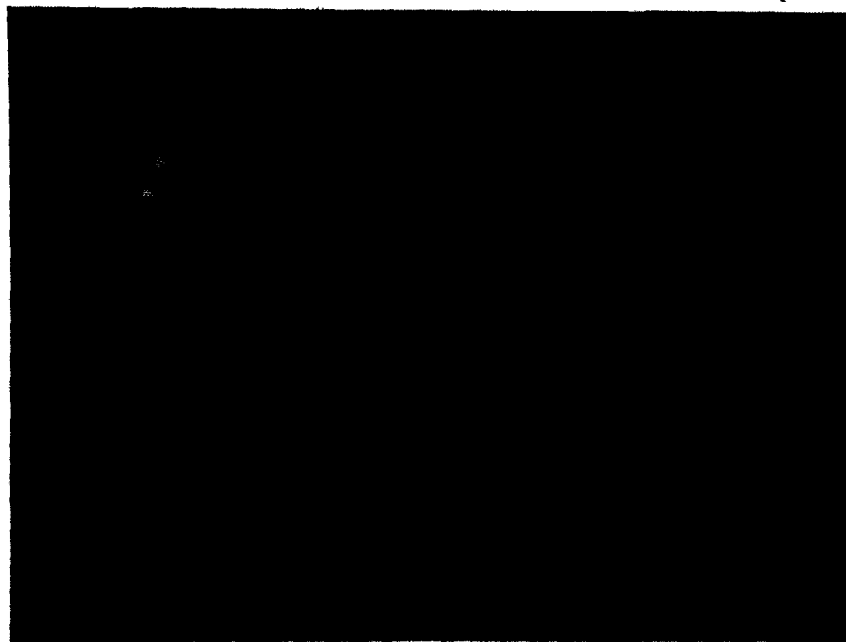
To determine the size of the sampling area and the efficiency of samplers, marked tags were released from two areas: an outer transect

Figure 9. Drift Sampling Net. (A) Close-up of permanently fixed net (0.91-m high X 0.46-m wide) and the removable nylon bag (B) . Two nets at high water.

(A)



(B)



located in the Laurencia Zone, and an inner transect found about midway between the Laurencia Zone and the nets (Fig. 6). Tags consisted of 45 mm² pieces of fluorescent Surveyor's Tape. About 10 tags were released for every meter of transect. This procedure was repeated under varied sea conditions to insure a close estimate of sampling area and sampling efficiency.

The biomass of A. spicifera and L. papillosa removed from the reef was calculated monthly by multiplying the proportion of each species from subsamples times the total biomass in each net, and summing these values over the five nets and the one-month period. The biomass for each species removed per unit area of reef was estimated from the biomass collected in nets, the area sampled by the nets, and the monthly occurrence of a species in the drift-sampling area. To estimate the percent occurrence of an alga in the drift sampling area, samples from the Reef Biomass Study were used but confined to the drift sampling area. The reef area occupied by a species was estimated from the product of its percent occurrence in the drift sampling area times the total area (m²) sampled by the nets. Dividing the species biomass removed from the reef by the reef area occupied by that species, the drift biomass was standardized to a one square meter plot.

Growth

Monthly Determinations

From January 1979 to February 1980, the growth of 30-mm apical fragments of A. spicifera was measured each month over a one-week period in the Laurencia and Acanthophora Zones (Fig. 6). Twenty fragments collected from the Laurencia Zone were placed into enclosures and measured for increases in length. Enclosures consisted of envelopes (0.15 m X 0.20 m); one side was made of 1-mm mesh cotton cloth, and the other of a clear, 1.5-mm thick, vinyl plastic through which numerous 3.4-mm diameter holes were drilled. Two enclosures were used in each zone and secured into depressions always open to seawater at a depth of 0.5 m.

Reciprocal Growth Experiment

In February and August 1979, the growth of apical fragments of A. spicifera, collected from the Acanthophora and Laurencia Zones, was measured to determine if growth was independent of collection location. Fifty apical fragments (30 mm in length) from the Acanthophora Zone were separated into two equal groups, placed into enclosures, and outplanted into the Acanthophora and Laurencia Zones. An additional fifty fragments of A. spicifera from the Laurencia Zone were treated in a similar fashion. After the one-week period, the increase in the length

of all fragments was determined.

Morphology

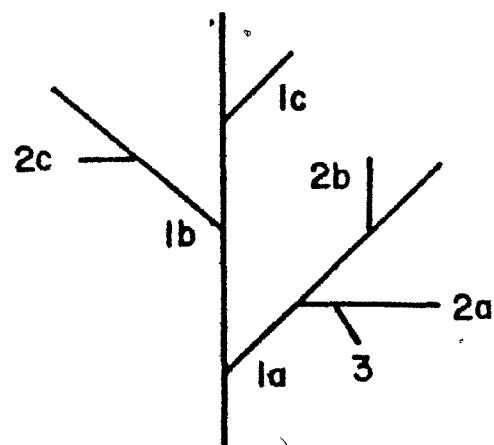
Botanical and Strahler Methods

Morphometric and meristic data, acquired from fronds of A. spicifera and L. papillosa in the Acanthophora and Laurencia Zones, were used to examine species- and habitat-specific differences in morphology. Twenty randomly located quadrats (0.15 m X 0.30 m) were harvested for A. spicifera and L. papillosa from 26 September to 1 October 1981 in the Acanthophora Zone and from 29 October to 5 November 1981 in the Laurencia Zone. All fronds in the quadrat were collected. The choice in sampling period maximized the time that A. spicifera and L. papillosa were not affected by periods of aerial exposures. The fronds were measured for numbers and lengths of branches. These data were later analyzed for branching structure using the two principal methods to number branches in a branching system: centrifugal and centripetal labelling (Uylings et al., 1975).

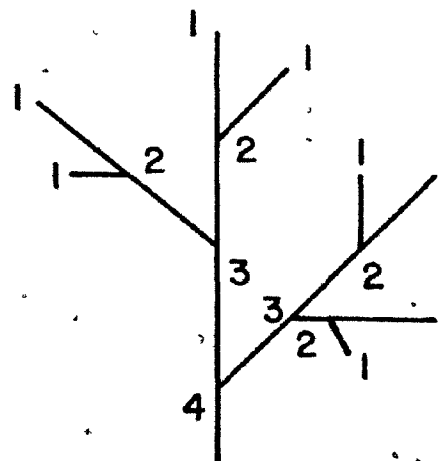
Botanists have traditionally ordered trees centrifugally by assigning order no. 1 (i.e., 1st-order branch) to the main stem and increasing order numbers in consecutive lateral branches (Wilson, 1966). In this instance, 1st-order branches originated at the main axis (Fig. 10). The "Botanical Method" permitted the assessment of branching complexity and compactness. Branching complexity was assessed from

Figure 10. Botanical and Strahler Methods of numbering branches in a branching system. 1 = 1st-order branch, 2 = 2nd-order branch, 3 = 3rd-order branch, 4 = 4th-order branch, 1a = first 1st-order branch; 1b = second 1st-order branch; 1c = third 1st-order branch; 2a = first 2nd-order branch on the first 1st-order branch; 2b = second 2nd-order branch on the first 1st-order branch; and 2c = first 2nd-order branch on the second 1st-order branch.

BOTANICAL METHOD (MODIFIED)



STRAHLER METHOD



several different forms of measurement: the numbers of different types of ordered branches; the percent composition of different ordered branches in the population (i.e., 1st-, 2nd-, 3rd-order, etc.); and the average number of branches at each order of branching. Measurements of branching compactness consisted of: (i) the distances from the holdfast to 1st-ordered branches; (ii) the distances from the main axis to the first 2nd-order branches; (iii) the lengths of 1st-order branches; (iv) the lengths of 2nd-ordered branches..

The second method of labelling branches, the "Strahler Method" (1953), is a centripetal ordering system: ordering begins at terminal, distal branches, and order is increased when two branches of equal order meet (Fig. 10). This method evaluated how the algae projected their branches into the water column. The 1st-order branch length (the distance from a terminal branch to the holdfast) was measured for all indeterminate branches comprising a frond.

Biomechanics of Breakage

In Vitro Study

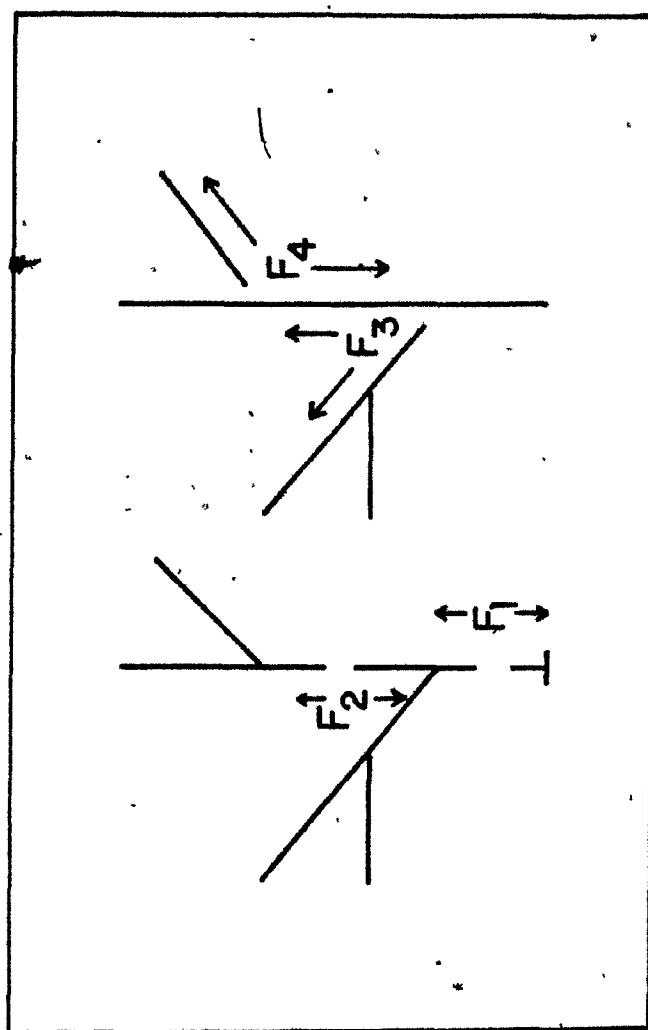
The breakage method of fracture by tension was used to measure the strength of A. spicifera at different locations on the thallus. Plants were secured with Velcro cloth to the arm and base of a pendulum balance. Lead balls of between 0.5 to 1.0 g were added every 20 to 40 seconds to the opposite end of the balance until breakage occurred.

Four different locations of breakage were assessed: (i) along the main axis of a branch; (ii) along the main axis of a branch adjacent to the holdfast; (iii) at a branch node when the holdfast and branch apex were secured (abaxial angle); (iv) at a branch node when the apices of the main axis and the branch were secured (branch axil; Fig. 11). The mass necessary to cause breakage and the frond diameter at the breakage point (measured with vernier calipers) were recorded for 50 fronds at each of the four locations mentioned above. For comparative purposes, branches of L. papillosa were also examined along their main axes, as in (i) above.

In Situ Study

Plants of A. spicifera of known size and branching pattern were outplanted into the Laurencia Zone to determine if breakage was independent of thallus location. A. spicifera that were growing on coral fragments were collected from the Thalassia Zone. The size and pattern of branching of each plants were traced onto plastic slates, so that any plants losing branches, when placed back onto the reef, were detected. Coral fragments containing these algae were secured by metal stakes into the Laurencia Zone (Fig. 6). The algae were then examined in the laboratory for losses at one-, four-, and six-day intervals. Into both calm and moderate seas, 40 plants were noted for: (i) the sizes of fragments broken off a plant; and (ii) whether the location of the break occurred at a branch node or internode.

Figure 11. Mechanical Measurements of Breakage. Position of algal attachment to pendulum balance when measuring the force required to cause breakage of: (F1) the main axis near the holdfast; (F2) the main axis; (F3) the branch node when the the distal ends of the main axis and branch are secured; and (F4) the branch node when the holdfast and the distal end of the branch were secured.



Frond Survivorship

The survivorship of A. spicifera was examined by tagging between 20 and 30 fronds in each of six permanent plots. Two plots were located at each of the Exposed, Sheltered, and Back-Reef Stations. Fronds were tagged with 5-cm long plastic coated "twist ties" that were loosely secured between branches and whose identity and number were maintained throughout the study. Branch losses were monitored twice weekly for a 4-month period from 19 September to 18 December 1981, under both wet- and dry-season conditions. Data were analyzed using the Biomedical Computer Program for Life Table Analysis at Dalhousie University (Anon., 1980). To assist in interpretation, Lethal Exposure 50 % (LE_{50}), the time required (days) to lose 50 % of the originally tagged fronds, was calculated as:

$$LE_{50} = (t_1 - t_0) + \frac{P_1 - 1/2}{F_1}$$

where (t_1, t_{1+1}) is the interval for which $P_1 \geq 1/2$ and $P_{1+1} < 1/2$; (t_0) is the time at the beginning of the first interval; (F_1) is the death-density function; and (P_1) is the estimate of the cumulative proportion surviving to the beginning of the 1st interval. Also, the mean survivorship period (μ) was calculated as:

$$u = \sum_{i=1}^N P(t_{i-1})(t_i - t_{i-1})$$

where $P(t)$ is the cumulative survival at each unique time of death.

Depletion curves were tested using an exponential scores test (or Savage statistic) proposed by Mantel (1966). For further information consult B.M.D.P. manual (Anon., 1981).

The percent cover of A. spicifera was measured along with survivorship from four 0.3-m X 0.5-m permanent quadrats, located adjacent to the survivorship stations. Each quadrat was divided into 20, 0.05-m X 0.15-m subsections that were visually estimated for Acanthophora coverage. The mean coverage of 80 subsections defined the percent cover for the station.

Phenology

From January 1979 to February 1980, seasonal and spatial information on the reproductive phenologies of A. spicifera and L. papillosa was collected. From a permanent 30-m transect in the Acanthophora Zone, 90 fronds (3 groups of 30) were collected in a stratified random manner (30 fronds for every 10 m) every fortnight. Similarly, an additional 90 fronds were collected from a transect of similar length in the Laurencia Zone (Fig. 6). Plants were categorized by reproductive phases (male, female, tetrasporic); mounted on herbarium paper, dried, and deposited at the National Research Council of Canada Herbarium (NRCC) in Halifax. To increase sample size, reproductive data

were lumped into monthly intervals (i.e., six samples of 30 plants for each location).

Colonization

Acanthophora Zone

The recruitment of Acanthophora fragments into the Acanthophora Zone was examined twice weekly from 10 September 1979 to 22 October 1979 and from 23 January 1980 to 6 March 1980. Six plots (0.3 m X 0.5 m) were chosen randomly in the Acanthophora Zone and cleared of Acanthophora plants to expose a Laurencia understorey. Around each site, a border of 0.50 m was similarly cleared of A. spicifera to serve as a buffer zone. Fragments of A. spicifera that were recruited into cleared plots and exceeding 30 mm in length were collected and measured for overall length. Smaller fragments were collected but assumed to be residual plant material and discarded.

Thalassia Zone

To test the substratum preference of fragments of A. spicifera and to examine how wave action influenced the colonization of these

fragments in the Thalassia Zone, coral rubble and L. papillosa were transplanted into Thalassia beds and examined for fragment recruitment. Five stations (I-V) were selected in the Thalassia Zone that represented: (i) an exposed fore-reef location; (ii) a sheltered fore-reef location; (iii-v) three back-reef locations (Fig. 6). Each station consisted of three adjacent square-meter plots of: (i) T. testudinum; (ii) T. testudinum with coral rubble; (iii) L. papillosa. L. papillosa was placed into the Thalassia meadow by removing a square meter of T. testudinum and by placing the hard substratum to which the L. papillosa was attached into the sediments. Neither the added coral rubble nor the L. papillosa represented an obvious obstruction for the current flowing through the Thalassia meadow. After four months, plots were scored for the numbers of fragments present. Two hypotheses were tested: (i) whether fragment colonization was independent of substrate; (ii) whether fragment colonization was independent of station location. The experiment commenced 17 September 1980.

Fragment Snagging and Attachment

Species and Habitat Comparisons

The snagging of 8- to 10-cm fragments of A. spicifera was measured in different current regimes and reef habitats. Between 20 and 70 fragments marked with acetate tape were released individually into three different current velocities (about 0.06, 0.18, and 0.24 m s⁻¹) from

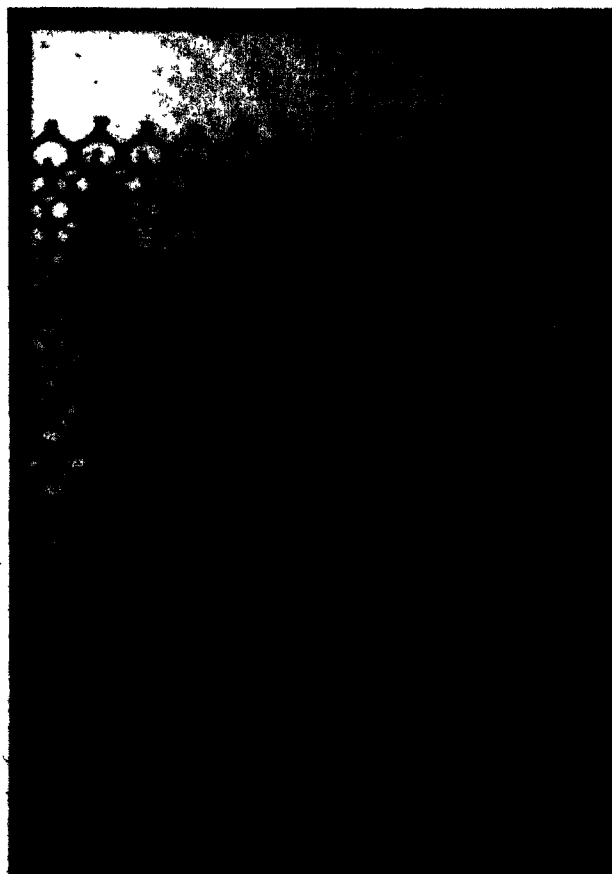
starting positions in the Acanthophora and Thalassia Zones and in a Thalassia-rubble area (Fig. 6). Marked fragments were noted for the distance travelled before snagging (i.e., remaining in the same position for greater than five minutes) and for their presence or absence after 72 hours. For comparative purposes, L. papillosa fragments were similarly evaluated in the Acanthophora Zone at current velocities of about 0.06 and 0.24 m s⁻¹.

Rates of Attachment

* The rates to which A. spicifera attached to another frond of A. spicifera or to L. papillosa, T. testudinum, or Porites-rubble were determined. For each combination, 40 pairs of plants were examined daily for attachment (i.e., the physical bonding of two fronds) over a 5-day period. The bases of each pair of plants were wrapped together with foam padding and fastened to 1.27-cm Vexar Netting (Fig. 12). Such an arrangement of plants insured close contact between species pairs. The Vexar Netting was then secured into the Thalassia Zone by metal stakes.

Figure 12. Illustrated usage of vexar netting and foam padding to pair fragments of A. spicifera with different substrata. The percent attachment (i.e., the physical bonding of two species) was noted each day from 40 plants of A. spicifera paired with A. spicifera, L. papillosa, T. testudinum, and Porites-rubble. Bar length = 33 mm.

(A)



2.4 The Maintenance and Persistence of A. spicifera

Seasonal Variation in Laurencia papillosa Biomass

L. papillosa is the most abundant species on the reef-flat at Galeta. Its importance to A. spicifera will be shown to be unmistakable. Accordingly, the information on the seasonal abundance of L. papillosa in the Acanthophora and Laurencia Zones was collected. Procedures were the same as those described previously for A. spicifera (see Spatial and Seasonal Distribution and Abundance).

Aerial Exposures

Daytime Tolerance

The susceptibility to aerial exposure of A. spicifera was measured by simulating a midday reef-flat exposure. Starting at midday, 45 fronds (5- to 8-cm in length) of A. spicifera were collected from the field, placed onto a damp slab of coral rubble, and allowed to dry in direct sunlight for either 15, 30, 45, or 60 minutes. Fifteen fronds were collected at each time interval, returned to seawater, and measured for apparent photosynthesis (net photosynthesis) and respiration after 24, 72, and 96 hours. Fronds collected from the field and not exposed in the air served as controls.

The apparent photosynthesis and respiration of A. spicifera were

measured in 1.19-l bottles in a Puffer-Hubbard Uni-Therm Incubator equipped with nine Sylvania cool-white fluorescent tubes. Bottles were filled with seawater collected in the early morning hours (0500 to 0700 h) to insure that seawater was unsaturated with oxygen. Fragments were incubated for one hour at 27°C, and at $180 \mu\text{E m}^{-2} \text{s}^{-1}$, and were agitated by mixing the seawater at a constant rate with magnetic stir bars. Oxygen determinations were made with a Yellow Spring Instrument Company (Model 57) Oxygen analyzer electrode. Apparent photosynthesis was expressed as $\text{mg O}_2 \text{ g (dry wt)}^{-1} \text{ h}^{-1}$. In bottles filled with seawater only, phytoplankton production was noted and subtracted from macro-algal production. Throughout the procedure, the recommendations of Littler (1979) were followed regarding the importance of container volume, thallus weight, oxygen tension, and water motion.

To compare the resistance of A. spicifera and L. papillosa to aerial exposures, 12 fragments of each species were simultaneously exposed on a partly cloudy day (50 % cloud cover) for 30 minutes at 1200 h on a damp piece of coral rubble. After exposure, fronds were placed into seawater tanks. An additional 12 fragments of each species that were not exposed in the air served as controls. Apparent photosynthesis was then determined for all fragments after 24 hours. A recovery period of 24 hours ensured that measurements of apparent photosynthesis reflected actual damage to the alga, rather than short-term effects immediately caused after injury.

Nighttime Tolerance

In addition to daytime exposures, nighttime exposures are common in late wet-season (August to October). Accordingly, the susceptibility to aerial exposures of A. spicifera during the night was assessed from two 0.4-m X 0.3-m X 0.1-m deep "mats" collected from the Acanthophora Zone. One "mat" was elevated out of the water on the reef-flat at 1900 h and returned to seawater (i.e., seawater tank) the following day at 0700 h. For a control, the second "mat" was placed into a seawater tank with running seawater at the beginning of the experiment. Six to 10 fronds were selected from the surface and underlying areas of each treatment and measured for apparent photosynthesis after 24 hours (see above). In the experimental treatment, fronds found on the surface of the "mat" were further categorized into partially and severely desiccated; when collected from the field, severely desiccated fronds appeared black and dehydrated, while partially desiccated plants were normal in appearance.

"Individual" versus "Aggregate"

In the Laurencia Zone, A. spicifera grows as an "individual" within the "aggregate" of L. papillosa. In doing so, "individuals" may be able to increase their resistance to withstanding aerial exposure. Because "individuals" of A. spicifera within L. papillosa "aggregates" could not be collected in sufficient numbers or without destroying the integrity of the "aggregate", comparisons of aerial exposure resistance were made

between "individuals" and "aggregates" of L. papillosa. "Individuals" of L. papillosa could then be compared with those of A. spicifera, which then could be related to the "aggregate" growth form of L. papillosa. An "aggregate" of L. papillosa was collected on a single piece of coral rubble (0.5 m^2) from the Laurencia Zone and pruned so that 24 single fronds were isolated within cleared patches from the rest of the "aggregate". Of the fronds removed to form these clearings, 12 fronds were placed into seawater tanks to serve as controls. Hence, the fronds used as the controls and those exposed in the air all came from the same "aggregate". Fronds were exposed in the air by elevating the piece of coral rubble just out of the water. At 15-minute intervals for the first 45 minutes, six fronds of L. papillosa ("individuals") were collected. Similarly, at 15-minute intervals for the first hour but then hourly for the next four hours, six fronds from the "aggregate" of L. papillosa were sampled. After exposure in the air, fronds were placed into seawater tanks and measured for apparent photosynthesis after 24 hours.

Photosynthetic Partitioning

Hay (1981a) found differences in apparent photosynthesis and respiration between uprights and holdfasts of three turf-forming algae, and concluded that the holdfasts acted as "resistant stages" because of their lower energetic costs. Similarly, the same mechanism could be operating in algae that grow as "individuals" or "mats". Hence,

apparent photosynthesis and respiration of holdfasts and uprights of A. spicifera were examined. Twenty intact plants were collected and cut with a razor blade to separate uprights from holdfast. The darker pigmentation of the holdfast permitted it to be easily distinguished from its uprights. Specimens were held for 24 hours in seawater tanks before measurements of apparent photosynthesis were made.

Holdfast versus Upright Tolerance

If the holdfast of A. spicifera is a "resistant stage", then the ability of the holdfasts to withstand aerial exposures should be significantly greater than that of their uprights. About 100 plants of A. spicifera each possessing both holdfasts and uprights were exposed to direct sunlight between 1200 and 1245 h. (i.e., the period of time previously determined to kill all uprights of A. spicifera). Prior to the initiation of the experiment, plants were pruned so that light was distributed evenly over the thallus. After exposure to air, thalli were returned to seawater tanks, cut with a razor blade to separate uprights from their holdfasts, and examined for the presence or absence of new branches after three weeks.

Competitive Interactions

Fore-Reef Biomass

Biomass samples were taken at the Exposed, Moderately Exposed, and Sheltered Stations. Transects perpendicular to incoming waves were sampled for biomass in a uniform manner; one sample was collected from every 0.5 m of transect. To increase sample size, two additional samples were taken 0.5 m to the right and left of the initial sample. These samples defined the abundance and spatial distribution of A. spicifera and L. papillosa at each of the wave exposure stations. Upon determining the location where the biomass of A. spicifera was most abundant (i.e., "center of distribution"); a 10-m transect parallel to incoming waves was sampled for biomass in a stratified random fashion; one sample was collected randomly from every 0.5 m of transect. Biomass samples were then treated as previously described (see Spatial and Seasonal Distribution and Abundance).

Biomass samples (February 1979 to March 1980) collected from the Reef Biomass Study, but restricted to the Laurencia Zone and to the area adjacent to the Exposed, Moderately-Exposed, and Sheltered Stations, were examined for the degree of association between A. spicifera and L. papillosa. The usual test for association, the X^2 test for independence in a 2 X 2 table, was done following the procedures of Pielou (1974). Using this method, two plants are said to be positively associated if "the presence of one species in any sampling plot makes it

more likely that the other will also be found". The sampling area around each station was defined by transects 5 to 10 at the Exposed Station, by transects 20 to 25 at the Moderately-Exposed Station, and by transects 28 to 32 at the Sheltered Station (Fig. 8). Because of the large number of samples containing neither A. spicifera nor L. papillosa, a negative association between the species was not possible. The large number of samples containing neither species was the result of sampling the entire Laurencia Zone and including samples collected during periods of aerial exposure, when algal biomass was at a minimum.

Apparent Photosynthesis

The rates of apparent photosynthesis of A. spicifera and L. papillosa were compared at temperatures ranging from 20° to 40°C. Thalli were exposed gradually, starting at 29°C, to increasing or decreasing water temperature (5°C every hour), and sustained for one hour at the desired temperature, before beginning the incubation period. Two groups of fronds were used: (i) for temperatures higher than 29°C; and (ii) for those lower than 29°C. Apparent photosynthesis was determined as previously described for six replicates at each temperature.

The apparent photosynthesis of A. spicifera and L. papillosa was measured in different light intensities outdoors in a transparent water bath which was fitted with magnetic stirrers and neutral density

filters. Photosynthetically active light was measured every five minutes with a photometer, while temperature was maintained between 28° and 29°C in a water bath. Six replicates were used for each one-hour incubation period. The mean apparent photosynthesis was then plotted against the average light intensity for each incubation period.

The rates of apparent photosynthesis of A. spicifera and L. papillosa were measured over daylight hours (0600 to 1900 h) to show the rates of oxygen production of the two algae under light and temperature combinations found on the reef-flat. One-hour incubations similar to those previously described were performed; flasks, however, were kept in a water bath that was continuously supplied lagoon water, and were agitated with a magnetic stir bar at 15-minute intervals. Water-bath temperature and available light were measured every 15 minutes.

Overgrowth

Algal Size

The size of A. spicifera and L. papillosa plants (the distance from the highest apical tip to the holdfast) were measured at the Moderately-Exposed Station following a period of aerial exposure. After about one week of continuous water cover on the reef-flat, plants of A. spicifera and those of L. papillosa growing beneath A. spicifera were collected from 20 quadrats (0.15 m X 0.30 m), randomly selected from

areas dominated by A. spicifera. All plants within the quadrats were used until approximately 100 plants of each species were collected. Similarly, an additional 100 plants of L. papillosa found nearby but not associated with A. spicifera were collected and measured. After five weeks the procedure was repeated. However, as a clear separation between plants of L. papillosa growing nearby and in association with A. spicifera could not be made, only the overall lengths of A. spicifera and L. papillosa were compared. Sample size was increased to about 200 fronds of each species. Plants were sampled initially on 10 September 1981 and later, on 15 October 1981.

Transmitted Light

A. spicifera and L. papillosa were observed to overgrow each other frequently. In doing so, the overstorey species restricts light to the understorey species. To examine the reduction in light through the overstorey species, "mats" of A. spicifera and "aggregates" of L. papillosa were collected from the reef-flat. At the Exposed, Moderately-Exposed, Sheltered, and Back-Reef Stations, two or three "aggregates" of L. papillosa were removed with a razor blade from the substratum, placed onto a glass pane, and measured for percent light transmittance with a photometer. Similarly, "mats" of A. spicifera were collected and measured from the Sheltered and Back-Reef Stations. An attempt was made to select "mats" and "aggregates" typically found at each of the stations.

Removal Experiment

With dense "mats" of A. spicifera covering L. papillosa in the Acanthophora Zone, the growth of Laurencia may be reduced significantly. Six plots (0.3 m X 0.6 m) were selected in the Acanthophora Zone to determine if the "mats" of A. spicifera inhibited the growth of L. papillosa. Stations were selected away from biomass transects and at locations where the cover of A. spicifera was uniform. The assumption was made that the biomass of L. papillosa beneath the canopy of A. spicifera was also uniform throughout the plot. Prior clearings of A. spicifera in the Acanthophora Zone gave credibility to this assumption. One-half of each plot was then randomly selected by a toss of a coin and removed of all A. spicifera on 2 September 1979. For six months, the L. papillosa in the cleared plots was maintained free from A. spicifera. Then, both halves of the quadrat were harvested and compared for differences in the biomass of L. papillosa.

Holdfasts versus Uprights

To determine if survivorship in low light intensities was independent of thallus location, individuals of A. spicifera possessing uprights and their holdfasts were subjected to: (1) total darkness in 0.09-m diameter X 0.16-m tall vessels filled with seawater; (2) total darkness in two vessels (0.09-m diameter X 0.16-m tall) with seawater pumped through the vessels at a two- to three-minute turnover rate;

(iii) low light intensities beneath four "aggregates" of L. papillosa that were fitted to the open sides of four darkened vessels (0.09-m diameter X 0.08-m tall), submerged in seawater just below surface level, and sprayed with a jet of seawater. Each treatment involved the use of 30 to 50 plants. Seawater temperature remained between 26° and 29°C throughout the experiments. After 24 hours in treatment one, and two weeks in treatments two and three, fronds were removed from their containers, sectioned into uprights and holdfasts, placed into outdoor seawater tanks, and examined for new branches at the end of three weeks.

3.0 RESULTS

3.1 Measurements of Environmental Variables

Water Temperature (Maximum-Minimum)

Seawater temperature varied between reef-flat locations, with monthly maximum and minimum temperatures generally occurring in the Acanthophora Zone rather than in the Laurencia Zone (Fig. 13). Temperatures in the Acanthophora Zone ranged from 23° to 37°C , while those in the Laurencia Zone ranged from 25° to 37°C . From December to April (dry season), minimum temperatures occurred when solar irradiance was at a minimum and when wind-generated waves pushed cooler offshore waters onshore. Conversely, maximum temperatures coincided with wet-season aerial exposures that occurred from May to November.

Solarimetry

Maximum solar irradiance occurred from January to April and minimum irradiance occurred from June to November. In 1979, March had the highest daily average of solar irradiance ($2.19 \times 10^3 \text{ J cm}^{-2} \text{ d}^{-1}$). From April to June, solar irradiance decreased to $1.56 \times 10^3 \text{ J cm}^{-2} \text{ d}^{-1}$, followed by a moderate increase to a wet-season high of $1.83 \times 10^3 \text{ J cm}^{-2} \text{ d}^{-1}$ in September. Solar irradiance then diminished to a minimum of $1.37 \times 10^3 \text{ J cm}^{-2} \text{ d}^{-1}$ in November, the beginning of the dry

Figure 13. Monthly maximum and minimum temperatures within the Acanthophora and Laurencia Zones (June 1979-80). Thermometers were secured into pools at 0.5 m depth. (●) Acanthophora Zone; (○) Laurencia Zone.

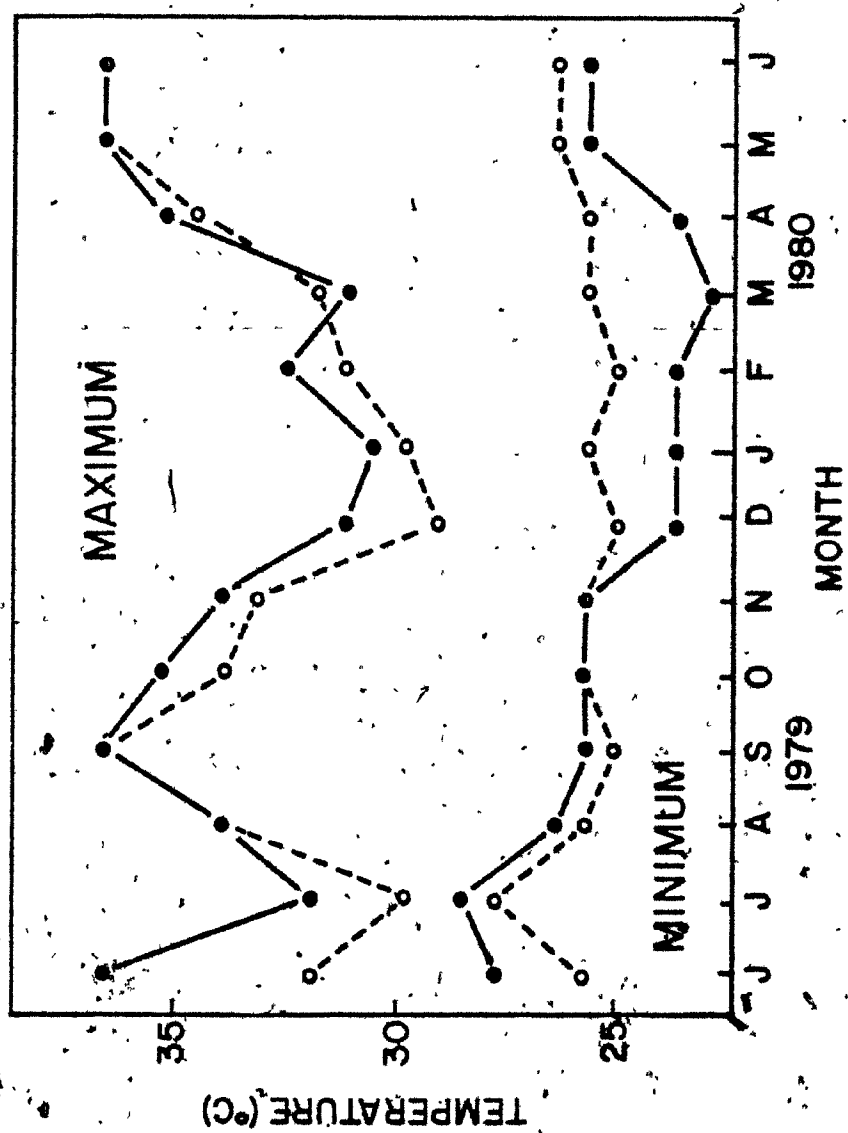
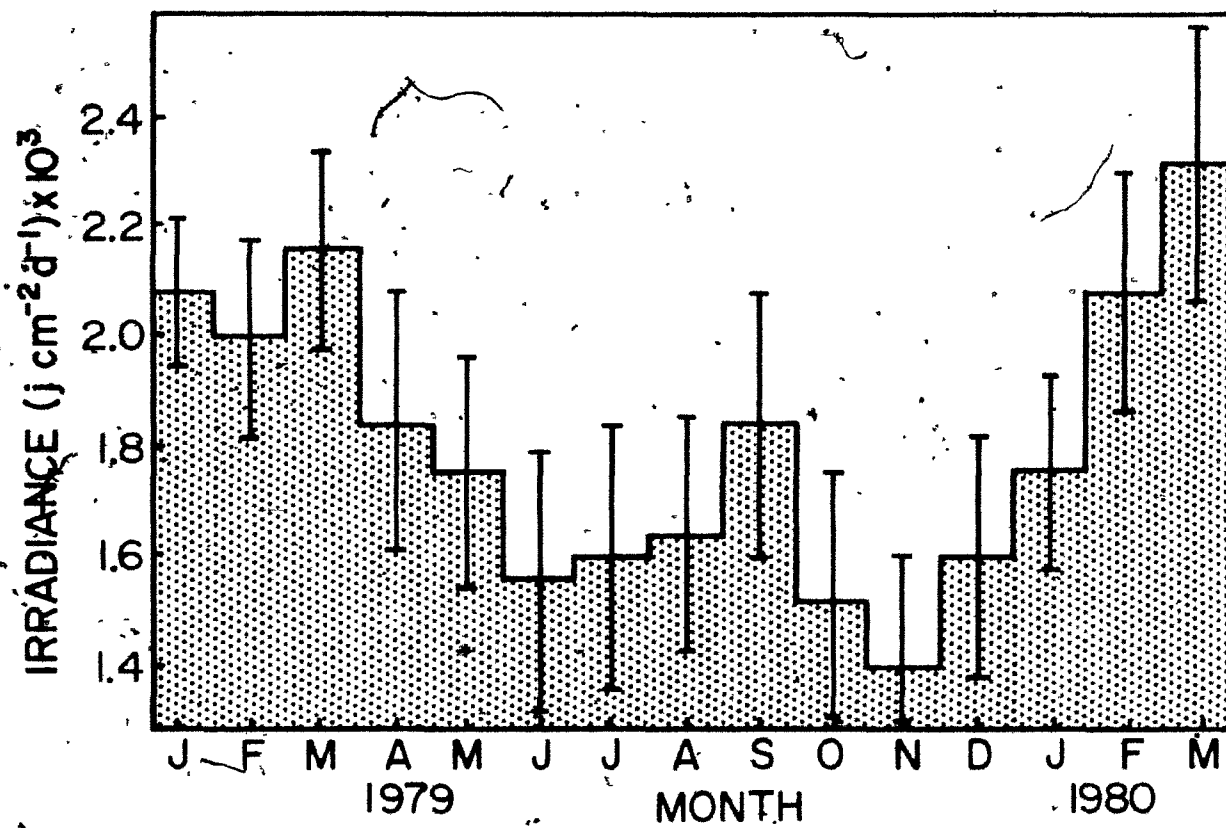


Figure 14. Solar Irradiance at Galeta Point, Panama (January 1979 to March 1980). Data were provided by J.D. Cubit, D. Windsor, and J. Thompson as part of the environmental monitoring data from Galeta Point, Smithsonian Institution Environmental Science Program, S.T.R.I. Vertical bars indicate $\pm$ the standard deviation. All values were converted from $\text{g cal cm}^{-2} \text{ h}^{-1}$ to $\text{J cm}^{-2} \text{ d}^{-1}$.



season. After November, solar irradiance increased to a maximum of about $2.30 \times 10^3 \text{ J cm}^{-2} \text{ d}^{-1}$ in February (Fig. 14).

Tidal Elevation and Aerial Exposures

In 1979 and 1980, the maximum tidal amplitude was 0.6 m at Galeta Point; 0.22 m was the minimum tidal elevation, as recorded on both 10 September 1979 and on 3 June 1980, while 0.82 m was the maximum tidal elevation, recorded on 19 December 1980. In general, the highest tides occurred during two periods: December through February; and July and August. Periods of low water that resulted in aerial exposures of the reef took place generally from May to November (Fig. 15).

Of the biotic zones on the reef flat, the Laurencia Zone was exposed the most frequently (Figs. 16 and 17). A typical aerial exposure averaged 5.2 hours in 1979 and 6.3 hours in 1980. In the Acanthophora Zone, aerial exposure averaged 4.3 hours in 1979 and 5.5 hours in 1980 and occurred in May and June (Fig. 18). When the Laurencia Zone is exposed in the air, seawater no longer flows over the reef surface. Accordingly, the Acanthophora and Thalassia Zones are either left in stagnant water or exposed in the air. In 1979 and 1980, such conditions prevailed for a maximum of 18 hours. The longest series of consecutive daytime exposures was 38 days in the Laurencia Zone and 9 days in the Acanthophora Zone. Daytime exposures were confined to two periods: May and June, and September and October. Nighttime exposures occurred primarily from September to November (Figs. 17 and 18).

Figure 15. Daily Tidal Elevation Range at Galeta Point, Panama (February 1979 to March 1980). Exposure in the air of the Laurencia Zone occurred at tide gauge elevations of below 0.30 m while those below 0.24 m exposed the Acanthophora Zone. Data were provided by J.D. Cubit, D. Windsor, and J. Thompson as part of the environmental monitoring data from Galeta Point, Smithsonian Institution Environmental Science Program, S.T.R.I.

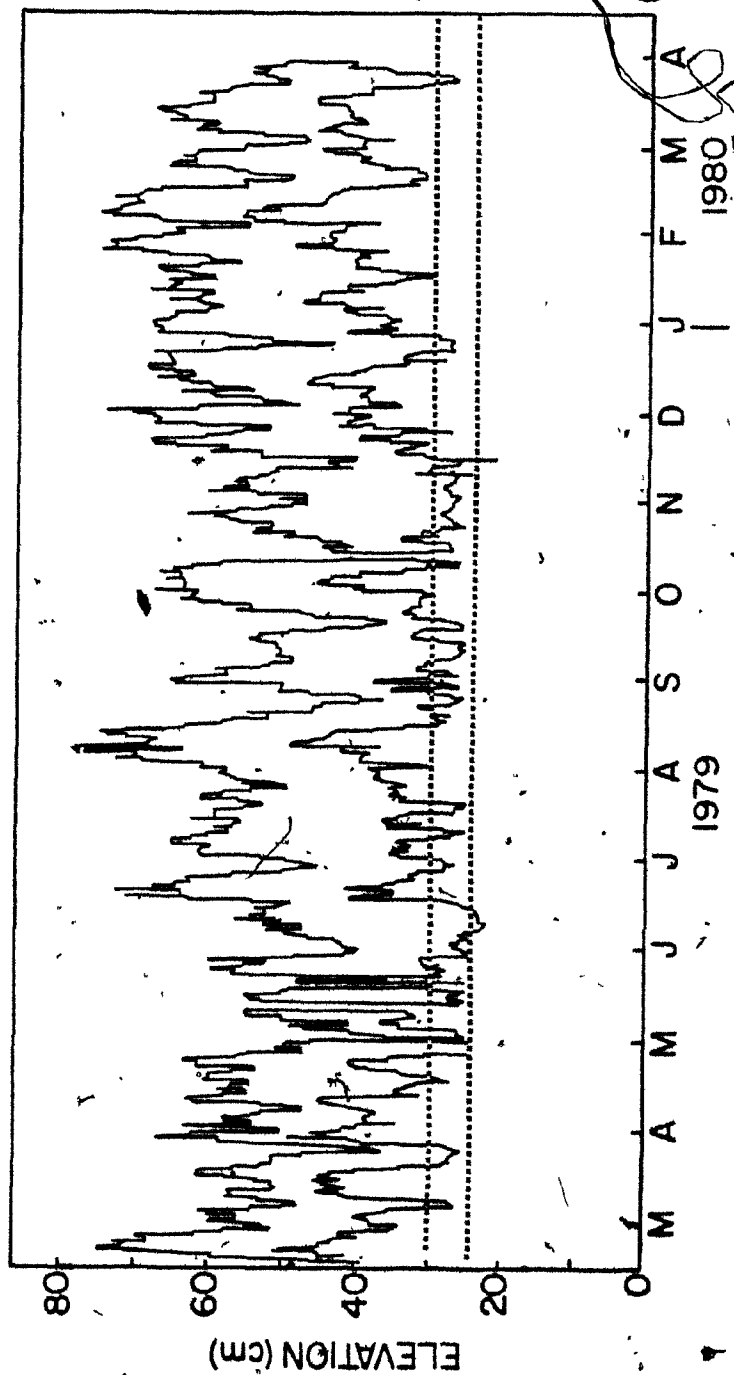


Figure 16. The frequency of Laurencia Zone exposures, in the air at Galeta Point, Panama (1979, 1980, and 1979-80 pooled data). Tidal elevation data were provided by J.D. Cubit, D. Windsor, and J. Thompson as part of the environmental monitoring data from Galeta Point, Smithsonian Institution Environmental Science Program, S.T.R.I.

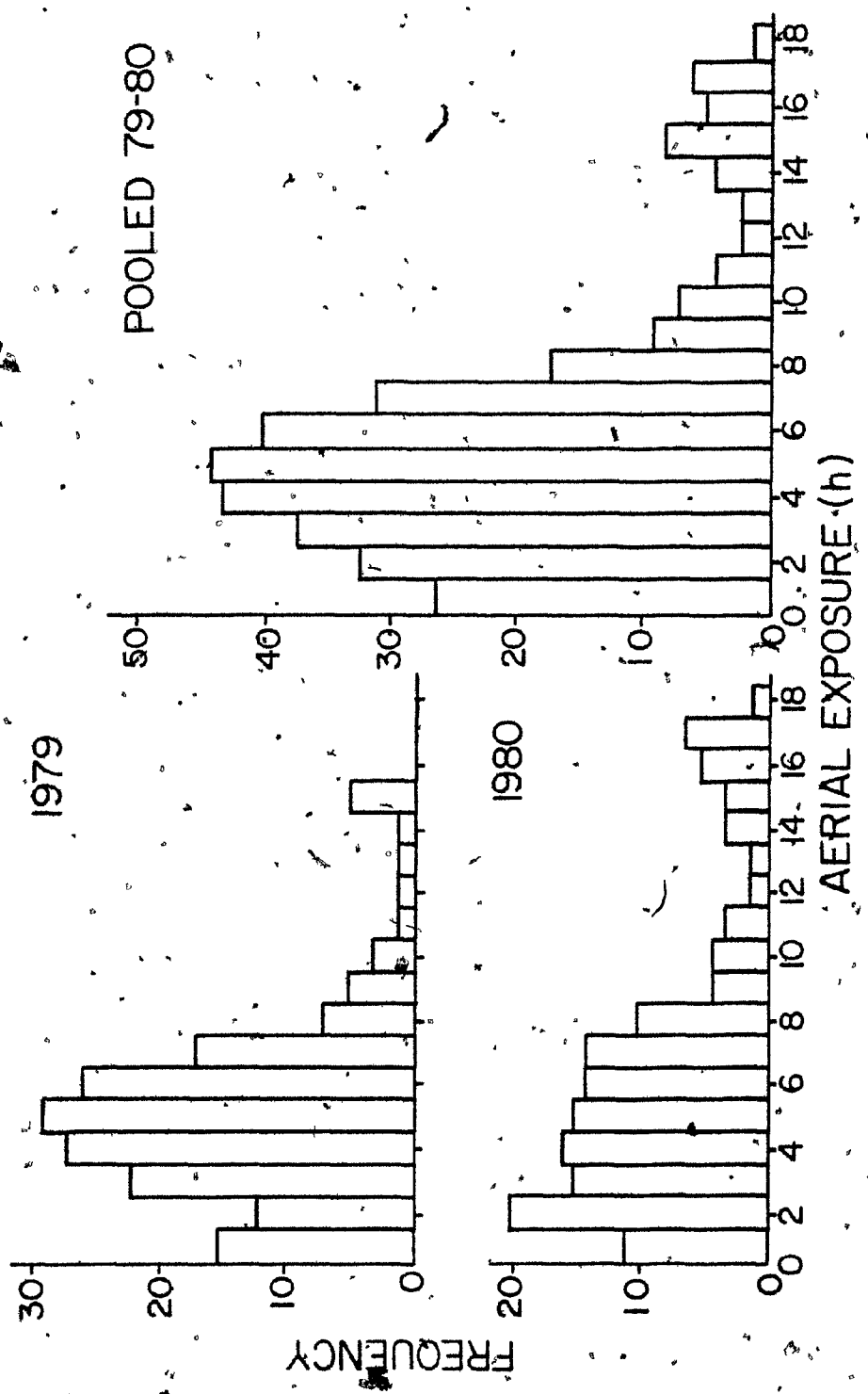


Figure 17. Daytime and Nighttime Aerial Exposures (h mo^{-1}) of the Laurencia Zone at Galeta Point, Panama (1979-80). Tidal elevation data were provided by J.D. Cubitt, D. Windsor, and J. Thompson as part of the environmental monitoring data from Galeta Point, Smithsonian Institution Environmental Science Program, S.T.R.I.

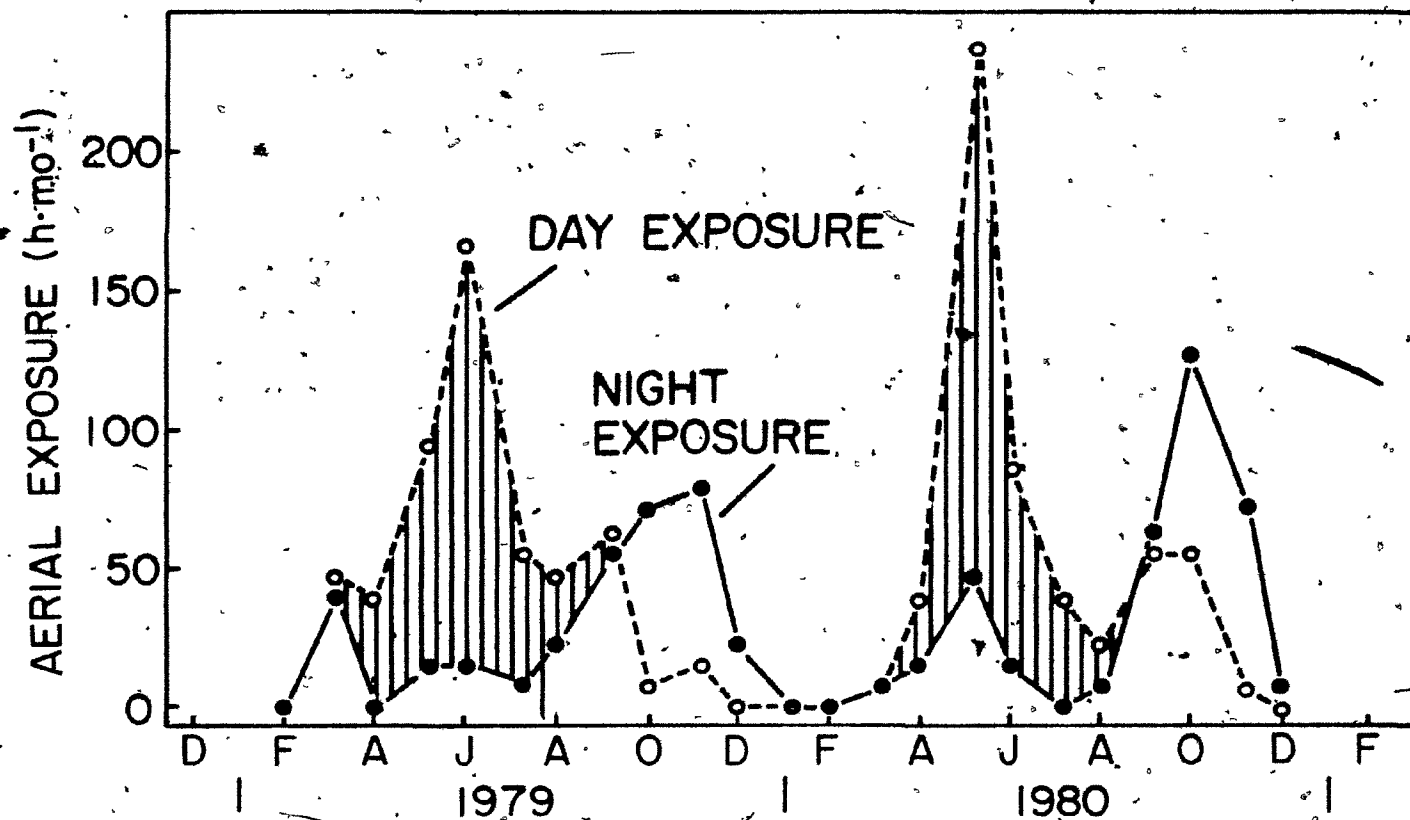
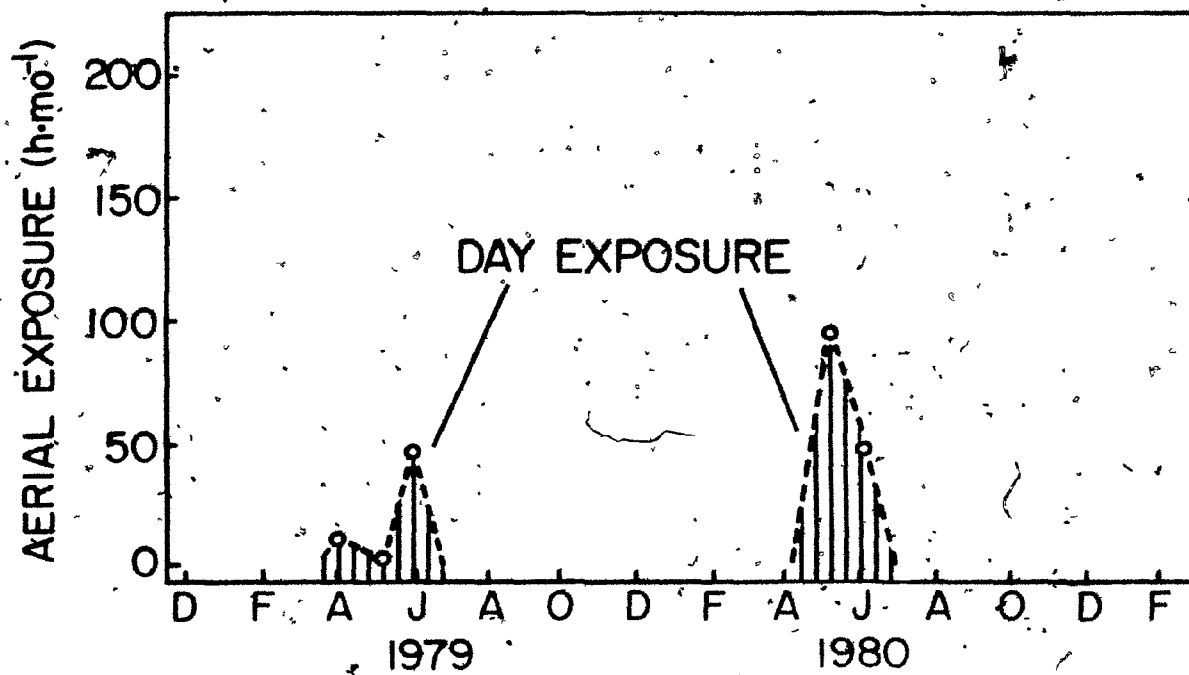


Figure 18. Daytime and Nighttime Aerial Exposures (h mo^{-1}) of the Acanthophora Zone at Galeta Point, Panama (1979-80). Tidal elevation data were provided by J.D. Cubitt, D. Windsor, and J. Thompson as part of the environmental monitoring data from Galeta Point, Smithsonian Institution Environmental Science Program, S.T.R.I.



Wave Exposure and Water Velocity

Wave-exposure gradients occurred along the fore-reef in the Laurencia Zone and from the Laurencia Zone into the Acanthophora Zone.

From 28 November to 12 December 1981, the wave forces (Newtons) that were exerted on 2.54-cm diameter spheres averaged 2.08 N at the Exposed Station, 1.25 N at the Moderately-Exposed Station, 0.88 N at the Sheltered Station, and 0.17 N at the Back-Reef Station; the differences in wave force at the Moderately-Exposed and the Sheltered Station were not significant (Table I). The Back-Reef Station, like the Sheltered Stations, was affected little by dry-season storms (Fig. 19). An increase in water depth during storms dampened the energy exerted on the reef surface.

At the fore- and back-reef stations, gradients of wave exposure measured by force meters were also indicated by measurements of water velocities. Water velocities were highest at the Exposed Station and lowest at the Back-Reef Station and were not significantly different between the Moderately-Exposed and Sheltered Stations (Table II and Figure 20). Velocities of water in the direction of incoming wave surge were higher than those in retreating water or backwash, and there was a net flow of water to the right of incoming wave surge (i.e., long shore current) with flow rates comparable to those of the backwash (Table II).

Water velocity in the direction of incoming wave surge had the most direct effect on algal populations, causing the fragmentation of A. spicifera and the removal of L. papillosa "aggregates" from the

Table I. Analysis of Variance Table evaluating wave force at the Exposed, Moderately Exposed, Sheltered, and Back-Reef Stations (November - December 1981). N = newton.

	df	ss	ms	F	P
Location	3	213229	71076	33.4	< 0.001
Error	41	87297	2129		
Total	44	300526			

(1)	Location	N	Force (N) $\bar{X}$	SD
	Exposed	9	2.08	0.89
	Moderately Exposed	12	1.25	0.29
	Sheltered	11	0.86	0.29
	Back-Reef	13	0.17	0.16

Vertical bars span groups that are not significantly different in exposure to wave force (Newman-Keuls Multiple Range Test $p < 0.05$).

Figure 19. Maximum force exerted by waves on 2.54-cm diameter sphere at the Exposed, Moderately-Exposed, Sheltered and Back-Reef Stations (29 November to 9 December 1981). (●) Exposed Station; (○) Moderately-Exposed Station; (▲) Sheltered Station; (△) Back-Reef Station.

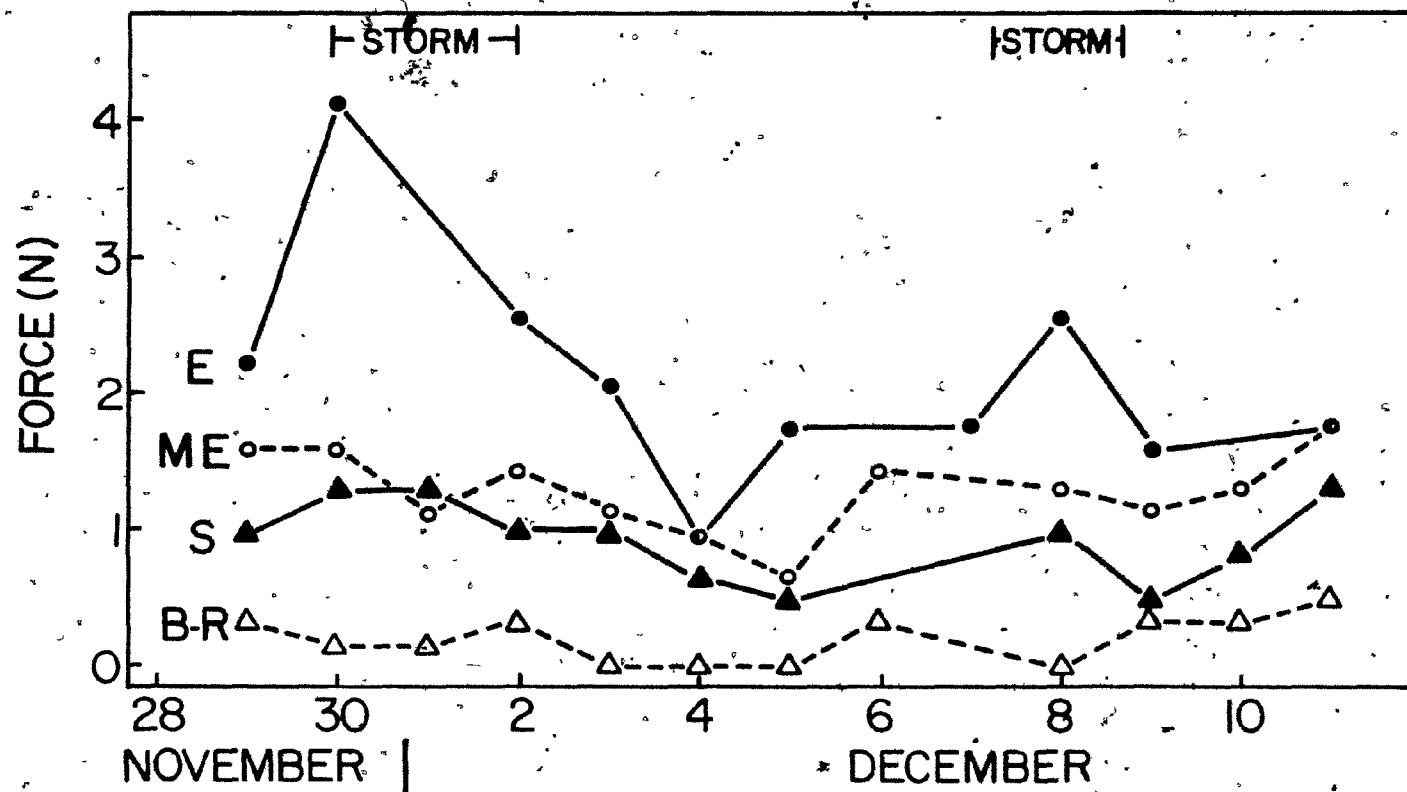


Table II. Two-way Analysis of Variance Table evaluating water velocity at the Exposed, Moderately Exposed, Sheltered, and Back-Reef Stations (November 1981).

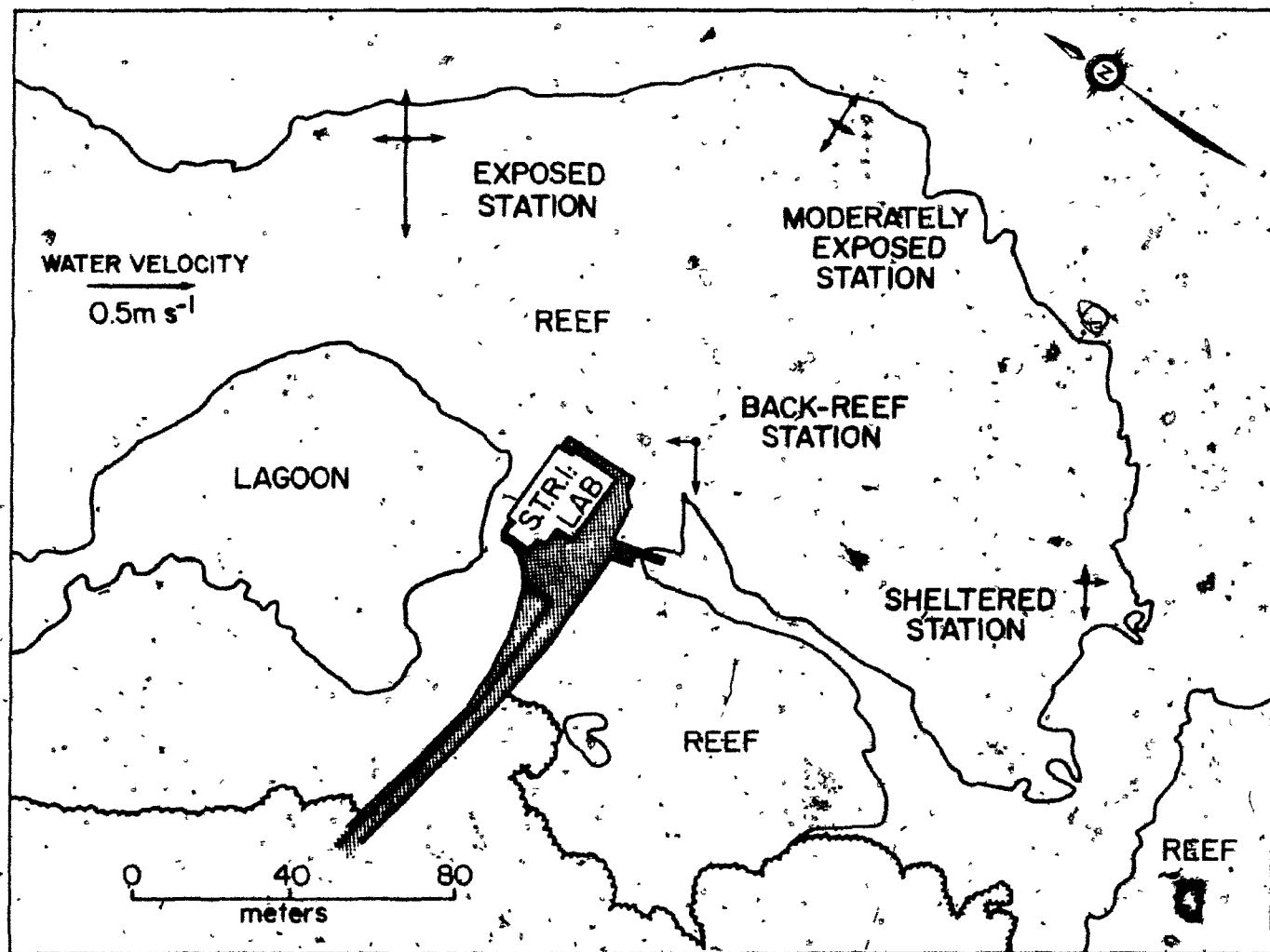
	df	ss	ms	F	p
Location	3	1.43	0.48	160.0	< 0.001
Direction	3	0.67	0.22	75.1	< 0.001
Error	240	0.71			
Total	255	4.44			

Current Direction:		Mean Current Velocity (m s^{-1})			
		1	2	3	4
Station:	Exposed	0.52	0.22	0.20	0.17
	Moderately Exposed	0.17	0.17	0.11	0.05
	Sheltered	0.02	0.14	0.20	0.07
	Back-Reef	0.21	0.00	0.00	0.14

(1) Vertical and horizontal bars span groups that are not significantly different in exposure to current velocities (Newman-Keuls Multiple Range Test, $p < 0.05$).

(2) Current direction: (1) is incoming wave surge, (2) is backwash, (3) is to the right of the station, and (4) is to the left of the station.

Figure 20. Mean velocity of water measured relative to incoming waves at the Exposed, Moderately-Exposed, Sheltered, and Back-Reef Stations (1 December 1981). Bar lengths (vectors) indicate the mean velocity and direction of water. Current velocities at each station were measured over a 15-min period during moderate, dry-season conditions.



substrata. Among fore-reef stations, water velocities were significantly different when measured in the direction of incoming wave surge; they decreased in intensity from the Exposed to the Sheltered Station (Table III). Water velocities averaged 0.52 m s^{-1} at the Exposed Station, 0.17 m s^{-1} at the Moderately-Exposed Station, 0.02 m s^{-1} at the Sheltered Station, 0.21 m s^{-1} at the Back-Reef Station. At the Back-Reef and the Moderately-Exposed Stations, water velocities were similar. These stations differed, however, in the type of water motion: the Back-Reef Station had a steady horizontal flow of water (current); and the Moderately-Exposed Station had a turbulent or violent flow of water that was generated by breaking waves.

Figure 21 shows measurements of water velocity taken throughout the reef flat during moderate sea conditions. On the reef flat, water velocities changed substantially over distances of a few meters (Fig. 21). Spill-off areas (locations where water was channelled off the reef) were detected in two fore-reef locations; here, water velocities frequently exceeded 0.7 m s^{-1} . In the back reef, current velocities were highest adjacent to the S.T.R.I. Laboratory, especially when large volumes of water surged over the reef flat. Water velocities of about 0.1 to 0.25 m s^{-1} normally occurred throughout the Acanthophora Zone and exceeded 0.64 m s^{-1} during some dry-season storms.

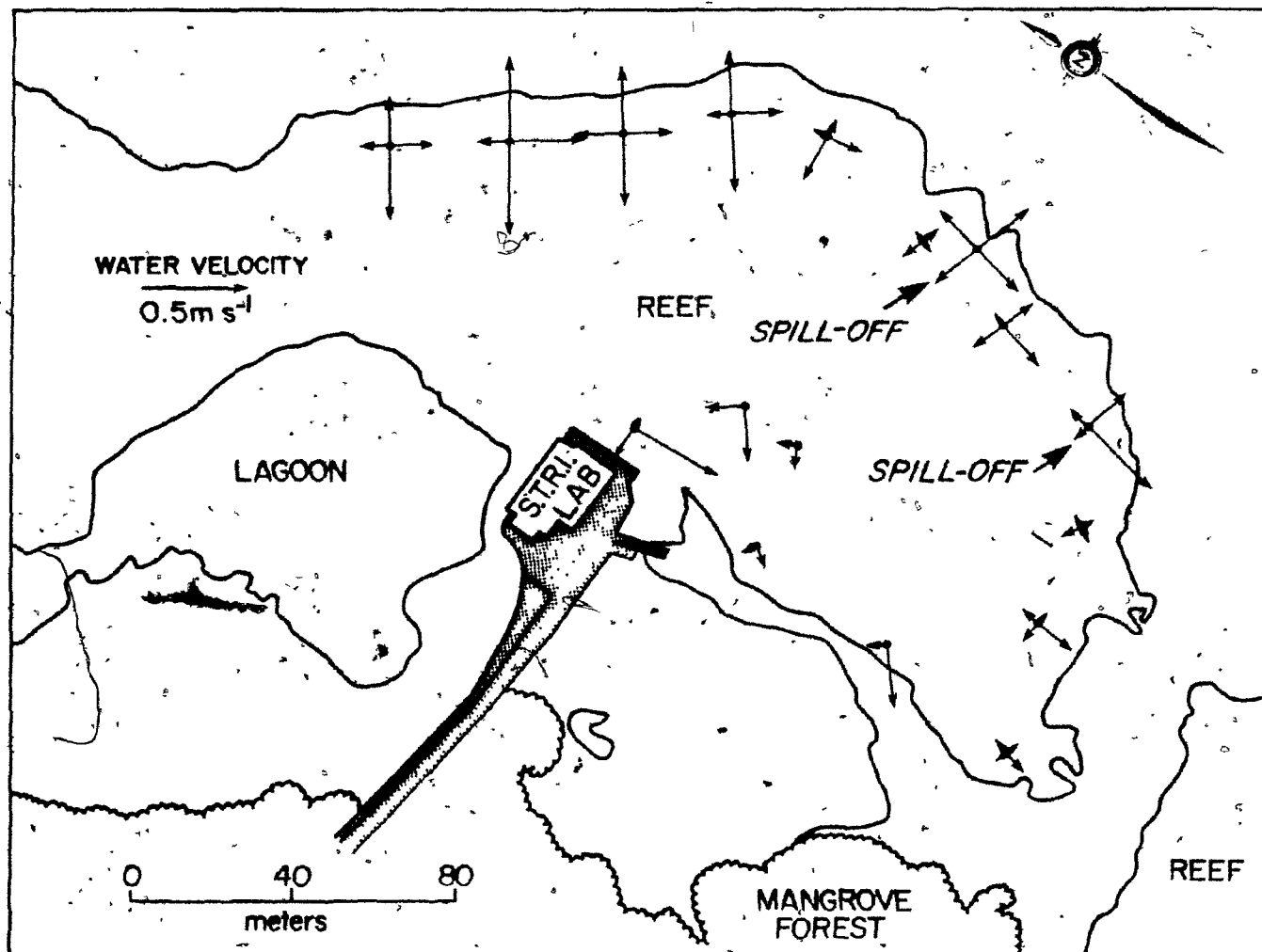
Table III. Analysis of Variance Table evaluating the water velocity of incoming wave surge at the Exposed, Moderately Exposed, Sheltered, and Back-Reef Stations (November 1981).

	df	ss	ms	F	p
Location	3	2.15	0.72	118.6	< 0.001
Error	60	0.36	0.01		
Total	63	2.52			

Location	N	Water Velocity (m s^{-1})	
		Mean	SD
Exposed	16	0.52	0.10
Back-Reef	16	0.21	0.11
Moderately Exposed	16	0.17	0.04
Sheltered	16	0.02	0.01

(1) Vertical bars span groups that are not significantly different in exposure to water velocity (Newman-Keuls Multiple Range Test, $p < 0.05$).

Figure 21. Mean velocity of water measured relative to incoming waves at selected locations on the reef flat at Galeta Point, Panama (5 December 1981). Bar lengths (vectors) indicate the mean velocity and direction of water. Current velocities at each station were measured over a 15-min period during moderate, dry-season conditions. Spill-off = A location where large volumes of water are channeled off the reef flat.

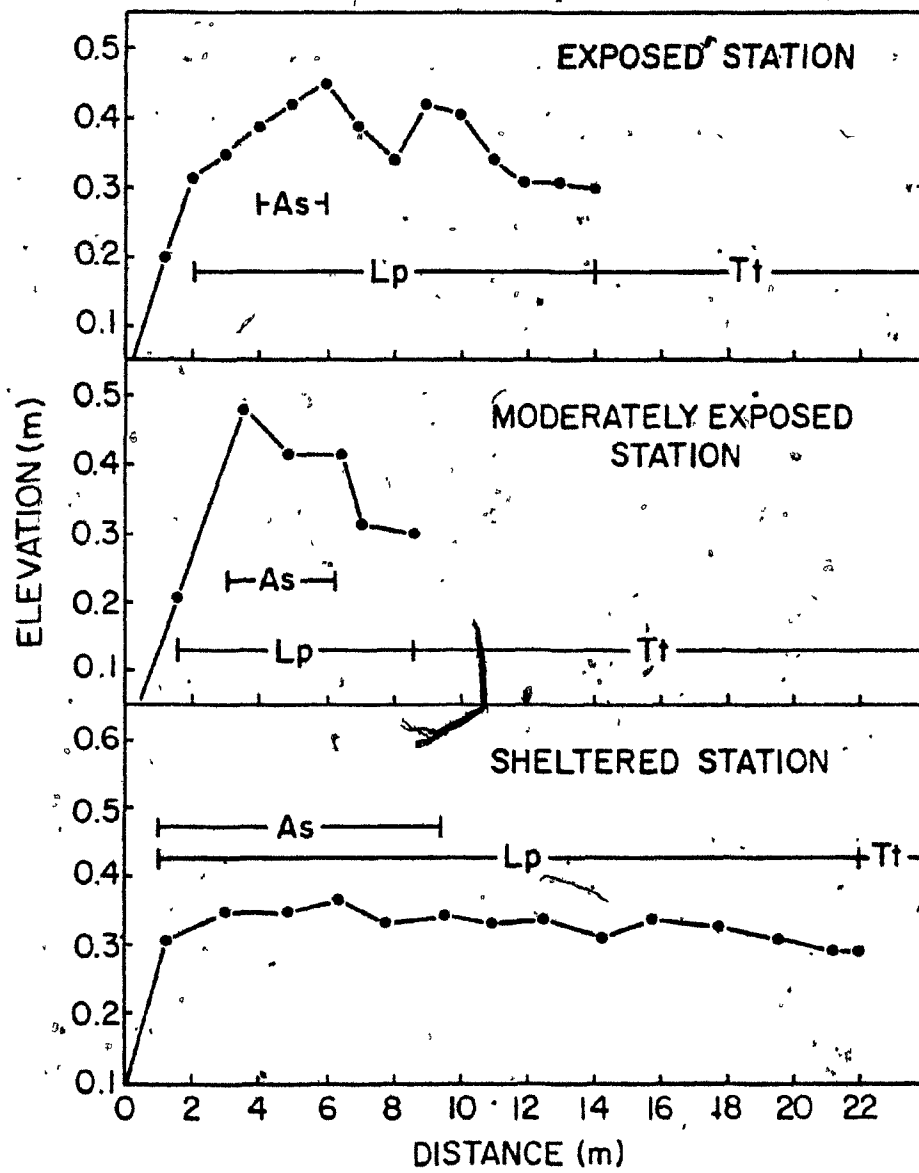


Fore-Reef Topography

The Exposed and Moderately-Exposed Stations were about 0.13 m higher in elevation than the Sheltered Station, and the Moderately-Exposed Station was a few centimeters higher in elevation than the Exposed Station (Fig. 22). The lower elevation of the Sheltered Station resulted from previous undercutting of the fore reef by an adjacent channel of water, which left large pieces of rubble on the reef slope. At the more exposed stations, logs regularly drifted ashore and abraded extensive areas of the fore reef, causing localized differences in reef elevation.

Substrate rugosity was significantly greater in the Laurencia Zone than in the Acanthophora Zone ($T = 10.73$, $df = 24$, $p < 0.001$). This unitless measurement of rugosity in the Laurencia Zone ($\bar{X} \pm SD$; 0.68 ± 0.11) was more than twice the estimate observed in the Acanthophora Zone ($\bar{X} \pm SD$; 0.31 ± 0.07). The greater rugosity of the Laurencia Zone was attributed to the numerous small depressions and crevices that occurred in the substratum. Otherwise a carpet of algae obscured the reef surface.

Figure 22. The distribution of A. spicifera and L. papillosa relative to reef elevation at the Exposed, Moderately-Exposed, and Sheltered Stations. Elevations are expressed relative to tide gauges at Galeta Point, Panama (September 1981). As = A. spicifera; Lp. = L. papillosa; Tt = T. testudinum.



3.2 The Fragmentation of A. spicifera

Spatial Distribution

A. spicifera was found predominantly in the Laurencia and Acanthophora Zones and displayed a spatial distribution on the reef flat similar to the distribution of L. papillosa (Figs. 23 and 24).

A. spicifera and L. papillosa occurred at the highest (Fig. 22) and lowest (Fig. 3) reef elevations. In the Laurencia Zone, A. spicifera occupied a narrow band within a much broader band of L. papillosa. As wave exposure diminished along the fore reef, the spatial distributions of both species expanded; this expansion, however, was not entirely uniform (Figs. 23 to 25), reflecting many microhabitat differences. As shown in Figure 22, the seaward margin of A. spicifera encroached upon that of L. papillosa as wave exposure decreased.

In the back reef, the distribution of A. spicifera was confined to the Acanthophora Zone or to beds of T. testudinum with coral rubble. In general, the Thalassia Zone contained little A. spicifera (Figs. 23 and 26). When T. testudinum was colonized by Centrocerus or Spyridia, however, A. spicifera was observed to recruit readily onto the Thalassia blades. In the back reef, L. papillosa had a wider distribution than A. spicifera (Figs. 23 and 24) and occupied most of the available hard substratum. L. papillosa served as the principal substratum for A. spicifera in the Acanthophora Zone.

Figure 23. Spatial distribution of A. spicifera on the reef flat at Galeta Point, Panama. Pooled data from Reef-Biomass Study (February 1979 to March 1980). Each mark indicates a location of a biomass sample containing A. spicifera.

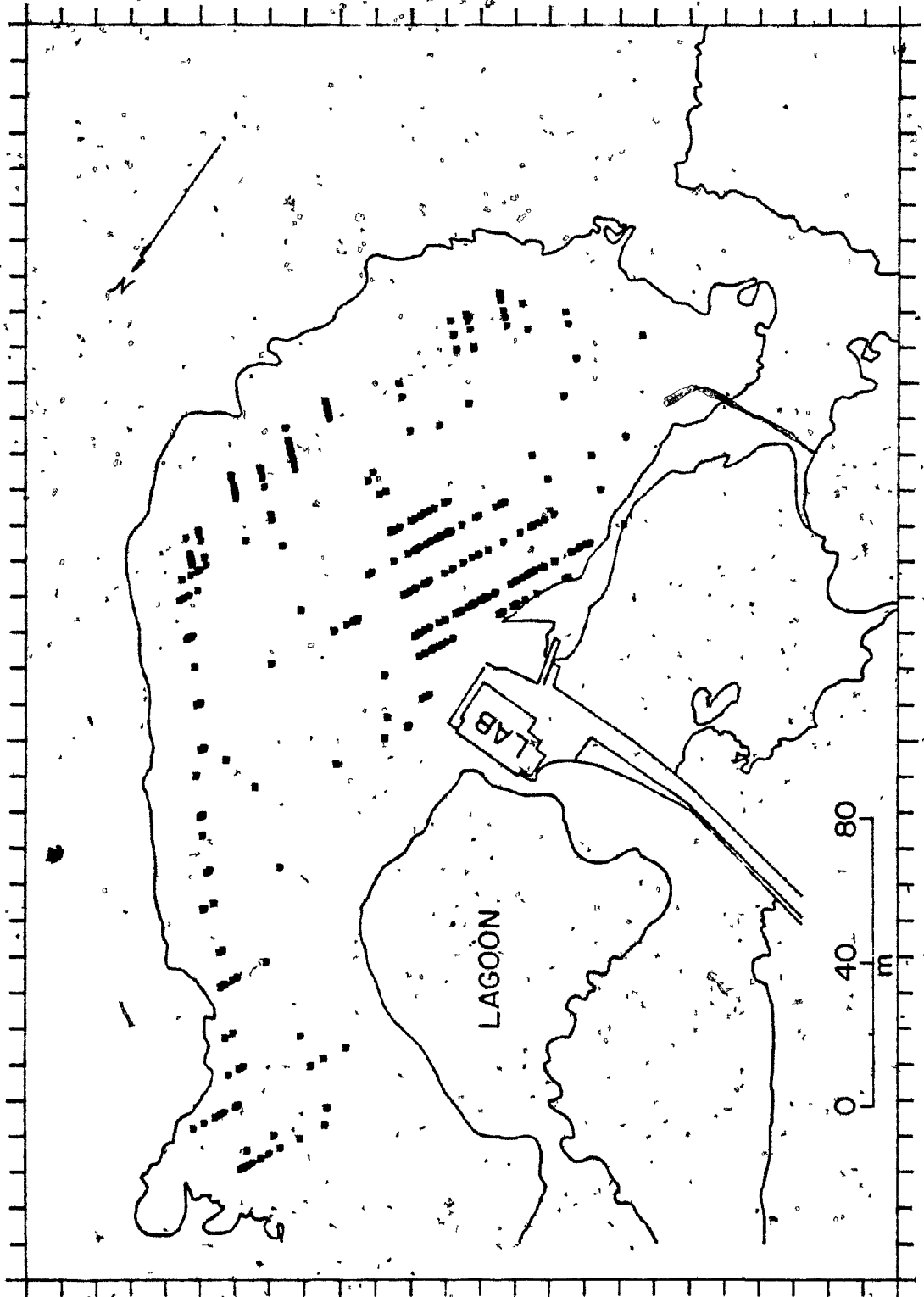


Figure 24. Spatial distribution of L. papillosa on the reef flat at Galeta Point, Panama. Pooled data from Reef-Biomass Study (February 1979 to March 1980). Each mark indicates a location of a biomass sample containing L. papillosa.

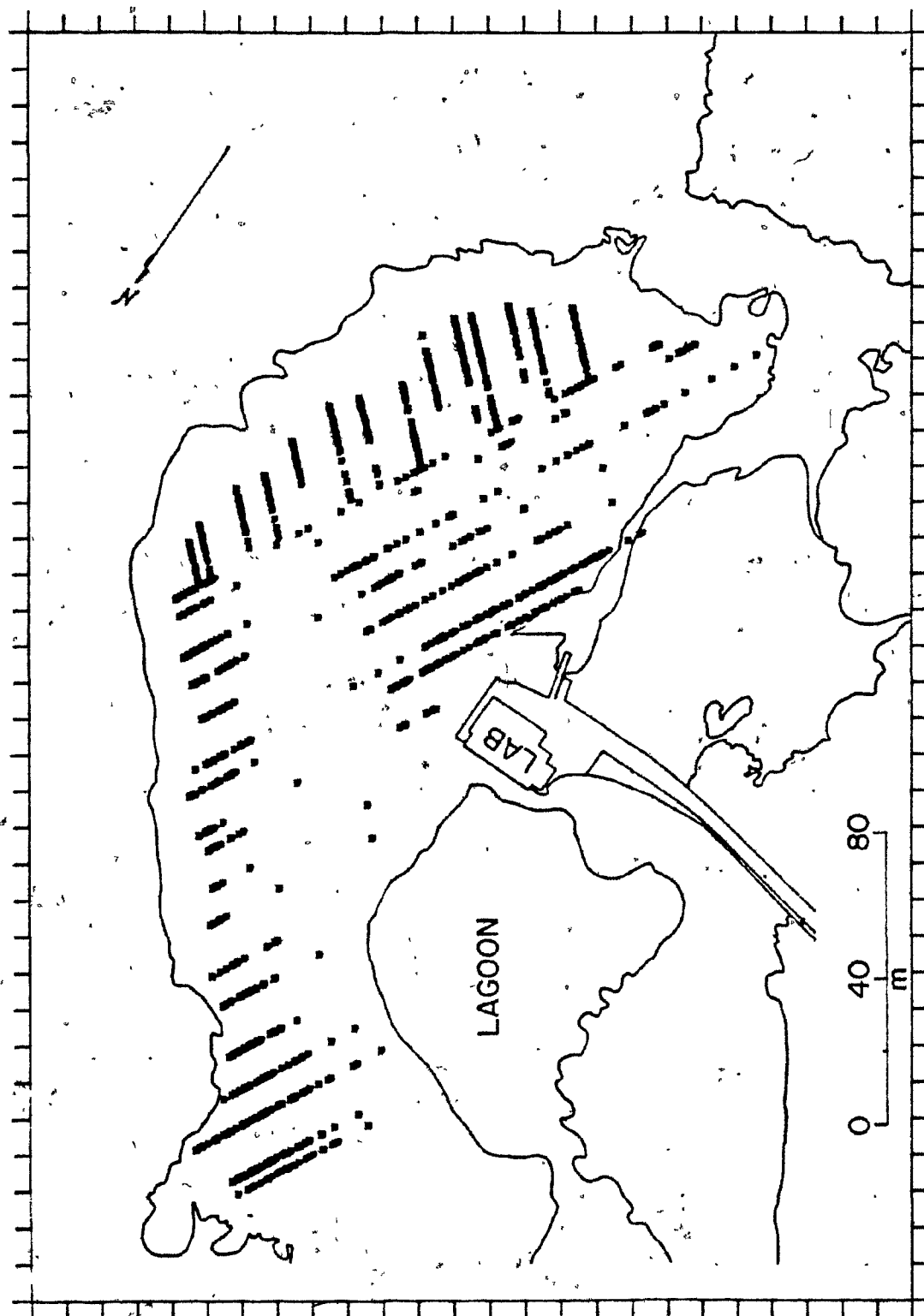


Figure 25. Distance in meters along Reef-Biomass Study and Wave-Exposure Station transects occupied by A. spicifera. Pooled data from Reef-Biomass Study (February 1979 to March 1980) and Wave-Exposure Stations (September 1981). E = Exposed Station; ME = Moderately-Exposed Station; S = Sheltered Station

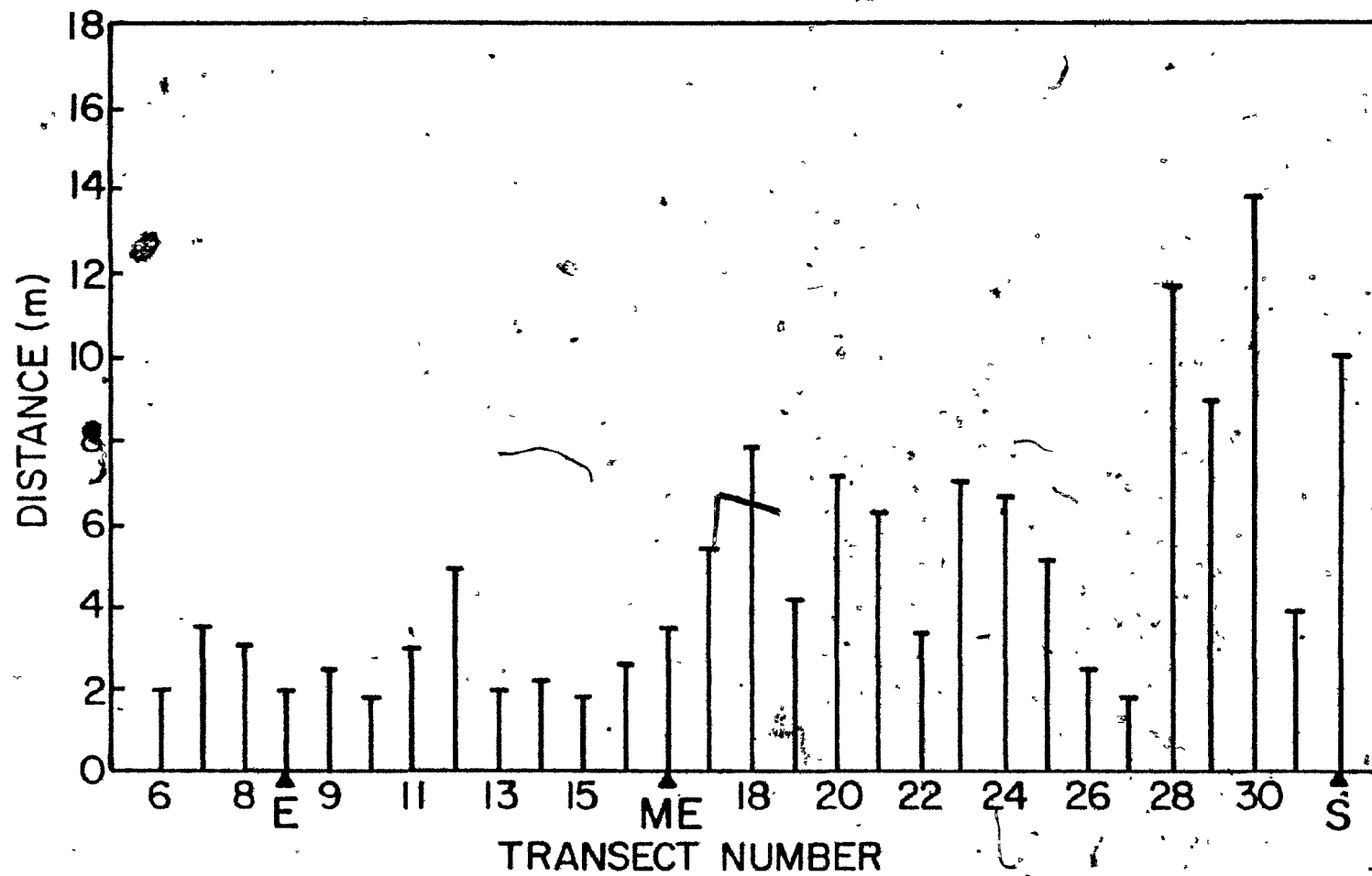
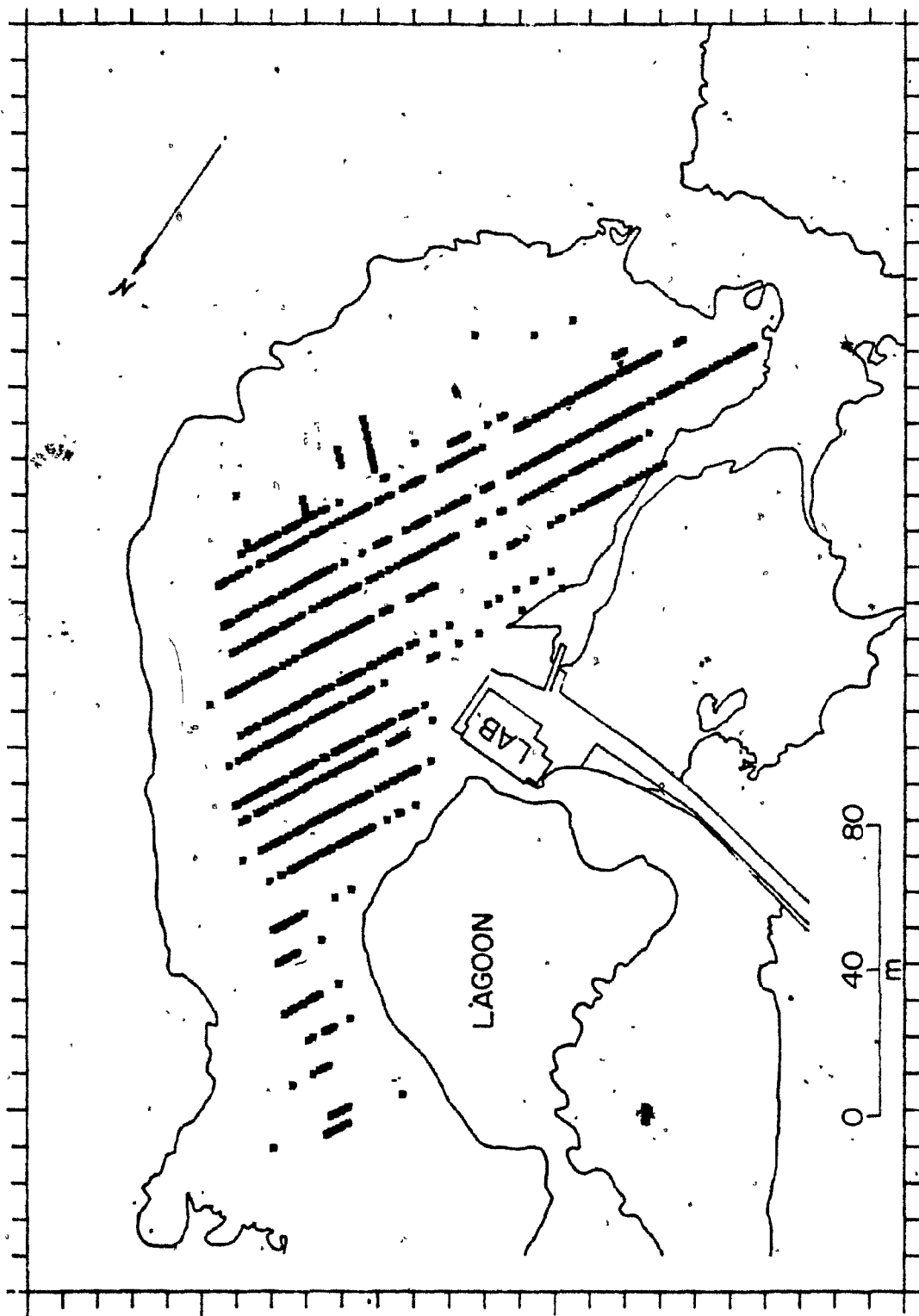


Figure 26. Spatial distribution of T. testudinum on the reef flat at Galeta Point, Panama. Pooled data from Reef-Biomass Study (February 1979 to March 1980). Each mark indicates a location of a biomass sample containing T. testudinum.

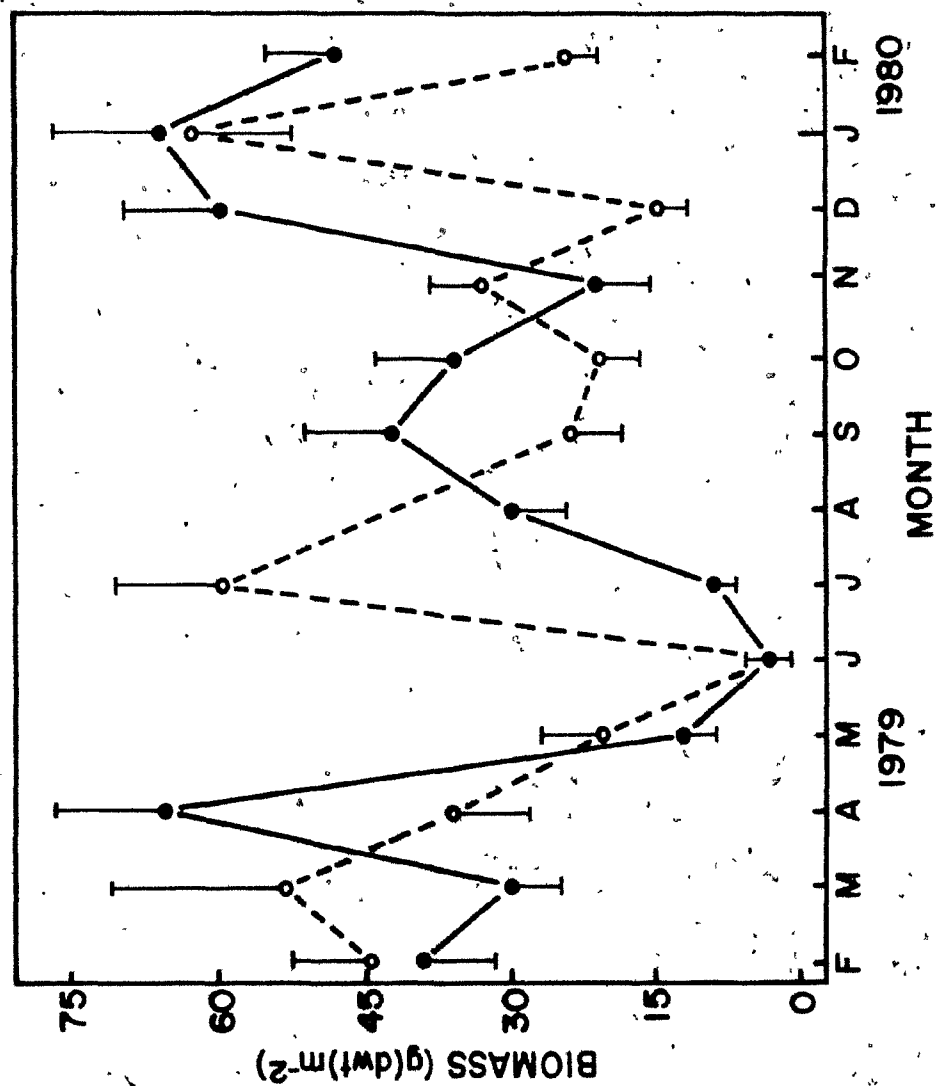


Seasonal Abundance

From February to August 1979, there was generally a greater biomass of A. spicifera in the Laurencia Zone than in the Acanthophora Zone. Conversely, from September 1979 to February 1980, there was a greater biomass of A. spicifera in the Acanthophora Zone than in the Laurencia Zone (Fig. 27). Also, increases in the biomass of A. spicifera in the Laurencia Zone generally preceded increases in the biomass of A. spicifera in the Acanthophora Zone.

From February to April 1979, conditions for the growth of A. spicifera were favourable (i.e., periods of maximum solar irradiance and minimum aerial exposures [Figs 14, 15, and 27]). A. spicifera obtained a maximum biomass of 64.6 and 53.8 g (d wt) m⁻² in the Acanthophora and Laurencia Zones, respectively. When aerial exposures were most intense (May-June), the abundance of A. spicifera was at a minimum. At that time, most uprights of A. spicifera were killed and removed from the plant, with only the holdfast of the plant remaining. Healthy plants were found only in areas splashed by waves. After June, A. spicifera in the Laurencia Zone rapidly recovered from the aerial exposures and increased to 59.0 g (d wt) m⁻² by July. The biomass of A. spicifera in the Acanthophora Zone, however, increased at a slower rate to 42.2 g (d wt) m⁻² by September. With the onset of the dry season, A. spicifera was again reduced to low abundance (about 25 g (d wt) m⁻²) both in the Acanthophora and Laurencia Zones, but later returned to maximum levels (about 66 g (d wt) m⁻²) by January.

Figure 27. Seasonality of A. spicifera biomass in the Laurencia and Acanthophora Zones (February 1979-80). Vertical bars indicate + or - one standard deviation from the mean. $n = 100$ for each point in the Acanthophora Zone (●). $n = 50$ for each point in the Laurencia Zone (○).



In February, stormy seas reduced the abundance of A. spicifera in the Laurencia Zone, but had little effect on A. spicifera in the Acanthophora Zone (Fig. 27).

Drift Sampling

It was deduced from recaptured tags that a sampling area of 1.32 ha remained stable throughout varied sea conditions. The five nets collected drift materials from roughly equivalent sampling areas; net 4 sampled the largest area of 4988 m² and net 3 sampled the smallest area of 3330 m² (Table IV and Fig. 28). The largest portion of the Laurencia Zone was sampled by net 5 (893 m²) and the smallest portion was sampled by net 3 (350 m²). As shown in Figure 28, tags that were released into the fore reef and captured by the nets were funnelled into the back reef. Nets 1, 2, and 3 sampled fore-reef areas from the Exposed to the Moderately-Exposed Stations, and Nets 4 and 5 sampled from the Moderately-Exposed Station to the Sheltered Station.

Nets 1, 2, and 3 collected 83% of the drift biomass, which included 90% of the drift Acanthophora. The sampling areas of these three nets included the entire Acanthophora Zone and delimited a narrow strip of reef through which most drift material passed (Tables V and VI, and Fig. 29). As drift biomass included many calcareous algae, and seeds, branches, and leaves of higher plants, A. spicifera constituted only 6.1% of the collected biomass. When drift materials were restricted to only reef-flat biota, T. testudinum, L. papillosa, and

Table IV. ² Sampling area of each net collecting drift biomass. Marked tags (45 mm pieces of Surveyor's Tape) were released from predetermined locations on the reef flat. Tags collected by the nets defined the sampling area.

Net no.	Laurencia Zone Sampled (m ²)	Total Sampling Area (m ²)
1	426	4719
2	382	4341
3	350	3330
4	530	4988
5	892	3378
Total 1-5	196	13,216 m ² = 1.32 ha.

Figure 28. Sampling area of each net collecting drift biomass. In different sea conditions, marked tags (45 mm² pieces of Surveyor's Tape) were released along two transects at predetermined locations. Tags collected by the nets defined the sampling area.

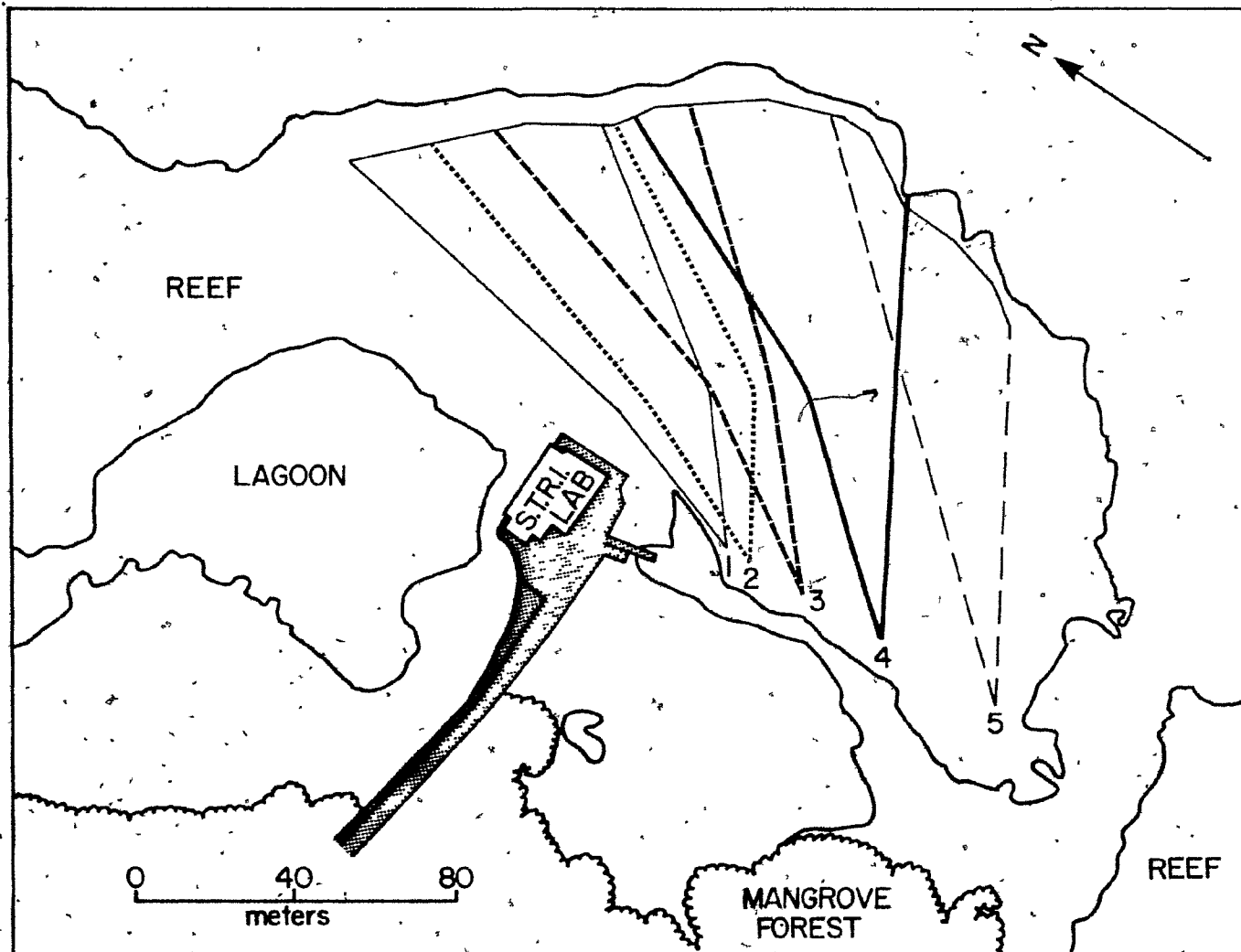


Table V. Analysis of Variance Table evaluating Total Biomass collected by Drift Nets (January 1979 to March 1980).

	df	ss	ms	F	p
Sampling Net	4	4355866	1088966	12.9	< 0.001
Error	315	26615349	84493		
Total	319	30971215			

Net no.	N	Total Biomass g (d wt)	
		Mean	SD
1	64	420	353
2	64	375	309
3	64	388	385
4	64	223	195
5	64	114	127

(1) Vertical bars span groups that are not significantly different in abundance (Newman-Keuls Multiple Range Test $p < 0.05$).

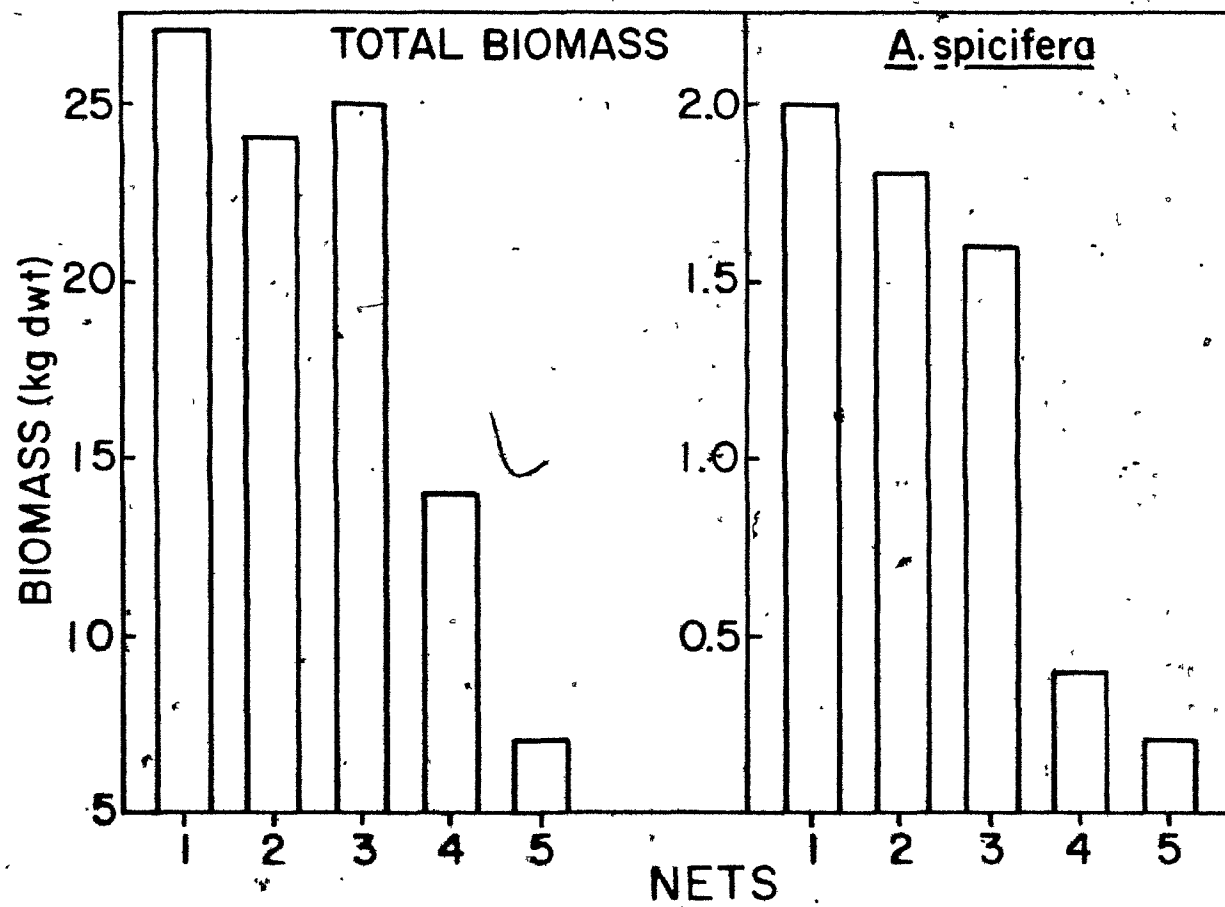
Table VI. Analysis of Variance Table evaluating A. spicifera collected in Drift Nets (January 1979 to March 1980).

	df	ss	ms	F	p
Sampling Net	4	43418	10854	15.5	< 0.001
Error	315	220488	700		
Total	319	263906			

Net no.	N	* <u>A. spicifera</u> Biomass g (d wt)	
		Mean	SD
1	64	30.9	41.4
2	64	27.8	31.5
3	64	25.2	26.4
4	64	6.7	9.1
5	64	2.5	4.3

(1) Vertical bars span groups that are not significantly different in abundance (Newman-Keuls Multiple Range Test $p < 0.05$).

Figure 29. Total Biomass and A. spicifera Biomass collected in Drift Nets (1 February 1979 to 31 March 1980). Five permanently fixed nets (0.91-m high X 0.46-m wide) continuously sampled drift as it was removed by a unidirectional current from the reef flat.



A. spicifera were the major components in decreasing order of abundance. Noteworthy was the observation that more L. papillosa was removed from the reef in large clumps (i.e., "aggregates") than as single fronds. In October and November, "mats" of A. spicifera were similarly torn from their substrata at the Sheltered and Back-Reef Stations.

Nets collected between 0.8 % and 3.6 % of the released tags, with a mean tag capture of 1.8 % (Table VII). Using 1.8 % as the collection efficiency of the nets, the total biomass of a species lost from the 1.32 ha sampling area was estimated. A maximum of about 245 kg (d wt) m^{-1} of algae was removed from the reef flat in February 1979, with L. papillosa being the major component, followed by A. spicifera. In general, more biomass of L. papillosa and A. spicifera was torn from the reef flat during the dry season than the wet season. L. papillosa lost more biomass from the reef flat than A. spicifera from January to July; A. spicifera, however, lost more biomass than L. papillosa from July to October. From November to March, more drift biomass of L. papillosa than of A. spicifera was collected. These cycles of biomass suggest that: during periods of intense wave-action (dry season), more biomass of L. papillosa than A. spicifera is removed from the reef flat; and, during periods of calm seas and minimum aerial exposures (July-October), more A. spicifera than L. papillosa is removed from the reef (Fig. 30).

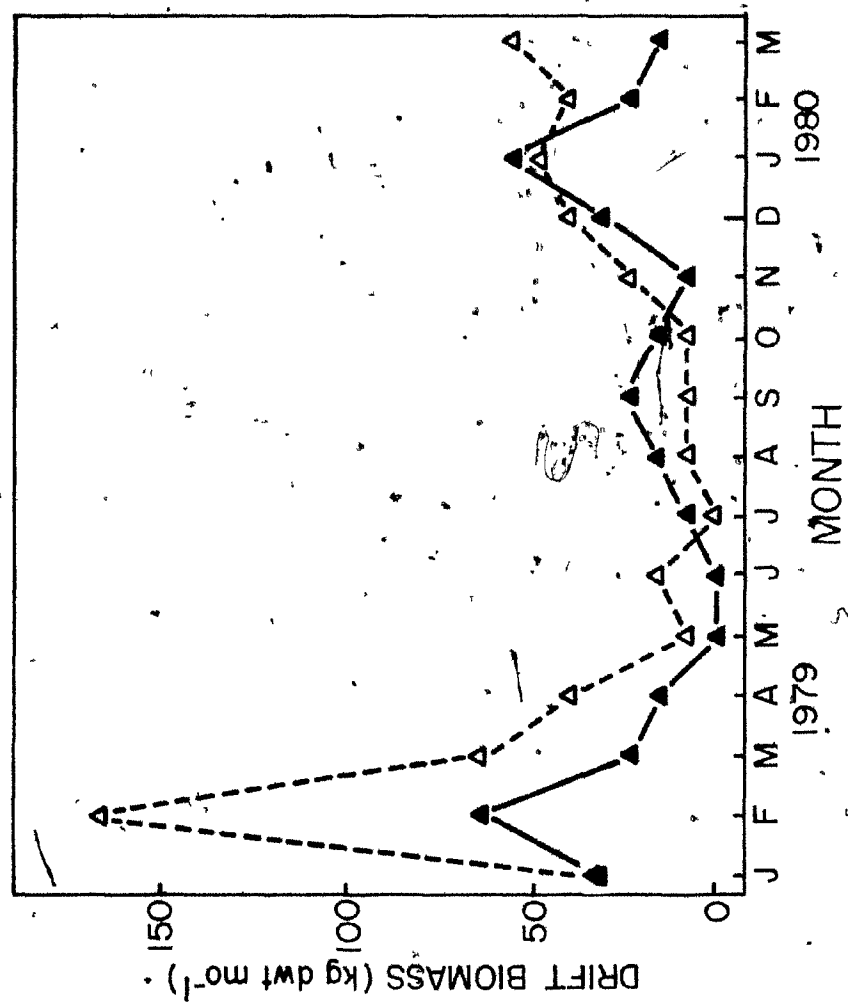
When the drift biomass of A. spicifera and L. papillosa was each standardized to one square meter of that species and expressed as wet weight, A. spicifera sustained greater losses of biomass than

Table VII. Sampling Efficiencies of Drift Nets based upon the release and capture of tags during different sea conditions.

Date	Transect	Sea State	Tags Released	Tags Captured	Efficiency
1/14/80	O	C	2600	39	0.015
1/23/80	O	C	1150	22	0.019
1/23/80	I	C	800	17	0.021
2/8/80	O	H	1400	47	0.036
2/8/80	I	H	800	8	0.010
3/7/80	O	M	1400	19	0.014
3/7/80	I	M	850	7	0.008
Capture Efficiency ($\bar{X} \pm SD$)					= 0.018 $\pm$ 0.009

- (1) O = Outer Reef Transect, I = Inner Reef Transect
 (2) Sea State: H = Heavy, M = Moderate, C = Calm

Figure 30. Biomass of A. spicifera and L. papillosa removed from the reef flat at Galeta Point, Panama (1 February 1979 to 31 March 1980). (Δ) L. papillosa; ($\blacktriangle$) A. spicifera.



L. papillosa. As A. spicifera has 5% more water per unit dry weight than L. papillosa, these data were expressed as wet weight to achieve a closer approximate of the quantity of drift in the water. As shown in Figure 31, A. spicifera had maximum losses of about 570 g (w wt) $m^{-2} mo^{-1}$ in February and September 1979 and January 1980. L. papillosa lost most of its biomass in February 1979 (360 g (w wt) $m^{-2} mo^{-1}$); for the rest of the year, maximum losses of L. papillosa were comparable with minimum losses of A. spicifera (105 g (w wt) $m^{-2} mo^{-1}$ [Fig. 31]). (See Appendix II and III for further sampling information.)

Growth

Monthly Determinations

With the exception of May, June, and July, A. spicifera grew at a rate of between 3.5 and 2.0 $mm d^{-1}$ (Fig. 32). For the 12-month period, fragments in the Laurencia Zone averaged 2.8 $mm d^{-1}$, while those in the Acanthophora Zone averaged 2.9 $mm d^{-1}$; these differences were not significant (ANOVA, $F = 0.44$, $p > 0.05$). Hence, the growth rate of fronds that were collected from the Laurencia Zone did not differ when measured for growth in the Acanthophora and Laurencia Zones. In May, growth decreased to 1.3 $mm d^{-1}$ in the Laurencia Zone and to 2.2 $mm d^{-1}$ in the Acanthophora Zone; this was presumably the result of increased seawater temperatures (Figs. 13 and 63). Periods of maximum growth

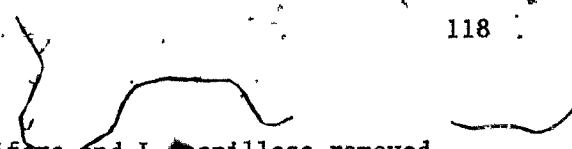


Figure 31. Biomass of A. spicifera and L. papillosa removed from the reef flat of Galeta Point, Panama, when the drift biomass of a species was standardized to a square meter and expressed as wet weight (1 February 1979 to 31 March 1980). (▲) L. papillosa; (▲) A. spicifera.

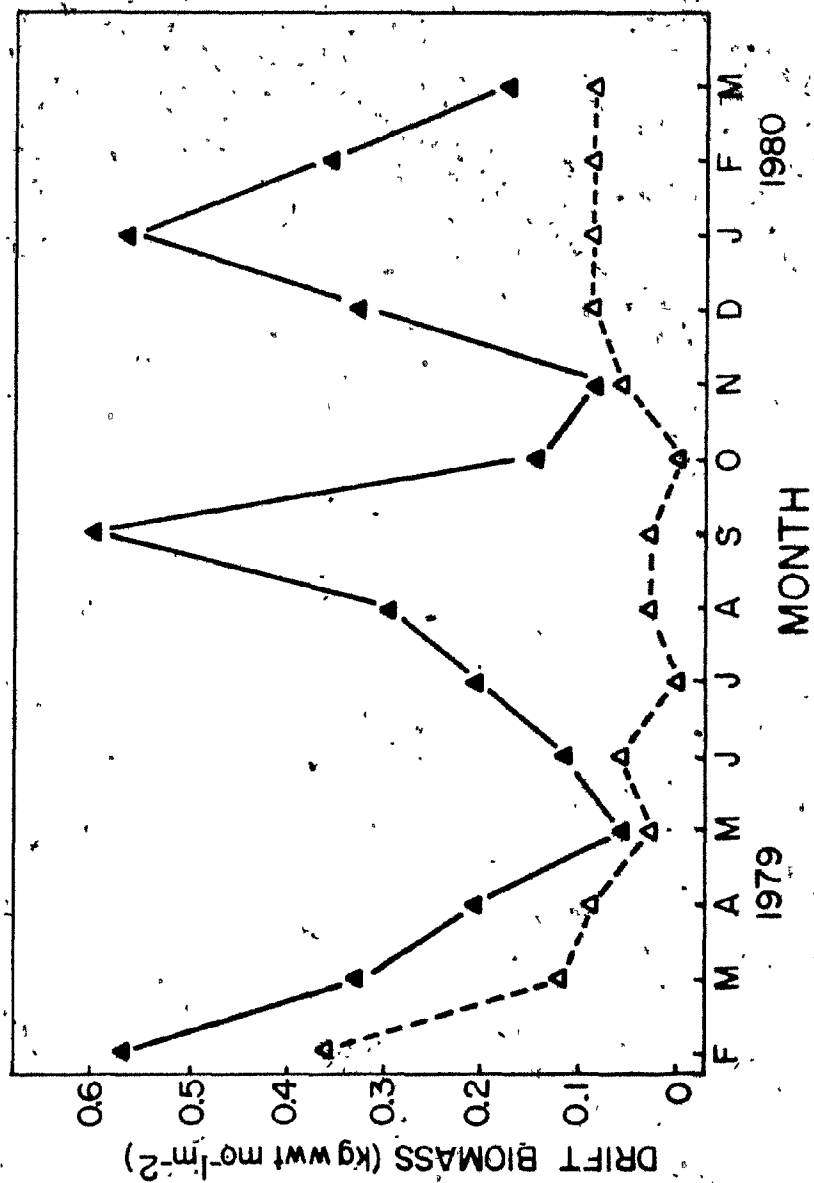
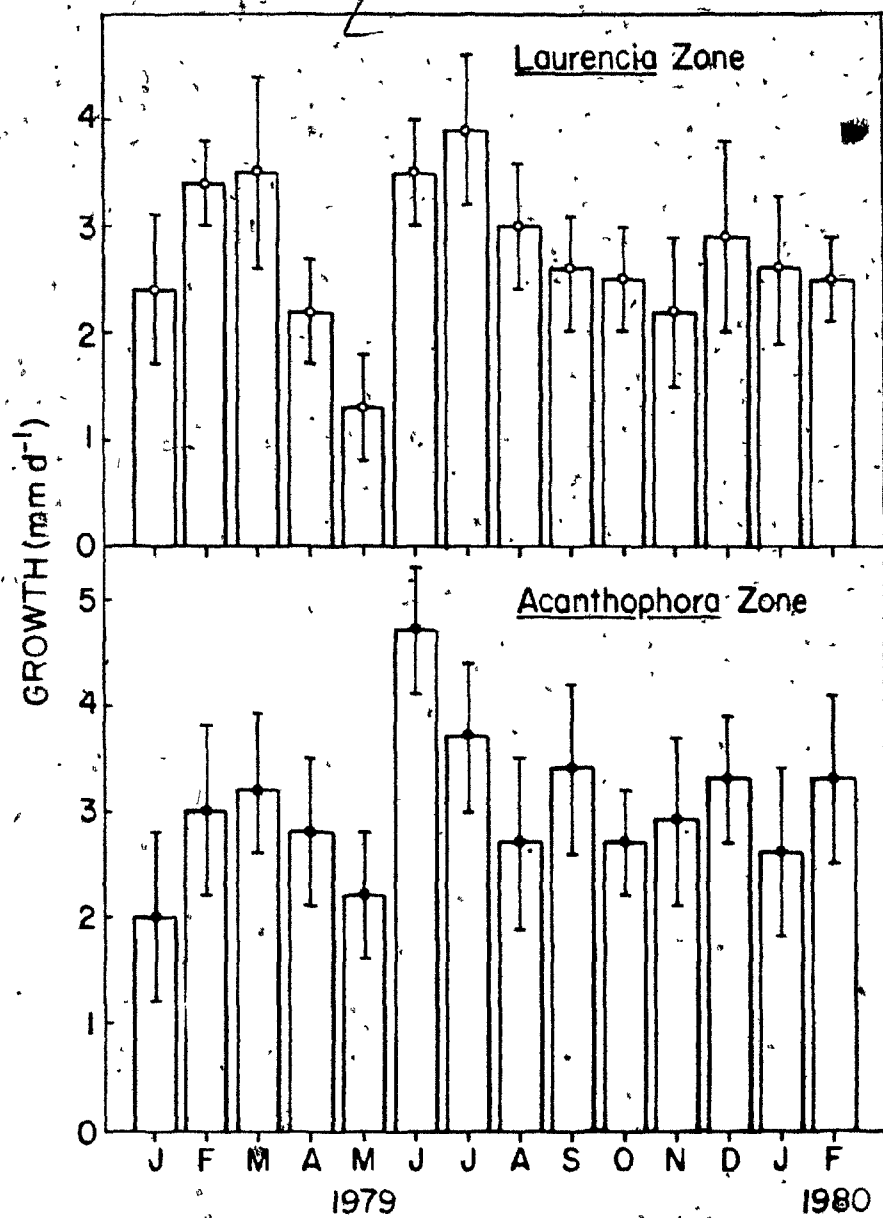


Figure 32. Seasonality of A. spicifera growth in the Acanthophora and Laurencia Zones. All fragments were collected from the Laurencia Zone. Vertical bars indicate $\pm$ one standard deviation from the mean. $n = 40$ for each point.



occurred in July in the Laurencia Zone (3.9 mm d^{-1}) and in June in the Acanthophora Zone (4.7 mm d^{-1}).

Reciprocal Growth Experiment

In February and August 1979, a reciprocal growth experiment was done using fronds of A. spicifera from the Acanthophora and Laurencia Zones. As shown in Table VIII, the growth of A. spicifera depended on the location from which the fronds were collected (Acanthophora and Laurencia Zone fronds) and the period of measurement (February and August). Station effects (Acanthophora and Laurencia Zone) were not significant. In February and August, the growth rate of fronds collected from the Acanthophora Zone was greater than that of those collected from the Laurencia Zone (Table VIII). Also, the growth rate of fronds was significantly greater in February than in August. With no significant station effects, the growth data of plants that were collected from the same location were pooled. The growth of A. spicifera from the Acanthophora Zone averaged 4.8 mm d^{-1} in February and 4.1 mm d^{-1} in August, while the growth of fragments from the Laurencia Zone averaged 3.2 mm d^{-1} in February and 2.9 mm d^{-1} in August.

Table VIII. Reciprocal Growth Experiments. Analysis of Variance Table evaluating the growth of A. spicifera. Fifty fronds were collected in the Acanthophora Zone, placed into enclosures, and transplanted into the Acanthophora and Laurencia Zones. An additional 50 fronds that were collected in the Laurencia Zone were similarly treated. Growth was measured over a one-week period in February and August 1979.

	df	ss	ms	F	p
Station	1	0.9	0.9	0.4	> 0.050
Fragment	1	25.8	25.8	10.1	< 0.001
Location					
Period	1	136.5	136.5	54.6	< 0.001
Error	204	523.4	2.6		
Total	207	686.6			

	<u>Acanthophora</u> Zone Fronds	<u>Laurencia</u> Zone Fronds
Period:	$\bar{X} \pm SD$	
February	4.80 $\pm$ 0.80	3.20 $\pm$ 0.76
August	4.13 $\pm$ 0.64	2.85 $\pm$ 1.82

(1) Units = mm d⁻¹

Morphology

Botanical Method

In general, fronds of A. spicifera in the Laurencia Zone were shorter, more compact, and had fewer branches than fronds in the Acanthophora Zone. Measures of branching compactness, the distances from the holdfast to 1st-order branches and from the main axis to the first 2nd-order branches were less in the Laurencia Zone than in the Acanthophora Zone (Fig. 33). Also, the distance from the holdfast to 1st-order branches increased with increasing degrees (i.e., first, second, third, etc.,) of 1st-order branches in the Acanthophora Zone; this pattern, however, was not observed in the fronds in the Laurencia Zone, where the distance from the holdfast to 1st-order branches averaged about 5 mm. As a second measure of compactness, the lengths of 1st- and 2nd-ordered branches were examined; they were shorter in the Laurencia Zone than in the Acanthophora Zone (Fig. 34). Together, these measures of branching compactness showed: (i) the fronds of A. spicifera in the Laurencia Zone were more tightly branched than fronds in the Acanthophora Zone; and (ii) fronds in the Laurencia and Acanthophora Zones differed in how branches emerged from the main axis.

The branching complexity of A. spicifera ranged from one to five orders of branches in the Acanthophora Zone and from one to three orders in the Laurencia Zone. In general, little difference was observed in the composition of ordered branches between the Acanthophora and

Figure 33. A. spicifera Branch Compactness. Distance from the holdfast to the 1st-order branches and the distance from the main axis to the first 2nd-order branch. Fronds were collected in the Laurencia Zone (○) at the Moderately-Exposed Station and in the Acanthophora Zone (●) at the Back-Reef Station (October-November 1981). Vertical bars indicate $\pm$ 95 % confidence intervals. 1a = first 1st-order branch; 1b = second 1st-order branch; 1c = third 1st-order branch; 2a = first 2nd-order branch on the first 1st-order branch; and 2c = first 2nd-order branch on the second 1st-order branch.

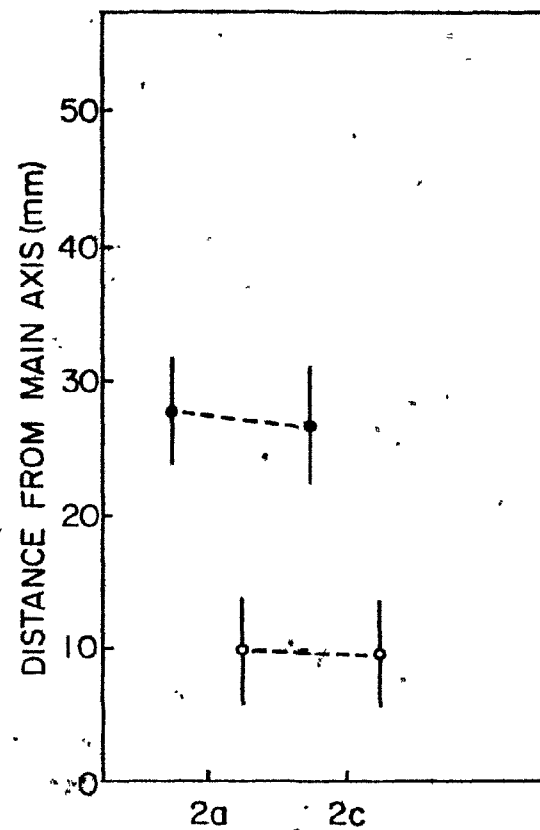
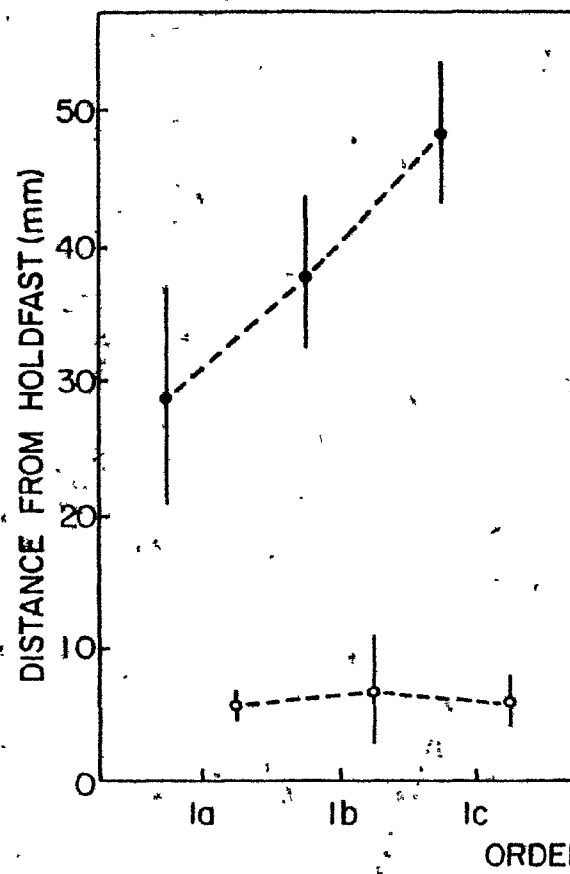
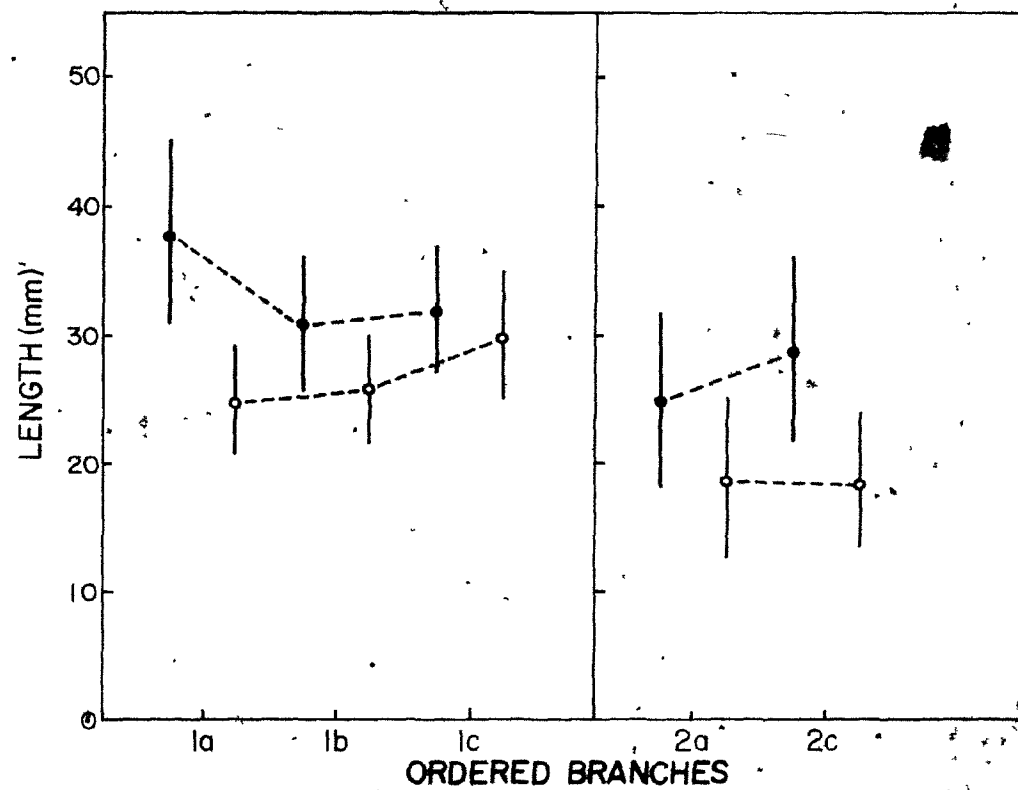


Figure 34. A. spicifera Branch Compactness. The mean length of the 1st-order branches and of the first 2nd-order branches. Fronds were collected in the Laurencia Zone (o) at the Moderately-Exposed Station and in the Acanthophora Zone (•) at the Back-Reef Station (October-November 1981). Vertical bars indicate $\pm$ 95 % confidence intervals. 1a = first 1st-order branch; 1b = second 1st-order branch; 1c = third 1st-order branch; 2a = first 2nd-order branch on the first 1st-order branch; and 2c = first 2nd-order branch on the second 1st-order branch.



Laurencia Zones (Fig. 35). For example, 84 % of the fronds of A. spicifera in the Acanthophora Zone had at least one 1st-order branch (i.e., at least one branch on the main axis), compared with 87.5 % of the fronds in the Laurencia Zone. In addition, the average numbers of branches found at each order of branching were similar in the Acanthophora and Laurencia Zones. Fronds of A. spicifera in the Acanthophora Zone averaged about three branches on the main axis, compared with two branches on the main axis in the Laurencia Zone. In effect, fronds of A. spicifera were: (i) larger and bushier (i.e., had more ordered branches) in the Acanthophora Zone, than in the Laurencia Zone; and (ii) generally similar in composition and number of branches in the Acanthophora and Laurencia Zones.

L. papillosa was shorter and more compact in branching structure in the Laurencia Zone than in the Acanthophora Zone. Measurements of compactness showed that: (i) the distances of 1st-ordered branches from the holdfast was less in the Laurencia Zone than those in the Acanthophora Zone; (ii) the distance of 1st-ordered branches from the holdfast increased with increasing degrees (primary, secondary,.....etc,) of 1st-ordered branches in both reef zones (Fig. 36); and (iii) the length of 1st-ordered branches was less in the Laurencia Zone than that in the Acanthophora Zone (Fig. 36). Like A. spicifera, L. papillosa was shorter and had a more compact branching design in the Laurencia Zone than in the Acanthophora Zone. Unlike A. spicifera, the way the branches emerged from the main axis was typical of a plant not affected by environmental disturbances: that is,

Figure 35. A. spicifera Branching Complexity. The percentage of fronds found with 1st-, 2nd-, 3rd-, 4th-, and 5th-order branches and the mean number of branches at each order of branching. Vertical bars indicate $\pm$ 95 % confidence intervals. $n = 99$ fronds. Fronds were collected in the Laurencia Zone (o) at the Moderately-Exposed Station and in the Acanthophora Zone (●) at the Back-Reef Station (October-November 1981).

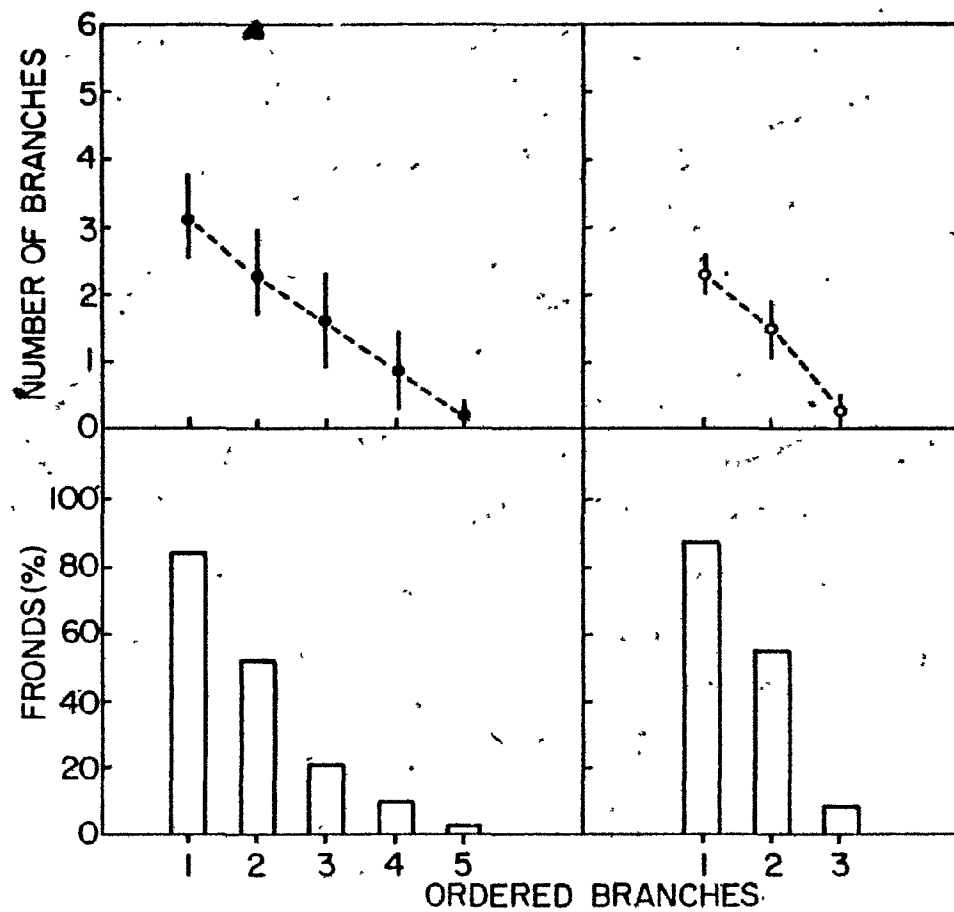
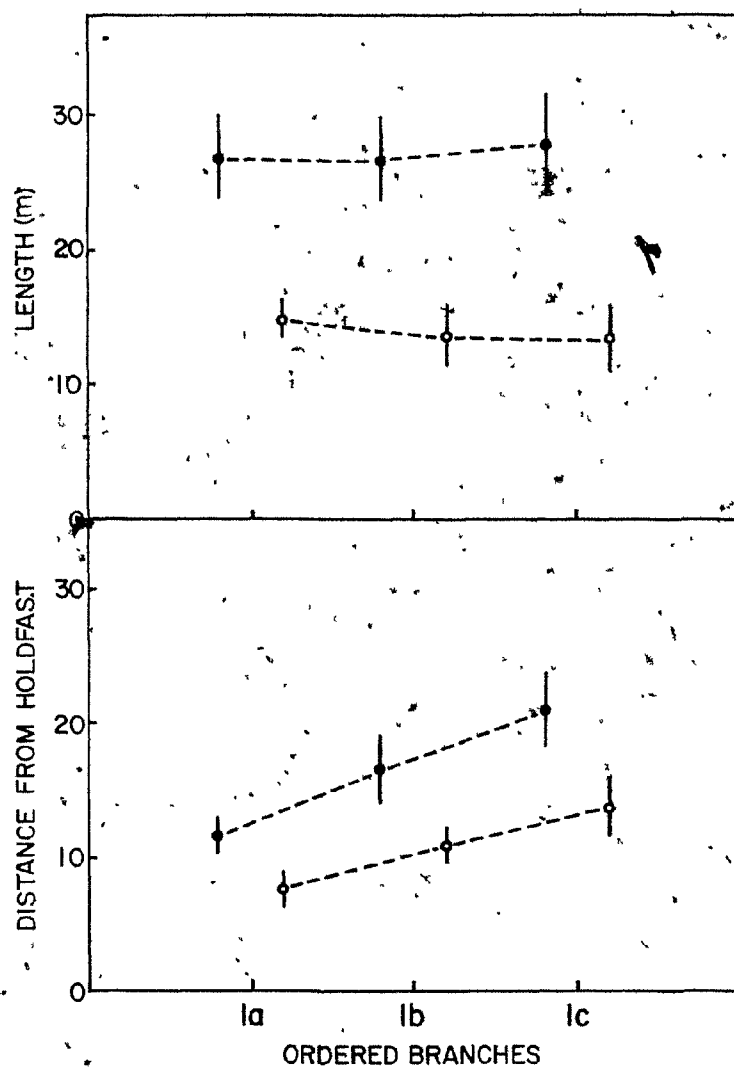


Figure 36. L. papillosa Branch Compactness. Distance from the holdfast to the 1st-order branches and the mean length of 1st-order branches. Fronds were collected in the Laurencia Zone (○) at the Moderately-Exposed Station and in the Acanthophora Zone (●) at the Back-Reef Station (October-November 1981). Vertical bars indicate $\pm$ 95 % confidence intervals. la = first 1st-order branch; lb = second 1st-order branch; and lc = third 1st-order branch.



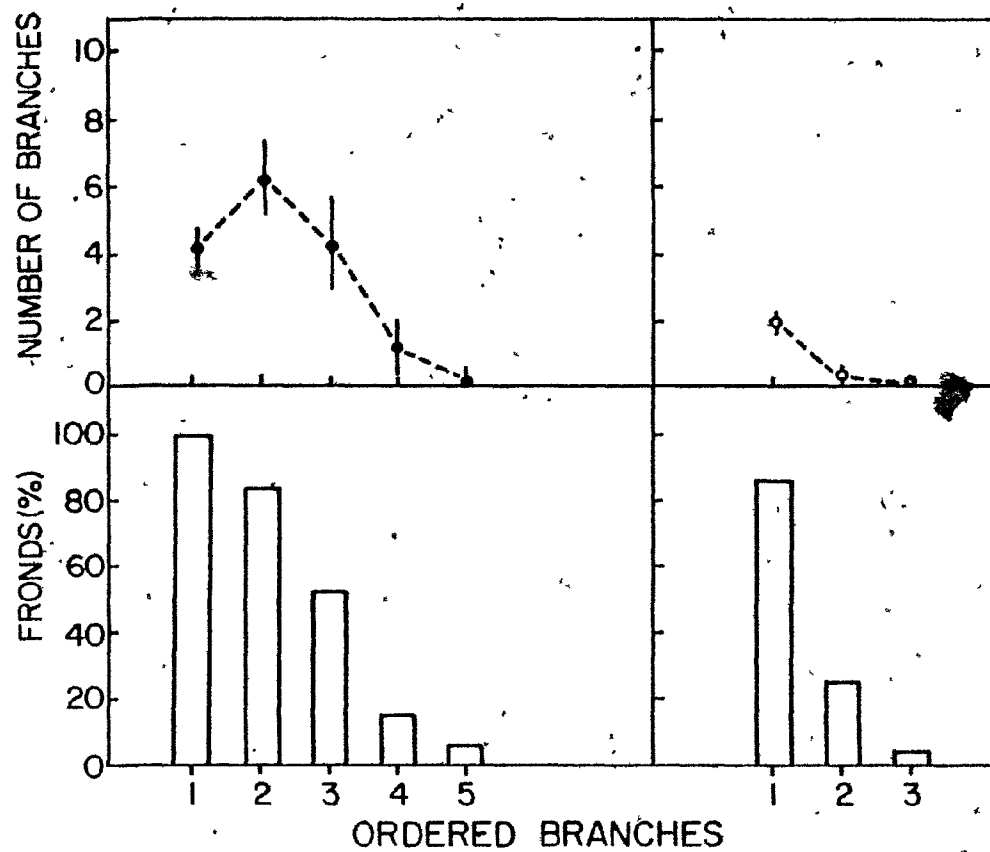
1st-ordered branches emerged from the main axis at progressively greater distances from the holdfast.

Fronds of L. papillosa ranged from one to five orders of branching in the Acanthophora Zone and from one to three orders of branching in the Laurencia Zone. The composition of ordered branches varied between the Acanthophora and Laurencia Zones. To illustrate, 84 % of the Laurencia fronds in the Acanthophora Zone had at least one 2nd-order branch compared with 25 % of the Laurencia fronds in the Laurencia Zone. As indicated in Figure 37, the number of branches at each order of branching was less in the Laurencia than in the Acanthophora Zones; for example, the average number of branches emerging from the main axis of L. papillosa in the Acanthophora Zone was 4.2 branches, compared with 2.0 branches in the Laurencia Zone. Also, Acanthophora Zone fronds of L. papillosa had more 2nd-order branches than any other ordered branch, while fronds of L. papillosa in the Laurencia Zone had predominantly 1st-ordered branches. Thus, L. papillosa was smaller and more compact in the Laurencia Zone than in the Acanthophora Zone, and had fewer and a smaller variety of branches in the Laurencia Zone than in the Acanthophora Zone. (See Appendix IV & V for further branching information.)

Strahler Method

A description of canopy structure was obtained by examining the distances of terminal branches from their basal holdfast (1st-order

Figure 37. L. papillosa Branching Complexity. The percentage of fronds found with 1st-, 2nd-, 3rd-, 4th-, and 5th-order branches and the mean number of branches at each order of branching. Vertical bars indicate $\pm$ 95 % confidence intervals. $n = 99$ fronds. Fronds were collected in the Laurencia Zone ($\circ$) at the Moderately-Exposed Station and in the Acanthophora Zone ($\bullet$) at the Back-Reef Station (October-November 1981).



branch length). Among fronds of A. spicifera, the 1st-order branch lengths averaged $113 \text{ mm} \pm 41 \text{ mm}$ ($\bar{X} \pm \text{SD}$) in the Acanthophora Zone, and $38 \text{ mm} \pm 14 \text{ mm}$ in the Laurencia Zone. With L. papillosa, 1st-order branch lengths averaged $70 \text{ mm} \pm 25 \text{ mm}$ in the Acanthophora Zone and $26 \text{ mm} \pm 8 \text{ mm}$ in the Laurencia Zone (Figs. 38 and 39). As shown in Table IX, the lengths of branches were significantly different among species and locations. Fronds of A. spicifera varied more in size than fronds of L. papillosa, and fronds of both species were larger in the Acanthophora Zone than in the Laurencia Zone. Differences in branch length reflected: (i) the ability of A. spicifera to grow taller than L. papillosa; and (ii) the carpet-like cover of L. papillosa, especially in the Laurencia Zone.

Biomechanics of Breakage

In Vitro Study

The mechanical strength of A. spicifera was evaluated and compared with L. papillosa. A. spicifera was strongest at its holdfast and weakest at a branch node within the branch axil (Fig. 40). The mass that was required to fracture a main axis or to fracture a lateral branch (when the holdfast and branch were secured) was not significantly different (Table X). Accordingly, branch nodes, the weakest part of the thallus, could potentially function as an abscission zone.

Comparisons of the mechanical strength of A. spicifera and L. papillosa showed that the main axis of L. papillosa was more

Figure 38. A. spicifera: The frequencies of 1st-order branches of different size classes (Strahler Method) in the Acanthophora and Laurencia Zone (October-November 1981).

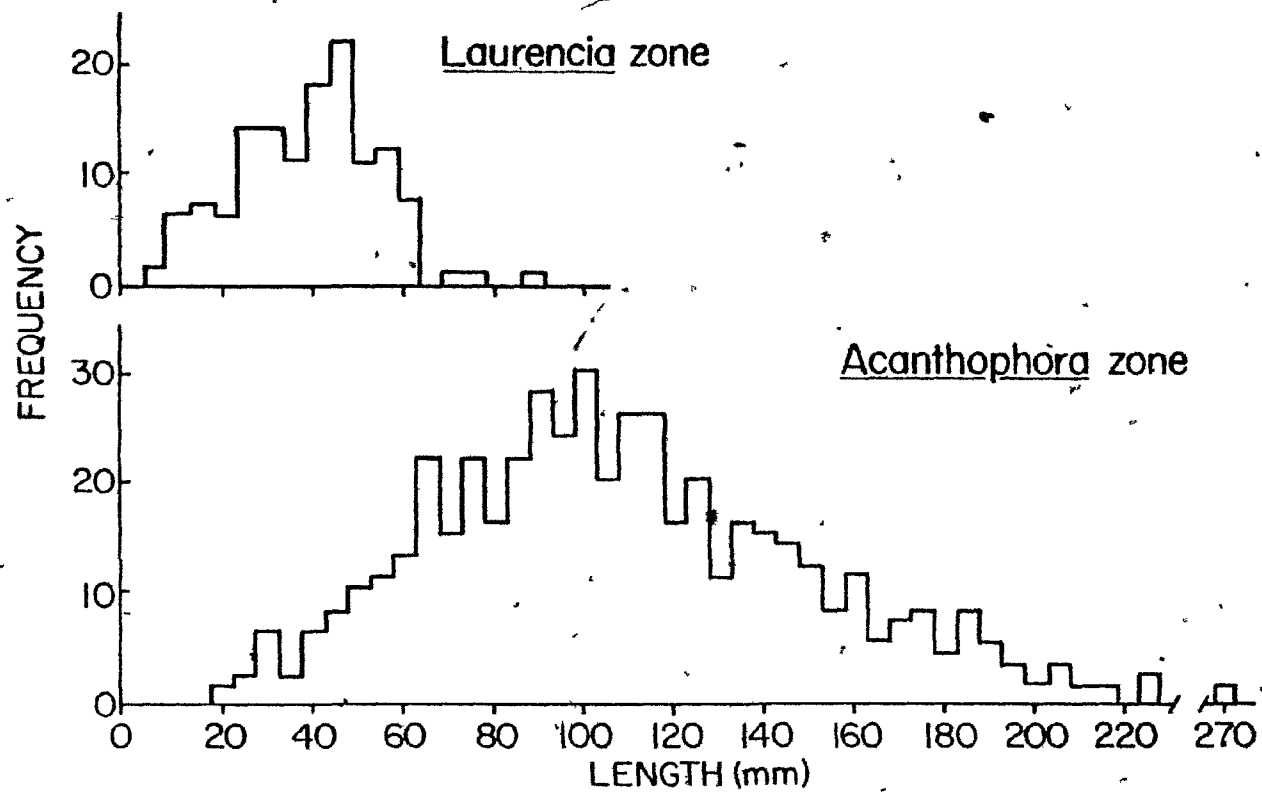


Figure 39. L. papillosa: The frequencies of 1st-order branches of different size classes (Strahler Method) in the Acanthophora and Laurencia Zone (October-November 1981).

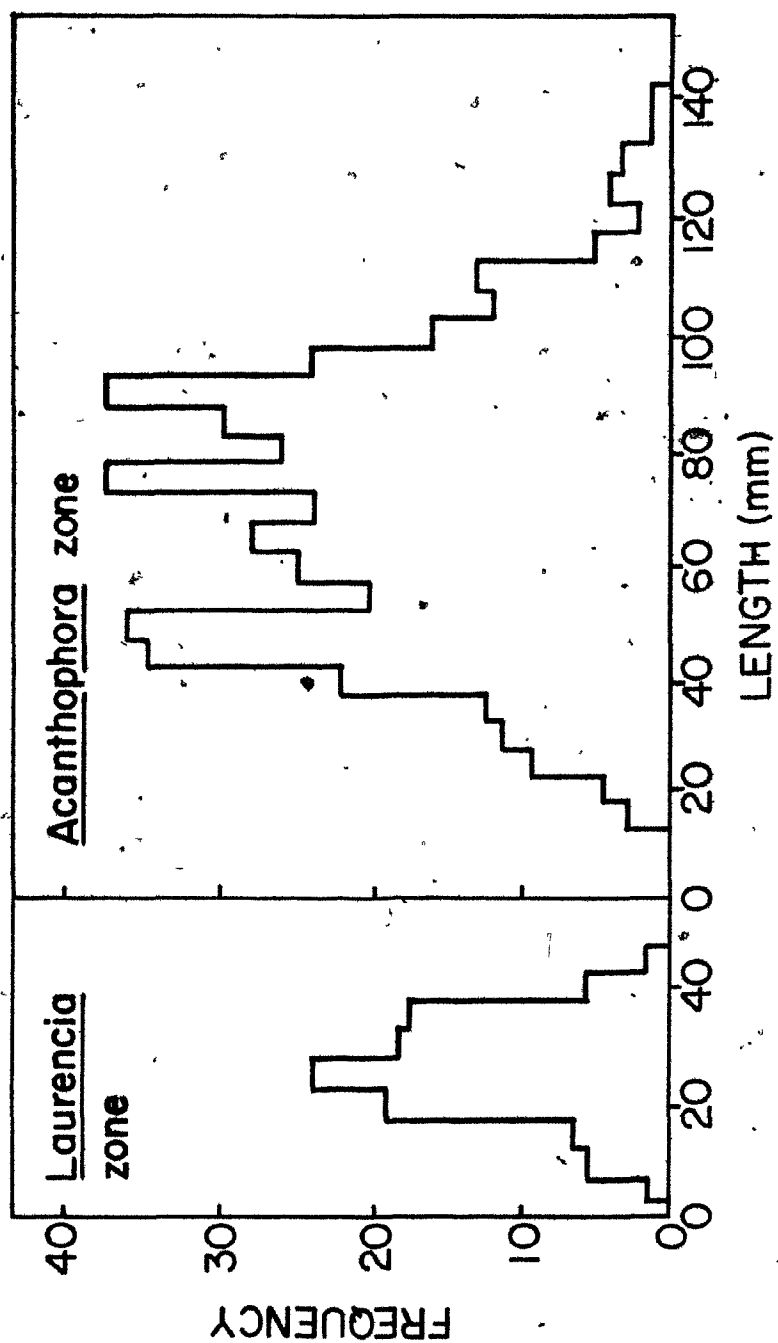


Table IX. Two-Way Analysis of Variance Table evaluating the length of 1st-order branches of A. spicifera and L. papillosa in the Laurencia and Acanthophora Zones (October 1981).

	df	ss	ms	F	p
Main Effects	2	3838.2	1919.1	184.9	< 0.001
Location	1	1950.7	1950.7	188.0	< 0.001
Species	1	192.3	192.3	18.5	< 0.001
Error	1099	11401.1	10.4		
Total	1101	15240.1	13.8		

	Location: ($\bar{X} \pm SD$)	
Species:	<u>Laurencia</u> Zone	<u>Acanthophora</u> Zone
<u>A. spicifera</u>	3.78 $\pm$ 1.44	11.26 $\pm$ 4.06
<u>L. papillosa</u>	2.60 $\pm$ 0.81	7.00 $\pm$ 3.47

(1) units = cm

Figure 40. Mechanical Measurements of Breakage. Scatter diagram of the mass (weight) required to break a cross-sectional area of A. spicifera. Force was applied on the main axis near the holdfast (Δ), at a branch node when the holdfast and the branch were secured ($\bullet$), and at a branch node when the distal ends of the main axis and branch were secured ($\circ$). $n = 50$ for each fracture location.

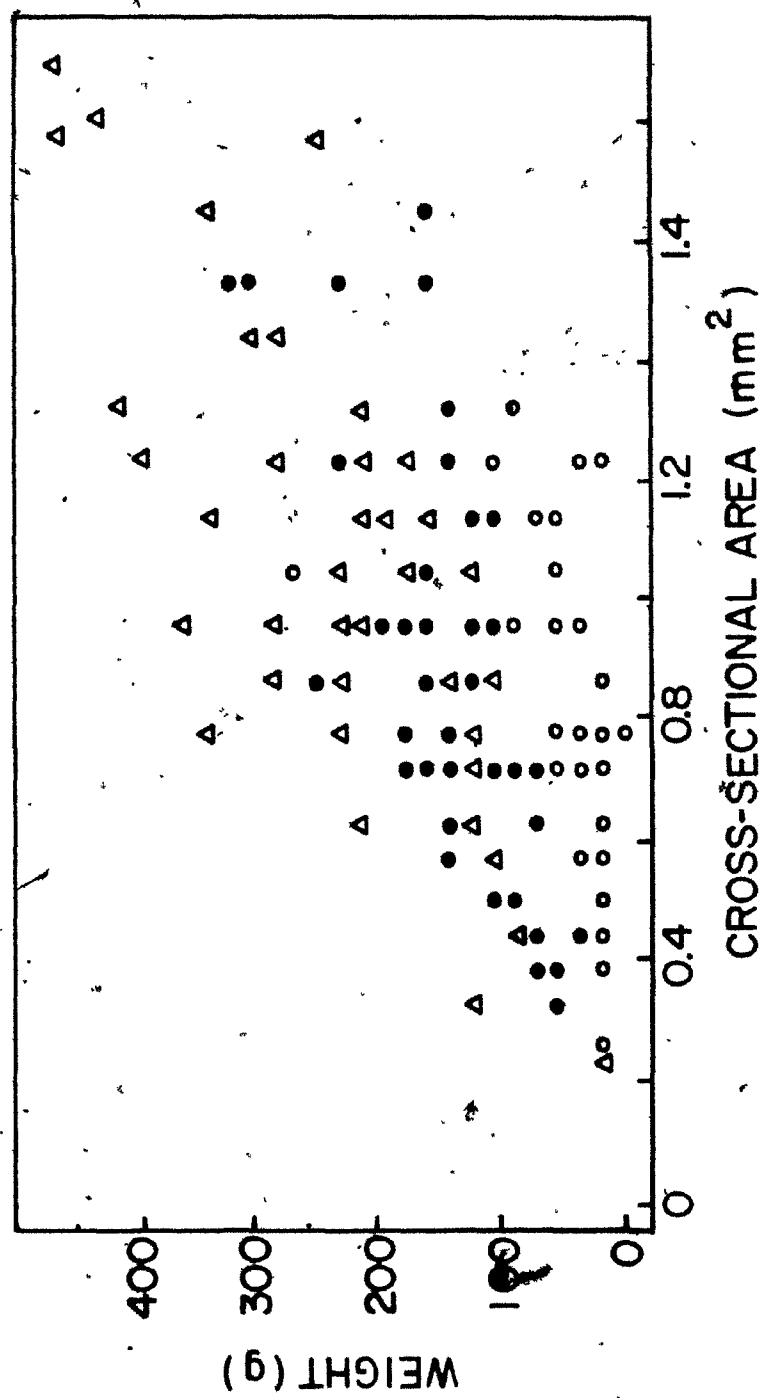


Table X. Mechanical Measurements of Breakage. Regression models of the mass (weight) required to cause breakage as a function of cross-sectional area (mm^2): B_0 = Y-intercept, B_1 = slope of the regression line, r^2 = regression coefficient, H_0 = null hypothesis

Plant:	Region:	$Y = B_0 + B_1X +$	r^2	F	p	N
<u>A. spicifera</u>						
	Main Axis	$y = -1.0 + 147x$	73.3	105.7	< 0.001	48
	Holdfast	$y = 95.9 + 113x$	25.2	15.5	< 0.001	49
	Branch Node*	$y = 12.4 + 146x$	49.8	47.6	< 0.001	49
	Branch Node**	$y = -13.9 + 54x$	34.7	25.00	< 0.001	49
<u>L. papillosa</u>						
	Main Axis	$y = 3.91 + 23.0x$	42.6	34.7	< 0.001	49
Regression Analysis:						
		($H_0 : B_0 = B_0$)		($H_0 : B_1 = B_1$)		
		N	F	p	t	p
<u>A. spicifera</u>						
	Main Axis x Holdfast	95	3.0	< 0.05	2.5	< 0.020
	Main Axis x Branch Node*	94	0.6	> 0.05	0.0	> 0.05
	Main Axis x Branch Node**	96	3.7	< 0.05	10.1	< 0.001
<u>A. spicifera x L. papillosa</u>						
	Main Axis x Main Axis	95	1.9	< 0.05	2.8	< 0.010

Branch Node* = branch axil
Branch Node** = abaxial angle

resistant to breakage (Table X and Fig. 41). Also, the maximum branch diameter of L. papillosa was larger (1.80 mm) than that of A. spicifera (1.65 mm). As the mass required to fracture the thallus was directly proportional to the cross-sectional area of the alga, the larger branch diameters of the older plants of L. papillosa were again mechanically stronger than those of A. spicifera.

In Situ Study

It was predicted that if the branch nodes represented an abscission zone, then more breaks should occur at branch nodes than within branch internodes. Of the 480 breaks recorded from outplanted A. spicifera, 280 occurred within branch internodes and 205 at branch nodes.

Over a six-day period, a greater number of fragments was formed from the outplanted A. spicifera during light sea conditions (297) than during moderate sea conditions (136). For both periods, the size distribution of fragments was highly skewed toward the smaller-sized fragments, with most of the fragments smaller than 50 mm (Fig. 42). Also, larger fragments were produced in moderate sea conditions than in light sea conditions (Test of Median; $X^2 = 4.75$; $p < 0.05$). The median fragment size was 20 mm in calm conditions and 25 mm in moderate sea conditions. Fronds of A. spicifera rarely fractured at or near the base of the holdfasts. Instead, a gradual erosion of the upper thallus resulted.

Figure 41. Mechanical Measurements of Breakage. Scatter diagram of the mass (weight) required to break the main axes of A. spicifera (○) and L. papillosa (●). $n = 50$ for each fracture location.

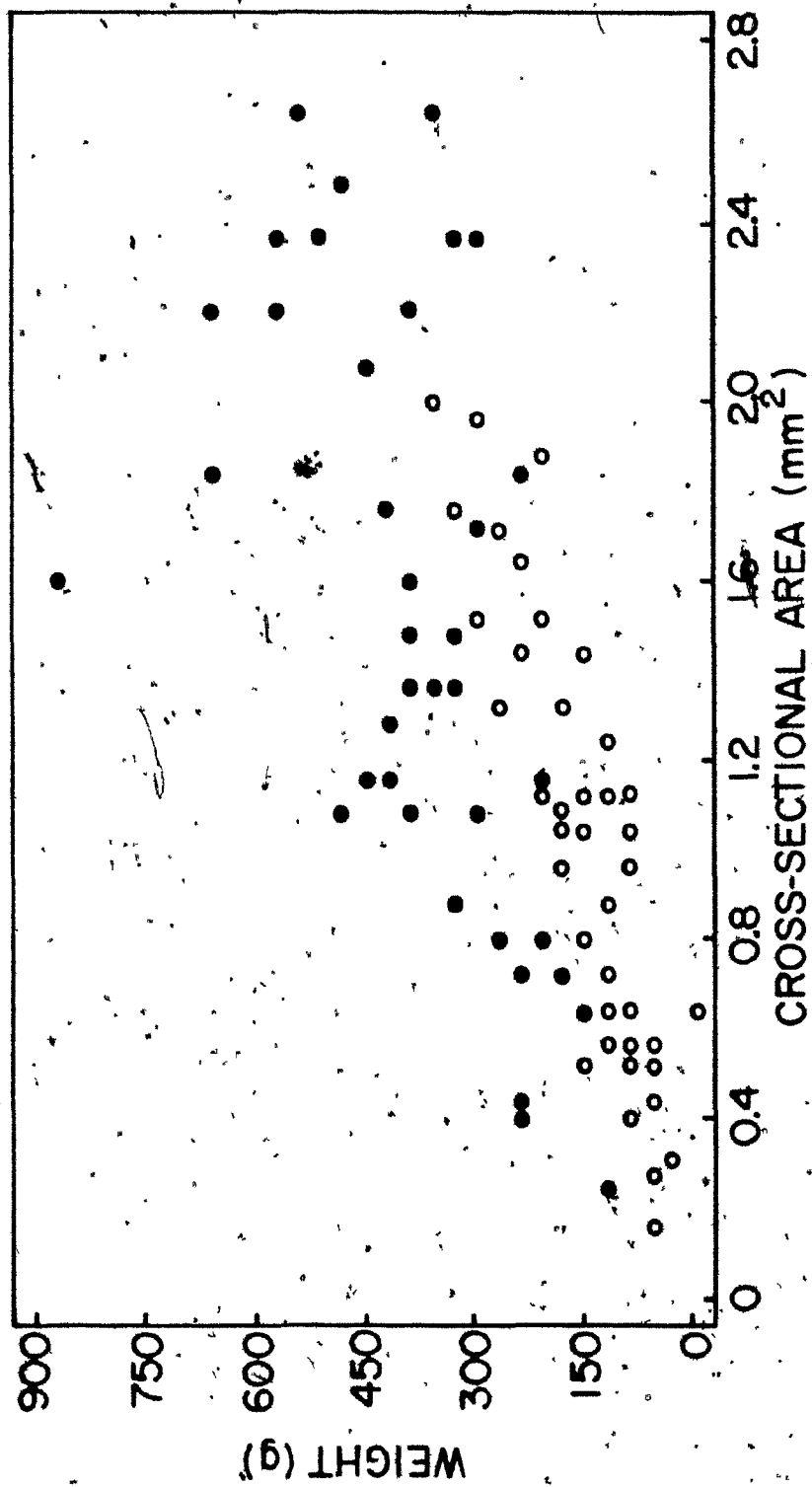
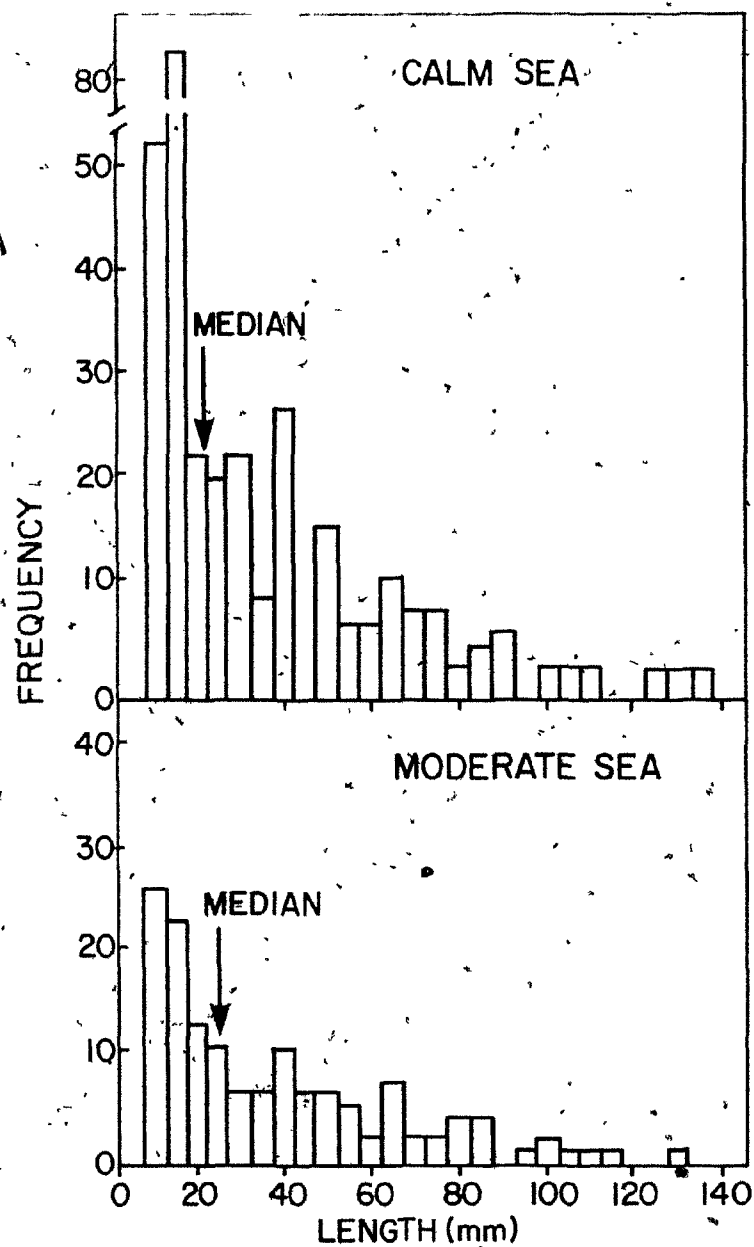


Figure 42. Numbers of fragments of different sizes of A. spicifera formed when transplanted into the Laurencia Zone during calm and moderate sea conditions. Arrows indicate the median fragment size.



Frond Survivorship

Depletion Curves

The survivorship of A. spicifera was assessed from depletion curves and found to vary among seasons and locations (Table XI and Fig. 43).

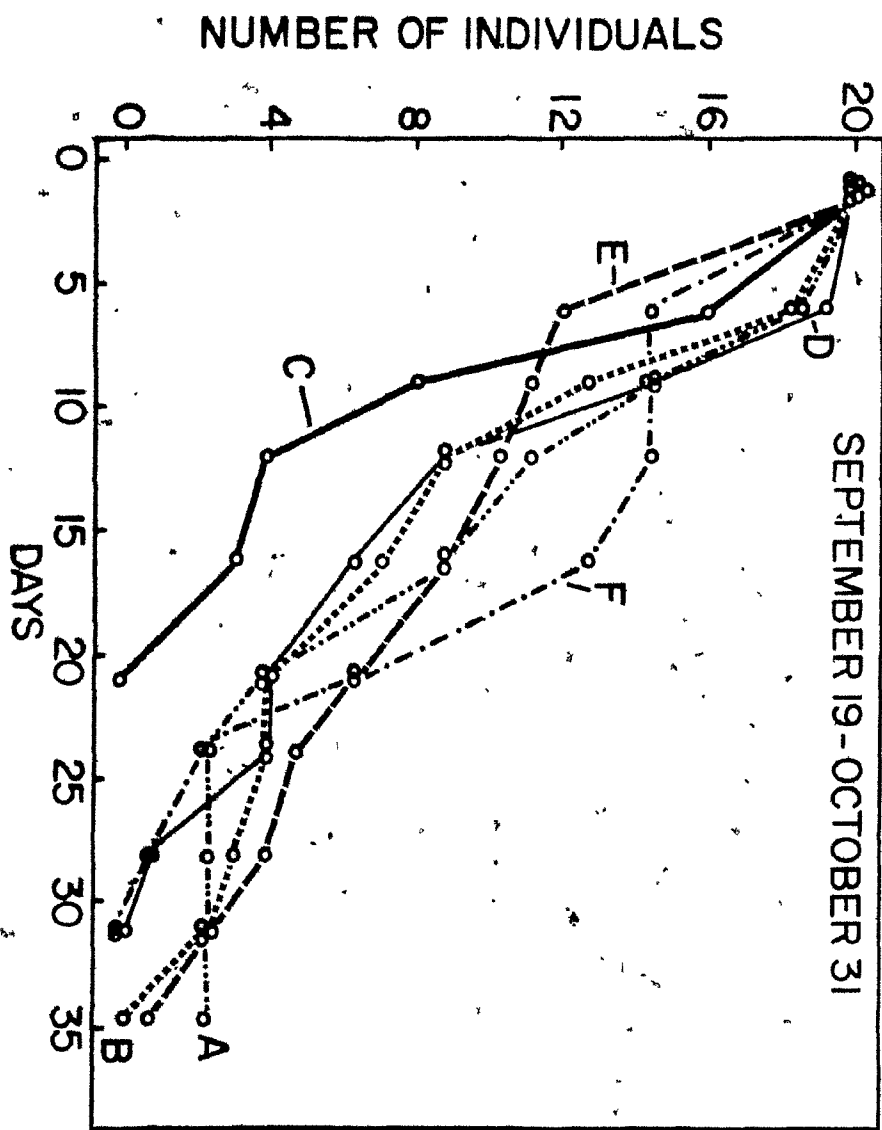
During the wet season, tagged fronds survived an average of 15.9 days at the Back-Reef Station and 14.9 days at the Exposed Station; these differences in frond survivorship were not significant (Table XI). At the Sheltered Station, tagged fronds survived an average of 12.0 days, a rate significantly lower than the survivorship at either the Back-Reef or Exposed Stations. The LE_{50} (length of time to lose 50 % of initial fronds) of A. spicifera at the Sheltered and Back-Reef Stations was 11 days, while fronds at the the Back-Reef Station had a LE_{50} of 20 days. The differences between the mean survival period and the LE_{50} suggested that frond losses at the Back-Reef and Exposed Stations were not uniform throughout the sampling period.

During the dry season (4 November to 16 December 1981), frond survivorship was related to wave exposure. Over the first 17 days, frond survivorship was not significantly different at the Sheltered and Back-Reef Stations, and fewer fronds were lost at the Sheltered and Back-Reef Stations than at the Exposed Station (Table XI). By day 6, all tagged fronds at the Exposed Station had been lost. The LE_{50} of fronds of A. spicifera was 11 days both at the Sheltered and Back-Reef Stations and 4 days at the Exposed Station. After day 17, the Back-Reef

Table XI. Mean Survival Period and LE/50 (time to lose 50 % of marked fronds) for tagged *A. spicifera* fronds at Wave-Exposure Stations (September to October 1981 [wet season] November to December 1981 [dry season]). (units = days)

Period:	Station:	LE ₅₀	Mean Survival $\bar{X} \pm \text{S.E.}$	Savage (Mantel-Cox) Test			
				Q	p	Q	p
Wet Season							
	Exposed	11	14.92 $\pm$ 1.321	3.47	< 0.05	0.34	> 0.05
	Sheltered	11	12.03 $\pm$ 0.90				
	Back-Reef	20	15.90 $\pm$ 1.53	6.54	< 0.01		
Dry Season							
	Exposed	4	4.85 $\pm$ 0.16	33.07	< 0.01	28.00	< 0.001
	Sheltered	11	12.15 $\pm$ 1.16				
	Back-Reef	11	11.60 $\pm$ 1.34	0.05	> 0.05		

Figure 43. Depletion curves of A. spicifera at the Exposed, Sheltered, and Back-Reef Stations (19 September to 31 October 1981 [wet season]). At each station, two groups of twenty fronds were tagged and noted for their presence or absence at 3- and 4-day intervals. (A-B) Exposed Station; (C-D) Sheltered Station; (E-F) Back-Reef Station.



Station incurred few frond losses, maintaining nearly half of its tagged fronds to the end of the sampling period. At the Sheltered Station, frond losses continued until day 30, when all tags had been lost (Fig. 44).

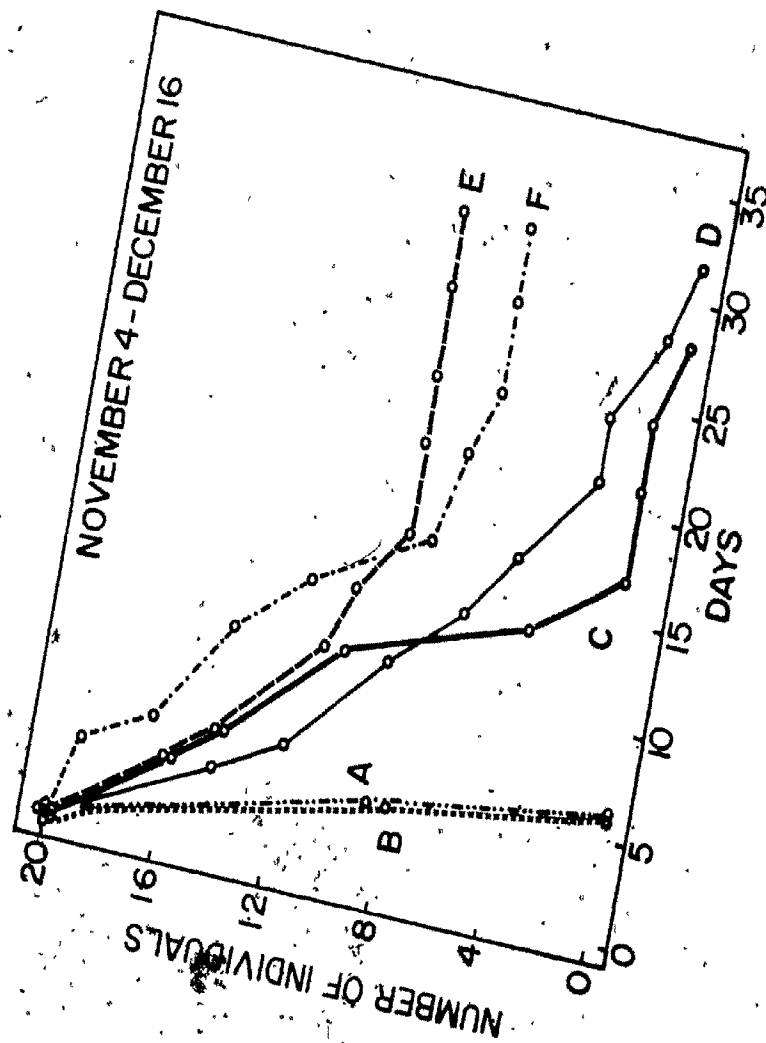
The mean survival period of tagged fronds from the wet to the dry season were shown to: decrease at the Exposed Station (Savage-Test, $p < 0.01$); remain stable at the Sheltered Station (Savage-Test, $p > 0.05$); and decrease at the Back-Reef Station during the initial 17-day dry-season period (Savage-Test, $p < 0.01$), and later to increase, incurring few frond losses.

Entire plants of A. spicifera were rarely lost to wave exposure. In general, such plants were not associated with "aggregates" of L. papillosa. Accordingly, plant losses appeared to be highest at the Exposed Station.

Wet and Dry Seasons

From 19 September to 16 December 1981, the results of the number of tagged fronds lost per 100 fronds per day from the Exposed, Sheltered, and Back-Reef Stations (Fig. 45) agreed with those of the depletion curves (Figs. 43 and 44). Statistical analysis indicated significant station ($F = 36.8$, $p < 0.001$) and period effects ($F = 12.1$, $p < 0.001$). Frond losses of A. spicifera at the Exposed and Sheltered Stations did not differ significantly, with an average daily loss of 9 % of tagged fronds at the Exposed Station and 8 % of the tagged fronds at the

Figure 44. Depletion curves of A. spicifera at the Exposed, Sheltered, and Back-Reef Stations (4 November to 16 December 1981 [dry season]). At each station, two groups of twenty fronds were tagged and noted for their presence or absence at 3- and 4-day intervals. (A-B) Exposed Station; (C-D) Sheltered Station; (E-F) Back-Reef Station.



Sheltered Station. Fronds at the Back-Reef Station survived longer than fronds at the fore-reef stations, with daily losses of 4 % of the tagged fronds (Table XII). Early in the wet season (19 to 29 September), little difference was observed between stations. From 9 October to 4 November, fronds at the Sheltered Station showed higher losses than those at the Exposed or Back-Reef Station. As dry season approached, wave exposure intensified, making the wave-exposure gradient more apparent and increasing the losses of fronds at stations more exposed to wave action (Fig. 45). Daily losses of tagged fronds were as high as 24 % during dry-season storms.

When evaluating survivorship data against percent cover, significant decreases in cover coincided with increases in frond losses; this was true, however, only at the Sheltered and Exposed Stations. During the first major dry-season storm for the 1981-82 season (9 to 13 November 1981 [days 48 to 52; Fig. 46]), the percent cover decreased at the Exposed and Sheltered Stations. At this time, the Exposed Station showed significantly higher losses in coverage than did the Sheltered Station ($T = 3.0$, $df = 10$, $p < 0.002$), coinciding with daily losses of 24 % of tagged fronds at the Exposed Station and 14 % of the tagged fronds at the Sheltered Station (Fig. 45). By 17 December (day 89; Fig. 46), the Exposed and Sheltered Stations had about a 20 % cover of A. spicifera, down from previous highs of 85 % cover at the Sheltered Station and 54.4 % cover at the Exposed Station. The Back-Reef Station remained at 100 % cover of A. spicifera throughout the sampling period, despite having daily losses of tagged fronds of 9 % during dry-season

Table XII. Analysis of Variance Table evaluating the survivorship of tagged fronds of A. spicifera to wave action (19 September to 16 December 1981).

	df	ss	ms	F	p
Station	2	1.44	0.72	36.8	< 0.001
Period	24	5.69	0.24	12.1	< 0.001
Error	75	1.47	0.02		
Total					

Station:	Exposed	Sheltered	Back-Reef
$\bar{x} \pm SD$	8.89 ± 5.74	8.41 ± 4.65	4.16 ± 2.67

(1) Horizontal bars span groups of similar survivorship (Newman-Keuls Multiple Range Test $p < 0.05$).

(2) Units = No. of fronds lost (100 fronds)⁻¹ d⁻¹

Figure 45. Numbers of tagged fronds lost per 100 fronds per day at the Exposed, Sheltered, and Back-Reef Stations (19 September to 16 November 1981). At each station, at least forty fronds were tagged and noted for their presence or absence at 3- and 4-day intervals. Missing tags were replaced. (Δ) Exposed Station; ($\circ$) Sheltered Station; ($\bullet$) Back-Reef Station.

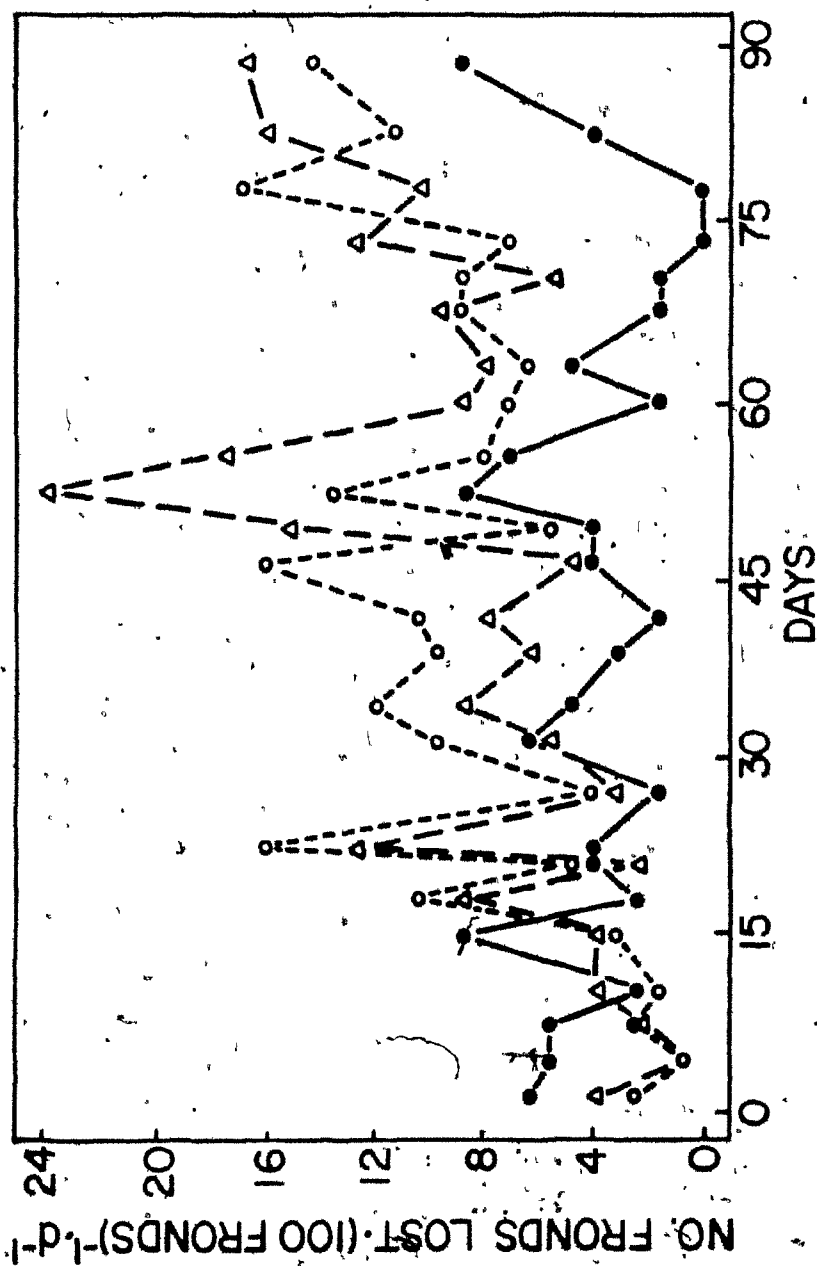
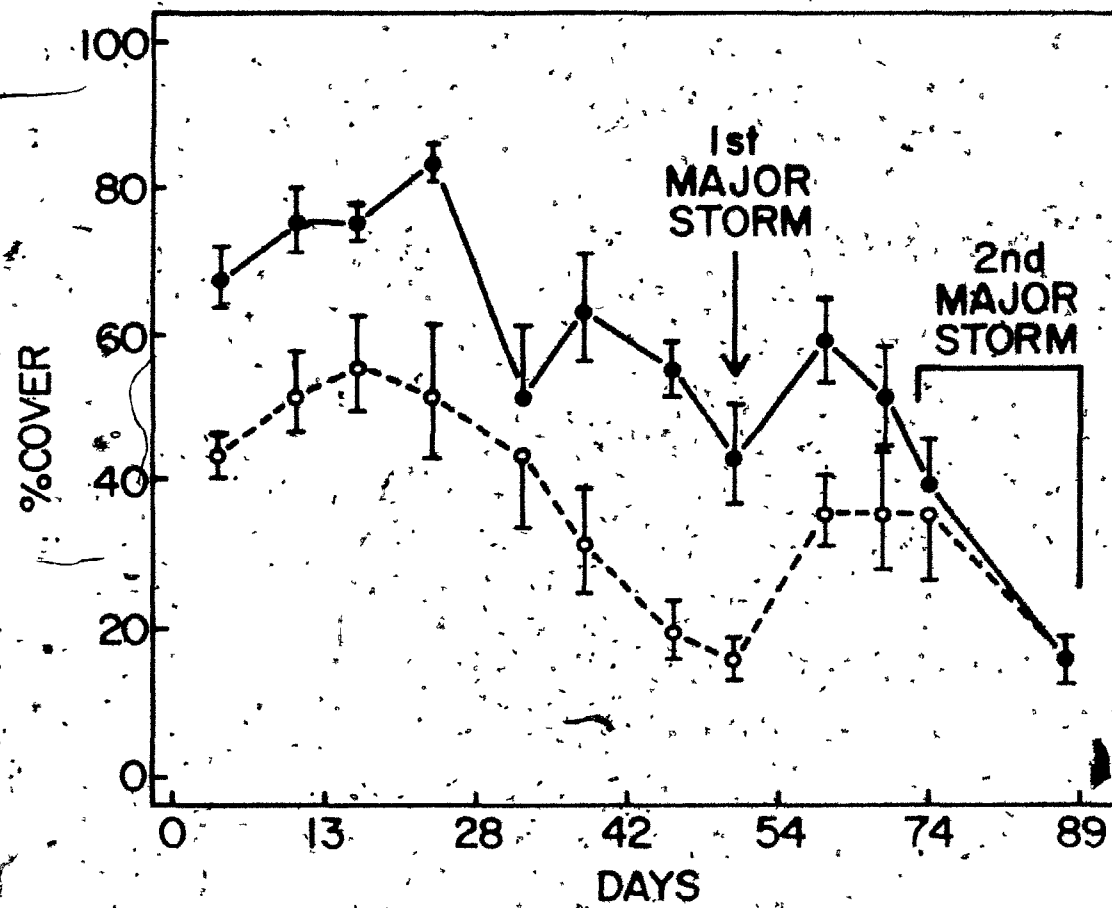


Figure 46. Percent cover of A. spicifera at the Exposed and Sheltered Stations (22 September to 16 December 1981). At the Back-Reef Station, the percent coverage remained at 100%. Vertical bars indicate $\pm$ the standard error. $n = 80$ for each point. (O) Exposed Station; (●) Sheltered Station.



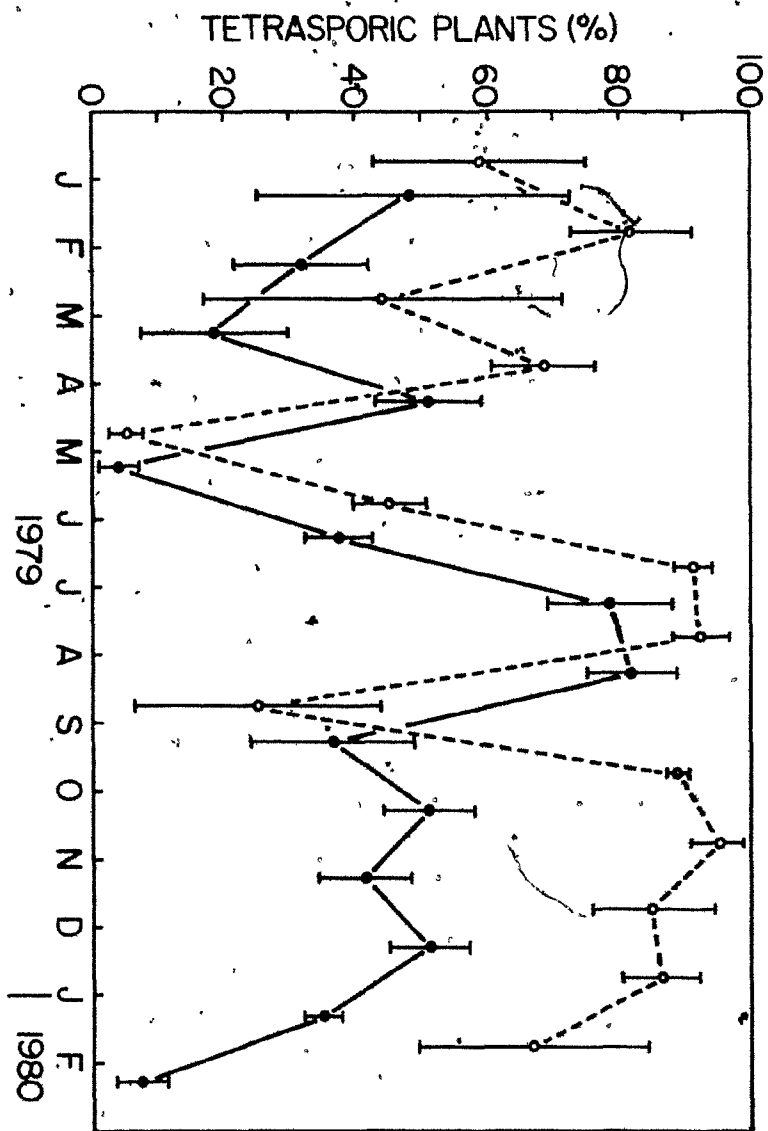
storms.

Phenology

Tetrasporic plants (i.e. plants possessing mature tetraspores) were, by far, more common than gametophytic plants both in the Acanthophora and Laurencia Zones. From January to May 1979, the composition of tetrasporic plants in the Laurencia Zone decreased from 83 % in February to 5 % in May (Fig. 47). All other plants were vegetative (not possessing tetraspores or carpospores). After May, the composition of tetrasporic plants increased to a maximum (greater than 80 %) for the remainder of the year, with the exception of September. Reduced levels of reproduction coincided with periods of increased aerial exposures of the reef flat. At this time, only the holdfasts of A. spicifera remained. In October, cystocarpic plants made up 3 % of the population; otherwise, no other gametophytic plants were collected during the 14-month period. A maximum of 96 % (November 1976) of the A. spicifera in the Laurencia Zone were found to be tetrasporic plants.

Comparisons in the reproduction of A. spicifera in the Acanthophora and Laurencia Zones showed a lower percentage of tetrasporic plants in the Acanthophora Zone than in the Laurencia Zone ($F = 13.1$; $P < 0.02$ [Fig. 47]). From October 1979 to February 1980, the difference in the percentage of tetrasporic plants was the greatest between the two algal zones. At this time, the Laurencia Zone population averaged about 40 % more tetrasporic plants than did the Acanthophora Zone population. Also, the distal determinate branches of A. spicifera in the

Figure 47. Percentage of fertile tetrasporic plants of A. spicifera in the Laurencia and Acanthophora Zones (January 1979 to February 1981). Four plants of A. spicifera possessing mature cytotocarps were collected in the Laurencia Zone in October 1979. Vertical bars indicate $\pm$ the standard deviation. $n = 6$ groups of 30 plants for each point. ($\circ$) Laurencia Zone; ($\bullet$) Acanthophora Zone.



Acanthophora Zone were for the most part always vegetative, while most determinate branches in the Laurencia Zone had tetrasporangia.

Otherwise, seasonal increases and decreases in the number of tetrasporic plants were similar between zones.

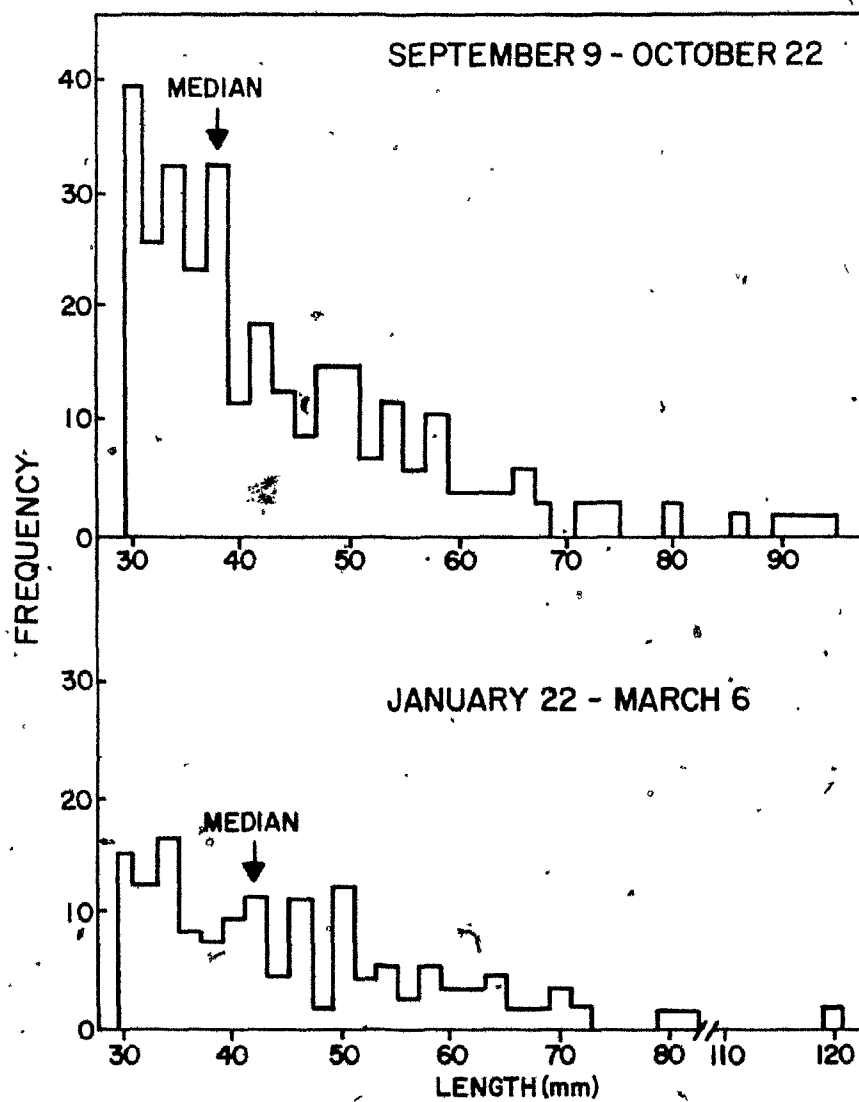
Colonization

Acanthophora Zone

Fragments of A. spicifera were readily recruited into the Acanthophora Zone. No difference in the rates of colonization was observed between wet- (9 September to 22 October 1979) and dry- (22 January to 6 March 1980) season periods ($T = 1.7$, $df = 22$, $p > 0.05$); however, distinct patterns in fragment colonization were recognized (Fig. 48). In the wet season, colonization rates increased from about $3.5 \text{ fragment m}^{-2} \text{ d}^{-1}$ in September to $9.6 \text{ fragment m}^{-2} \text{ d}^{-1}$ in October, coinciding with an increase in wave exposure. Starting on 16 October and lasting for four days, low colonization rates reflected a period of calm seas.

In the dry-season period (23 January to 6 March 1980), colonization rates decreased from a high of $16.1 \text{ fragment m}^{-2} \text{ d}^{-1}$ in January to a low of $0.8 \text{ fragment m}^{-2} \text{ d}^{-1}$ in March, representing maximum and minimum rates of colonization for the wet and dry seasons (Fig. 48). Despite the high colonization rates during the dry season, nearly twice the number of fragments was recruited into cleared plots in the Acanthophora Zone

Figure 48. Mean number of fragments of A. spicifera settling in the Acanthophora Zone (9 September to 22 October 1979 [wet season]; 21 January to 6 March 1980 [dry season]). Six plots (0.3 m X 0.5 m) were chosen randomly and cleared of Acanthophora plants to expose a Laurencia understorey. Around each plot, a border of 0.5 m was similarly cleared to serve as a buffer zone. Vertical bars indicate $\pm$ the standard error.



during the wet-season period (236 fragments) than during the dry-season period (136 fragments). In effect, this suggested that the transitional period from wet to dry season (November-December), with its moderately high biomass of A. spicifera and increased wave exposure, should be the optimum period for fragment colonization.

The lengths of A. spicifera fragments that were recruited into cleared plots in the Acanthophora Zone diminished steadily during the wet- and dry-season periods (Fig. 49). Fragments of A. spicifera collected during the dry-season period were significantly longer than fragments collected during the wet-season period (Test of Median; $\chi^2 = 5.1$, $p < 0.025$). The median fragment size of A. spicifera was 42 mm in the dry season and 38 mm in the wet season (Fig. 50), and the size distribution of recruited fragments was skewed toward smaller-sized fragments during both sampling periods.

Thalassia Zone

The recruitment of A. spicifera fragments into a Thalassia meadow was examined experimentally and varied among stations and substrata (Table XIII). More A. spicifera fragments were found at Stations II, III, and IV, which were in close proximity to the Acanthophora Zone, than at Stations I and V. Station I was located in the fore reef and exposed to the most wave activity, while station V was also located in the fore reef and exposed to little wave activity and minimal current velocities. Significantly more fragments of A. spicifera colonized the

Figure 49. Mean size (length) of fragments of A. spicifera settling in the Acanthophora Zone (9 September to 22 October 1979 [wet season]; 21 January to 6 March 1980 [dry season]). Six plots (0.3 m X 0.5 m) were chosen randomly and cleared of Acanthophora plants to expose a Laurencia understorey. Around each plot, a border of 0.5 m was similarly cleared to serve as a buffer zone. Vertical bars indicate $\pm$ the standard deviation.

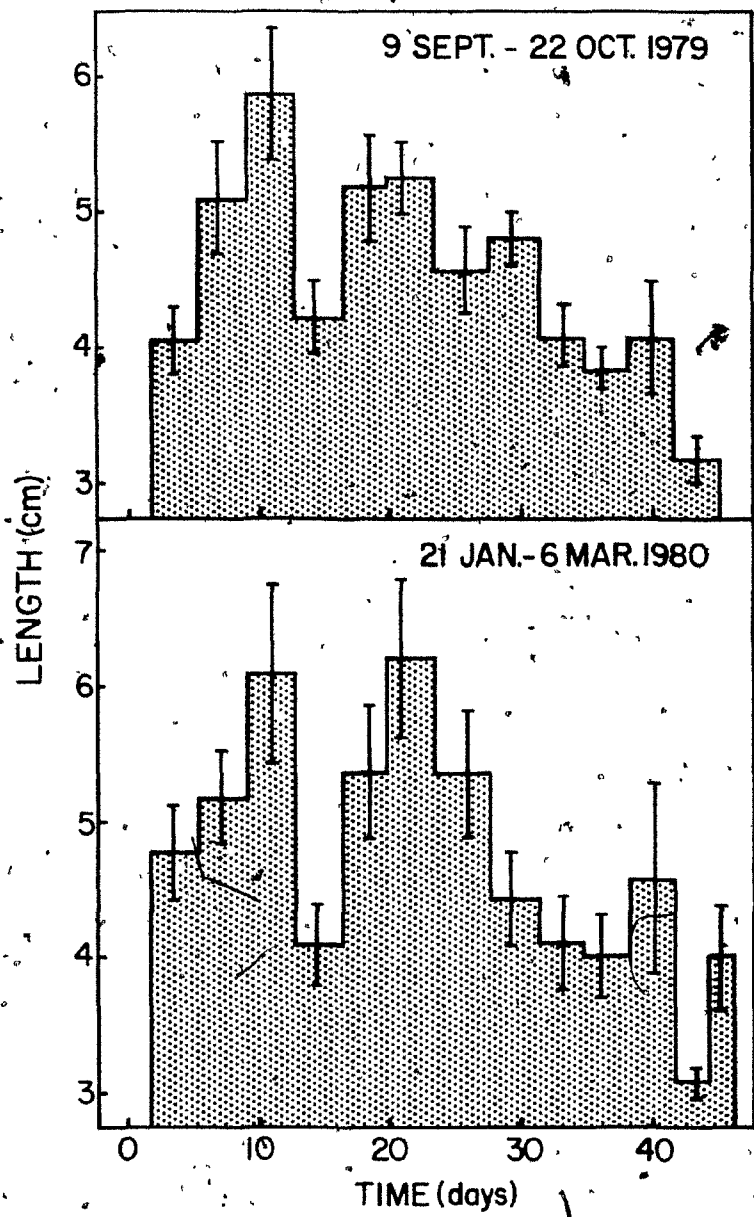


Figure 50. Numbers of A. spicifera fragments of different size classes settling in the Acanthophora zone (9 September to 22 October 1979 [wet season]; 21 January to 6 March 1980 [dry season]). Six plots (0.3 m X 0.5 m) were chosen randomly and cleared of Acanthophora plants to expose a Laurencia understorey. Around each plot, a border of 0.5 m was similarly cleared to serve as a buffer zone.

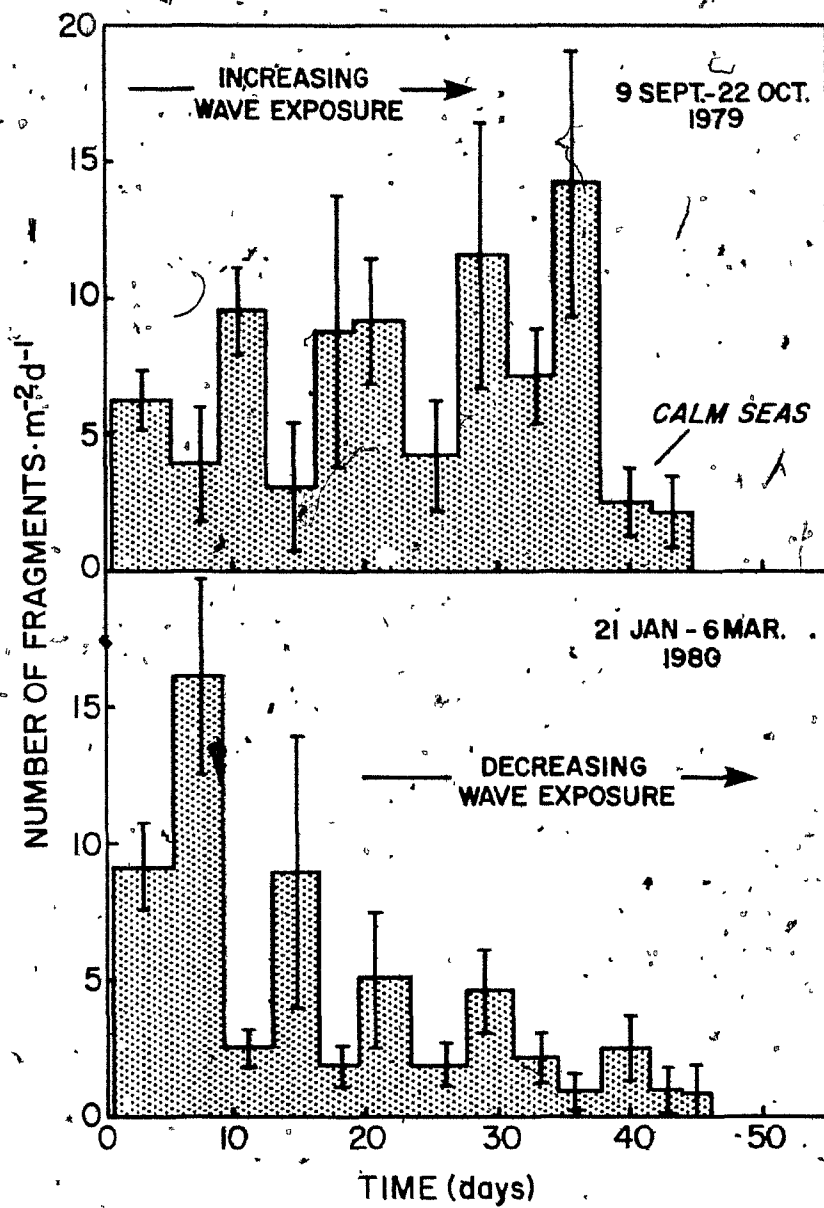


Table XIII. Thalassia Zone Colonization. Number of A. spicifera fragments recruited onto T. testudinum, L. papillosa, and Porites-rubble at five Thalassia Zone Stations. Each station consisted of a square meter plot of each substratum that was examined at the end of six months for the number of fragments present (September 1979 to February 1980).

Substratum	Stations (no. of fragments)					Total
	I	II	III	IV	V	
<u>T. testudinum</u>	0	0	0	0	0	0
<u>Porites</u> -Rubble	0	7	1	19	0	27
<u>L. papillosa</u>	0	18	46	34	0	98
Total	0	25	47	53	0	125

Null Hypothesis (Ho) :

- (1) No difference in settlement of fragments onto the different substratum: Reject Ho at $\alpha = 0.001$: $X^2 = 122.9$: $df = 2$.
- (2) No difference in the settlement of fragments at different stations: Reject Ho at $\alpha = 0.001$: $X^2 = 100.8$: $df = 4$.
- (3) No difference in settlement of fragments onto:
 - T. testudinum and Porites: Reject Ho at $\alpha = 0.001$: $X^2 = 27.0$: $df = 1$.
 - T. testudinum and L. papillosa: Reject Ho at $\alpha = 0.001$: $X^2 = 98.0$: $df = 1$.
 - L. papillosa and Porites: Reject Ho at $\alpha = 0.001$: $X^2 = 40.3$: $df = 1$.

Table XXIII. (cont'd)

Null Hypothesis (Ho) :

(4) . No difference in the settlement of fragments between stations:

I and II;	Reject Ho at $\alpha = 0.001$; $X^2 = 25.00$; df = 1.
I and III;	Reject Ho at $\alpha = 0.001$; $X^2 = 47.00$; df = 1.
I and IV;	Reject Ho at $\alpha = 0.001$; $X^2 = 53.00$; df = 1.
I and V;	Accept Ho at $\alpha = 0.050$; $X^2 = 0.00$; df = 1.
II and III;	Reject Ho at $\alpha = 0.010$; $X^2 = 6.72$; df = 1.
II and IV;	Reject Ho at $\alpha = 0.010$; $X^2 = 10.09$; df = 1.
II and V;	Reject Ho at $\alpha = 0.001$; $X^2 = 25.00$; df = 1.
III and IV;	Accept Ho at $\alpha = 0.050$; $X^2 = 0.36$; df = 1.
III and V;	Reject Ho at $\alpha = 0.001$; $X^2 = 47.00$; df = 1.
IV and V;	Reject Ho at $\alpha = 0.001$; $X^2 = 53.00$; df = 1.

substratum of L. papillosa than any other substratum. Of the three substrata, 98 fragments were found in the plots of L. papillosa, followed by 27 fragments in the Porites-rubble plot, while no fragments of A. spicifera colonized the blades of T. testudinum. It was observed that filamentous green, brown, and red algae aided in fragment recruitment onto Porites-rubble. After 3 to 4 weeks, most of the coral rubble was colonized by opportunistic species that became entangled with fragments of A. spicifera.

Fragment Snagging and Attachment

A. spicifera versus L. papillosa

Most fragments of A. spicifera and L. papillosa snagged at current velocities of about 0.08 m s^{-1} , while 93 % of the A. spicifera and 92 % of the L. papillosa snagged at 0.24 m s^{-1} (Table XIV). Differences in snagging ability between species were not significant; the snagging of fragments, however, decreased significantly with increased current velocity (Table XV). Similarly, the distance used by for a fragment to snag did not differ between species, but increased with increased current velocity (Table XVI).

After 72 hours, the number of fragments remaining in position on the reef did not differ between A. spicifera and L. papillosa, or between different current velocities (Table XV). At low current velocities (0.06 to 0.09 m s^{-1}), 21 % of the A. spicifera and 23 % of the L. papillosa were still present after 72 hours. Similarly, at high

Table XIV. The effect of current velocity on drifting fragments of A. spicifera and L. papillosa: (i) in their ability to snag, (ii) in their ability to remain in position for 72 hours, and (iii) in their distance traveled before snagging in the Acanthophora Zone. Each fragment was released from a starting position and followed until snagged (i.e., remaining in the same position for more than 5 min.). After 72 hours, fragments still in position were counted.

Species	Current Velocity m s^{-1}	N	Snagged (%)	Remaining at 72 h (%)	Snagging Distance (m) ($\bar{X} \pm \text{SD}$)
<u>A. spicifera</u>	0.09	47	100	21	3.2 $\pm$ 1.4
	0.24	29	93	31	10.1 $\pm$ 5.6
<u>L. papillosa</u>	0.06	66	100	23	3.8 $\pm$ 1.7
	0.24	25	92	20	9.2 $\pm$ 5.4

N = no. of fragments

Table XV. Chi-square Analysis evaluating the effects of current velocity on drifting fragments of A. spicifera and L. papillosa in their ability to snag and remain in position for 72 hours in the Acanthophora Zone. Each fragment was released from a starting position and followed until snagged (i.e., remaining in the same position for more than 5 min.). After 72 hours, fragments still in position were counted.

Period:	Species:	<u>A. spicifera</u>		<u>L. papillosa</u>		Total
		Snagged	Not Snagged	Snagged	Not Snagged	
	Current: m s^{-1}					
5 min	0.06 to 0.09	47	0	66	0	113
	0.24	27	2	23	2	54
72 h	0.06 to 0.09	10	37	15	50	110
	0.24	9	20	5	20	54
Total		93	59	109	72	333

Null Hypothesis (H_0):

- (1) There are no differences in snagging ability between A. spicifera and L. papillosa. Accept H_0 at $\alpha = 0.05$; $X^2 = 0.03$; $df = 1$.
- (2) There are no differences in the numbers of fragments that snagged and remained in position for 72 hours. Reject H_0 at $\alpha = 0.001$; $X^2 = 191.61$; $df = 1$.
- (3) There are no differences in the number of fragments that snagged at 0.09 m s^{-1} and 0.24 m s^{-1} . Reject H_0 at $\alpha = 0.001$; $X^2 = 19.99$; $df = 1$.
- (4) There are no differences in the number of snagged fragments that remained in position for 72 hours at 0.09 m s^{-1} and 0.24 m s^{-1} . Accept H_0 at $\alpha = 0.05$; $X^2 = 0.26$; $df = 1$.

Table XVI. Analysis of Variance Table of Snagging Distance of A. spicifera and L. papillosa in the Acanthophora Zone under varied current regimes.

	df	ss	ms	F	p
Main Effects	2	1305.1	652.6	60.6	< 0.001
Species	1	0.6	0.6	0.5	> 0.817
Current	1	1293.6	120.1	11.2	< 0.001
Error	159	1712.2	10.8		
Total	162	3036.7	18.7		

Current Velocity: (1) 0.06 to 0.09 m s⁻¹, and (2) 0.24 m s⁻¹
 Species: (1) A. spicifera, and (2) L. papillosa

current velocity (0.24 m s^{-1}), 31 % of the A. spicifera and 20 % of the L. papillosa remained in position. These results suggested that more than 25 % of the snagged fronds had more than 3 days to become secured to new substrata. Tagged fronds that were not found in the position of snagging after 72 hours were frequently observed farther downstream. In all cases, A. spicifera always attached to L. papillosa. The converse situation, L. papillosa attaching to A. spicifera, was never observed. At the time of the manipulation (February 1980), the percent cover of A. spicifera was at a maximum, covering most available surfaces in the Acanthophora Zone.

Reef-Flat Comparisons.

A. spicifera fragments were the most successful in colonizing the Acanthophora Zone. The number of snagged fragments, the distance required by a fragment to snag, and the number of snagged fragments remaining in position for 72 hours decreased significantly outside of the Acanthophora Zone (Table XVII). Small changes in current velocity in the Thalassia beds, from 0.08 to 0.09 m s^{-1} , decreased the snagging ability of fronds from 100 % to 15 % and increased the distance required to snag from 2.2 to 11.8 m. After 72 hours, no fragments were found in the Thalassia beds. At current velocities of 0.18 m s^{-1} , A. spicifera was not able to snag onto the Thalassia substratum. When releasing fragments into currents of 0.12 m s^{-1} in the Thalassia-rubble area, 76 % of the fragments snagged and 7 % of the released fragments were still

Table XVII. Chi-square Analysis evaluating the effects of current velocity on drifting fragments of A. spicifera in their ability to snag and in their ability to remain in position for 72 hours in the Acanthophora Zone. Each fragment was released from a starting position and followed until snagged (i.e., remaining in the same position for more than 5 min.). After 72 hours, fragments still in position were counted.

Period: Current: $m s^{-1}$	5 min		72 h	
	Snagged	Not Snagged	Snagged	Not Snagged
0.09	47	0	10	37
0.18	50	4	12	42
0.24	27	2	9	20
Total	124	6	31	99

Null Hypothesis (H_0):

- (1) There are no differences in the number of fragments that snagged and remained in position for 72 hours at different current velocities. Reject H_0 at $\alpha = 0.001$; $\chi^2 = 138.17$; $df = 1$.
- (2) There are no differences in the number of fragments that snagged at different current velocities. Accept H_0 at $\alpha = 0.050$; $\chi^2 = 3.57$; $df = 2$.
- (3) There are no differences in the number of fragments that remained in position for 72 hours at different current velocities. Accept H_0 at $\alpha = 0.05$; $\chi^2 = 1.07$; $df = 2$.

present after 72 hours. Of the fragments that remained for 72 hours, all were attached to pieces of coral rubble rather than to blades of Thalassia. In contrast to the two areas of Thalassia, 93 % of the fragments snagged and 21 % of the released fragments remained for 72 hours in the Acanthophora Zone at a current velocity of 0.18 m s^{-1} . At current velocities of 0.24 m s^{-1} , 93 % of the fragments snagged and 31 % of the released fragments were still present after 72 hours. These differences, in snagging between current velocities of 0.18 and 0.24 m s^{-1} were not significantly different (Table XVIII). At current velocities of 0.18 and 0.24 m s^{-1} , about 10.5 m of reef were required to snag a fragment of A. spicifera in the Acanthophora Zone.

The probability of an Acanthophora fragment successfully colonizing a back-reef habitat was estimated from: (i) the mean distance across each back reef habitat (this was determined to be 36 m for the Acanthophora Zone, 22 m for the Thalassia-Rubble Area, and 45 m for the Thalassia Zone); (ii) the distance required by a fragment to snag (Table XVII); (iii) the percentage of released fragments that did not snag (Table XVII); and (iv) the percentage of fragments successfully remaining for 72 hours. Fragments remaining for 72 hours were assumed permanently attached (this was later confirmed; Fig. 51). The probability of A. spicifera colonizing the Acanthophora Zone at different current velocities was estimated to be 93 % at 0.09 m s^{-1} , 49 % at 0.18 m s^{-1} , and 62 % at 0.24 m s^{-1} . Fragments of A. spicifera had no chance of recruiting into the Thalassia Zone at current velocities between 0.08 and 0.18 m s^{-1} and had only a 7 % chance of

Table XVIII. The effect of current velocity and reef-flat location on drifting fragments of A. spicifera: (i) in their ability to snag, (ii) in their ability to remain in position for 72 hours, and (iii) in their distance traveled before snagging in the Acanthophora Zone. Each fragment was released from a starting position and followed until snagged (i.e., remaining in the same position for more than 5 min.). After 72 hours, fragments still in position were counted.

Reef Habitat	Current Velocity m s^{-1}	N	Snagged (%)	Remaining at 72 h (%)	Snagging Distance (m) $\bar{X} \pm \text{SD}$
<u>Acanthophora</u> Zone					
	0.09	47	100	21	3.2 ± 1.4
	0.18	54	93	22	10.9 ± 5.8
	0.24	29	93	31	10.1 ± 5.6
<u>Thalassia</u> -Rubble Area					
	0.12	29	76	7	14.0 ± 5.6
	0.18	20	0	0	
<u>Thalassia</u> Zone					
	0.08	42	100	0	2.2 ± 0.3
	0.09	20	15	0	11.8 ± 6.8
	0.18	20	0	0	

N = no. of fragments

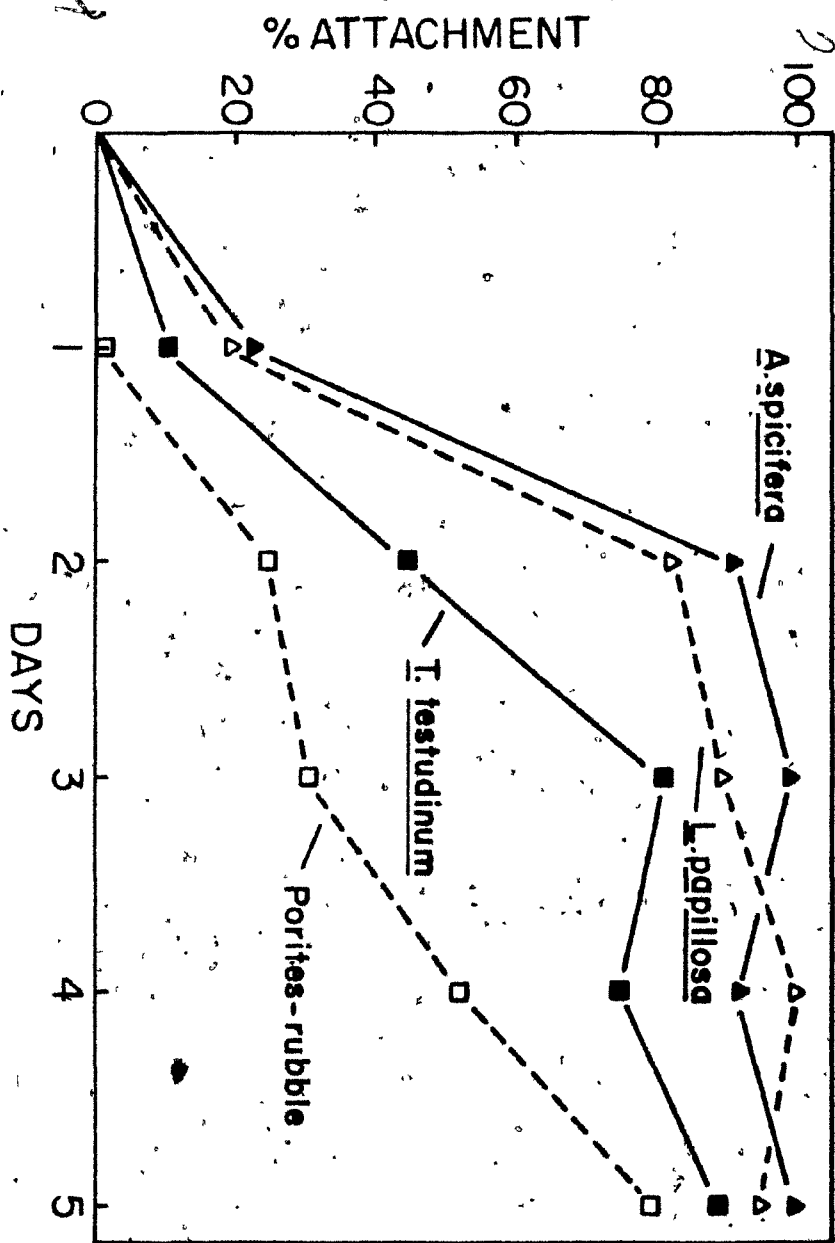
colonizing a Thalassia-Rubble Area at 0.12 m s^{-1} .

Rates of Attachment

A. spicifera attached the most rapidly to another frond of A. spicifera or to a frond of L. papillosa. By the end of the second day, between 91 to 83 % of the fragments of A. spicifera had attached to A. spicifera and L. papillosa, respectively (Fig. 51). At this time, more fragments of A. spicifera attached to the substrata of A. spicifera and L. papillosa than to T. testudinum or Porites-rubble (Test of Percentages, $p < 0.001$); the differences observed between A. spicifera and L. papillosa and between T. testudinum and Porites-rubble were not significant (Test of Percentages, $p > 0.05$). After five days, about 90 % of the A. spicifera fragments were attached to Thalassia blades, and about 80 % of the A. spicifera fragments were attached to Porites-rubble. Accordingly, Figure 51 shows blades of T. testudinum are, in general, a better substratum for fragment colonization than Porites-rubble.

The attachment of A. spicifera to a surface involves the contact of determinate branchlets with a substratum, followed by a period of growth. The growth of determinate branchlets took three forms: (i) a stimulation of the branchlet to produce a spineless branch or branches which encircled the contacted substratum; (ii) the same spineless branches terminating in a discoid holdfast; and (iii) the branchlets interlocking with and adhering to the branches of their host. The

Figure 51. Percent Attachment (i.e., the physical bonding of two individuals) of A. spicifera with another frond of A. spicifera, L. papillosa, T. testudinum, and Porites-rubble. Each point represents 40 species pairs.



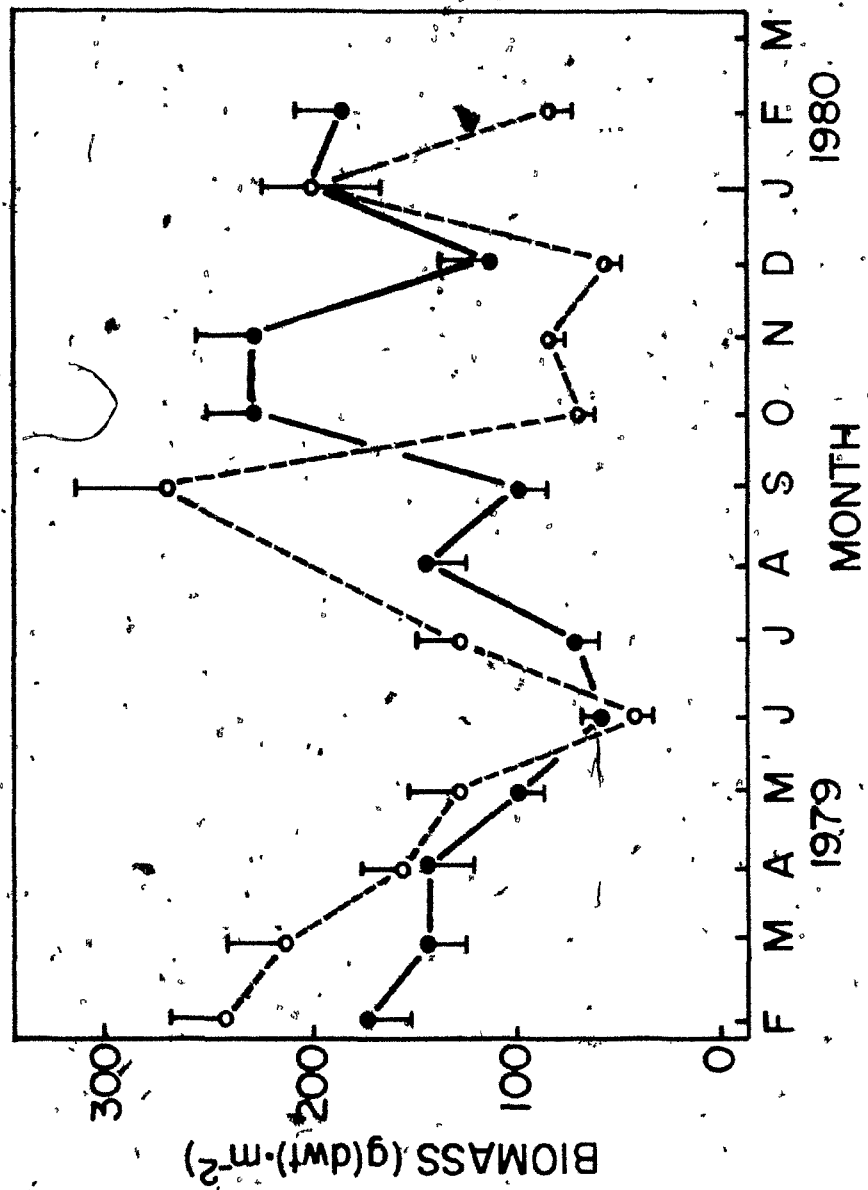
second method was extensively used with Thalassia, and the other methods were employed separately or together with remaining species.

3.3 The Maintenance and Persistence of A. spicifera

Seasonal Variation in L. papillosa Biomass

From February 1979 to September 1979, there was a greater biomass of L. papillosa in the Laurencia Zone than in the Acanthophora Zone. Conversely, from October 1979 to February 1980, the opposite was true (Fig. 52). The biomass of L. papillosa decreased steadily from February to June, with the increase in occurrence of aerial exposures (Fig. 15) and the lower solar irradiance (Fig. 14). At that time, L. papillosa decreased in biomass by 81 % in the Laurencia Zone and by 69 % in the Acanthophora Zone. From June to September, the biomass of L. papillosa in the Laurencia Zone increased in abundance to $268 \text{ g (d wt) m}^{-2}$. In the Acanthophora Zone, L. papillosa biomass rose to a maximum of $229 \text{ g (d wt) m}^{-2}$ in November and, for the most part, maintained this biomass for the remainder of the sampling period (Feb. 1980). After September and continuing until December, aerial exposures and dry-season storms reduced the Laurencia Zone biomass of L. papillosa to a minimum of about $70 \text{ g (d wt) m}^{-2}$. In January 1980, the Laurencia Zone biomass of L. papillosa increased to about $200 \text{ g (d wt) m}^{-2}$, but soon decreased to a minimum in February. Two important observations deserve mention: (i) in the Acanthophora Zone, the canopy of A. spicifera appeared to protect the understorey plants of L. papillosa from desiccation and thermal stress; and (ii) the low reef elevation of the Acanthophora Zone resulted in less frequent aerial exposures (Fig. 17). Together, these

Figure 52. Seasonality of L. papillosa biomass in the Laurencia and Acanthophora Zones (February 1979 to March 1980). Vertical bars indicate + or - one standard deviation from the mean. $n = 100$ for each point in the Acanthophora Zone (•). $n = 50$ for each point in the Laurencia Zone (o).



observations can account for the greater biomass of L. papillosa in the Acanthophora Zone than in the Laurencia Zone from October 1979 to February 1980.

Aerial Exposures

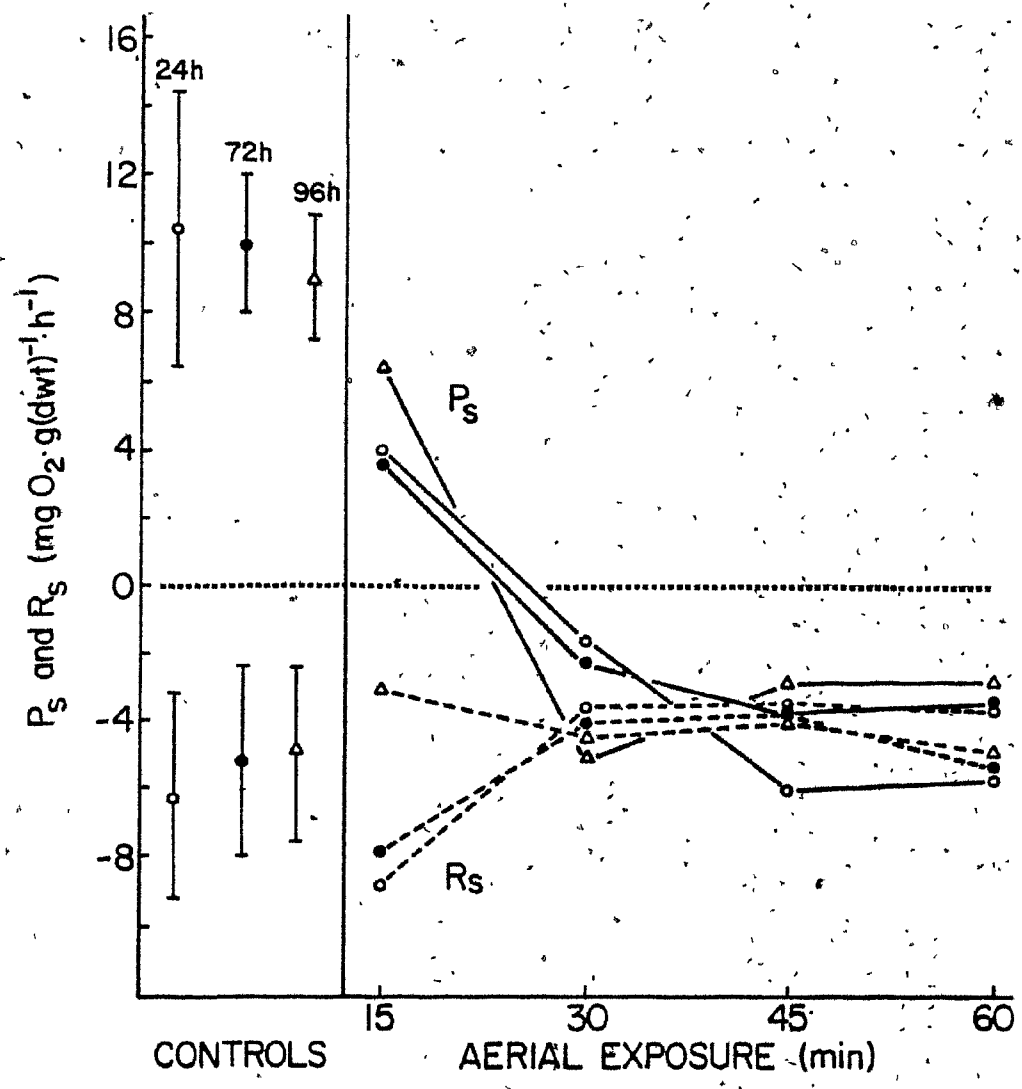
Daytime Tolerance

When placed on a moistened piece of coral rubble, individual fronds of A. spicifera survived 15 minutes of direct sunlight. No fronds survived periods of more than 30 minutes in the air (Fig. 53). Fronds showing no net oxygen production did not recover, losing all their pigments and breaking apart. After 96 hours, surviving fronds of A. spicifera were not fully recovered from the aerial exposure, showing significantly less oxygen production than did the controls ($T = 3.3$, $df = 13$, $p < 0.01$). Measurements of respiration provided little information regarding frond survival, with few respiration rates in the experimental treatments differing from the controls. Apical regions of branches were most susceptible to desiccation and thermal effects, with the fronds consistently dehydrating and breaking apart basipetally.

A. spicifera versus L. papillosa

When L. papillosa and A. spicifera were exposed simultaneously in the air for 30 minutes, fronds of L. papillosa showed the least amount

Figure 53. Mean rate of apparent photosynthesis and respiration of A. spicifera fronds after different aerial exposure and recovery periods. Fronds used as controls were not exposed in the air. Vertical bars indicate ± the standard deviation. $n = 15$ for each point.



of injury after 24 hours. The photosynthetic capacity of A. spicifera fronds decreased by 83 %, while fronds of L. papillosa decreased by 61.5 % (Fig. 54). Also, all fronds survived the exposure period of 30 minutes on a partly cloudy day (i.e., about 50 % cloud cover).

Night Tolerance

When "mats" of A. spicifera were exposed in the air at night, significant injuries to fronds on the surface of the "mats" occurred, but no injuries were sustained among fronds within the "mats" (Table XIX). In addition, no frond mortality resulted during the 12-hour exposure period. Fronds on the surface of the "mat" showed different degrees of desiccation; the most severely desiccated areas appeared as dark, dehydrated patches. After 24 hours in seawater, fronds collected from these dark patches showed a reduction of 82 % in photosynthetic capacity, while fronds on the surface of the "mat" that showed no outward signs of desiccation were reduced by 22 % in photosynthetic capacity (Table XIX and Fig. 55).

Individual versus Aggregate

The injury to L. papillosa fronds increased as exposure to air and direct sunlight increased. "Individuals" of L. papillosa survived 30 minutes of aerial exposure, while fronds of Laurencia "aggregates" survived longer than five hours (Fig. 56). After 45 minutes of exposure

Figure 54. Changes in the rate of apparent photosynthesis of of A. spicifera and L. papillosa "individuals" after a 30-min exposure in the air and a 24-hour recovery period. Aerial exposures began at midday on a partly cloudy day (50 % cover). Also shown, is the percent reduction in apparent photosynthesis. Vertical bars indicate ± 95 % confidence intervals. $n = 12$ for each point. C = Control; Exp = Experimental.

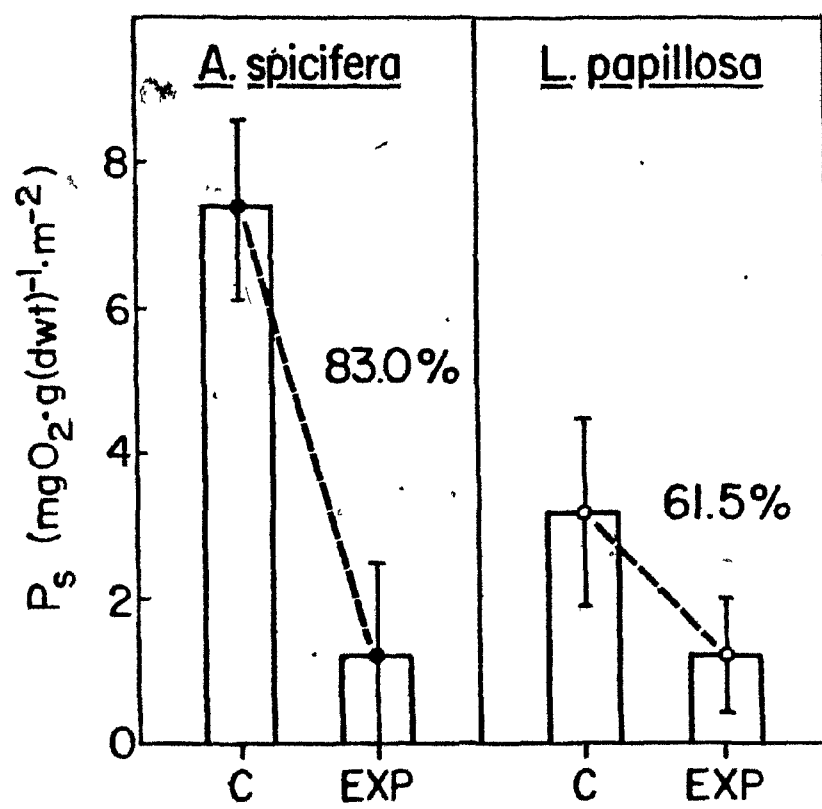


Table XIX. Two-tailed Students t-test evaluating the effect of Nighttime Aerial Exposures on the apparent photosynthesis of A. spicifera (October-December 1981).

Treatment:		t	df	p
Control	Experimental			
Upper Mat	X Upper Mat			
	Least Desiccated	5.6	16	< 0.001
	Most Desiccated	17.8	24	< 0.001
Lower Mat	X Lower Mat	1.3	11	> 0.050

Figure 55. Nighttime Aerial Exposures: A. spicifera mats were collected from the field and either placed into seawater tanks (control) or just above water level on the reef flat (experimental treatment). After 12 hours (1500 to 0700 h), fronds from the experimental treatment were return to seawater and allowed to recover for 24 hours. All fronds were then measured for for apparent photosynthesis. In the experimental treatment, fronds were further divided into partially and severely desiccated; severely desiccated fronds were black and dehydrated when removed from the field, while partially desiccated fronds appeared normal. Vertical bars indicate $\pm$ 95 % confidence intervals. N = 10 for experimental treatments. n = 6 for controls: C = Control; Exp = Experimental.

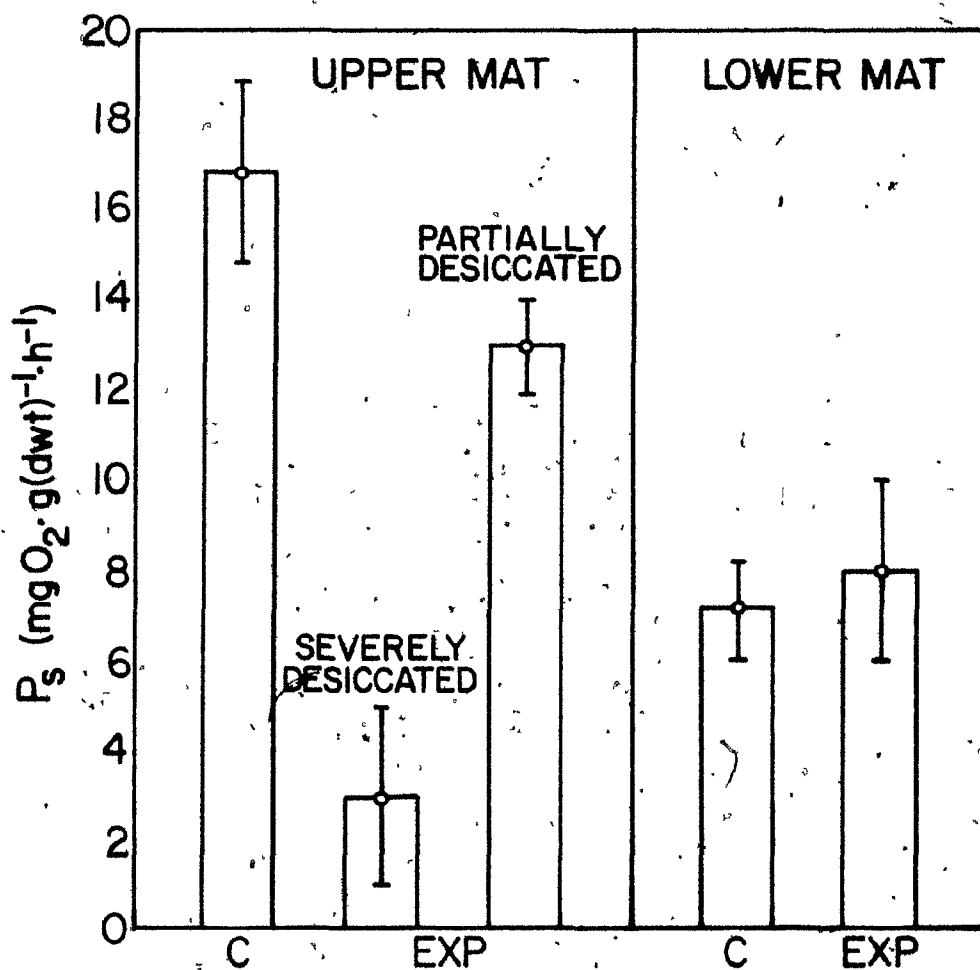
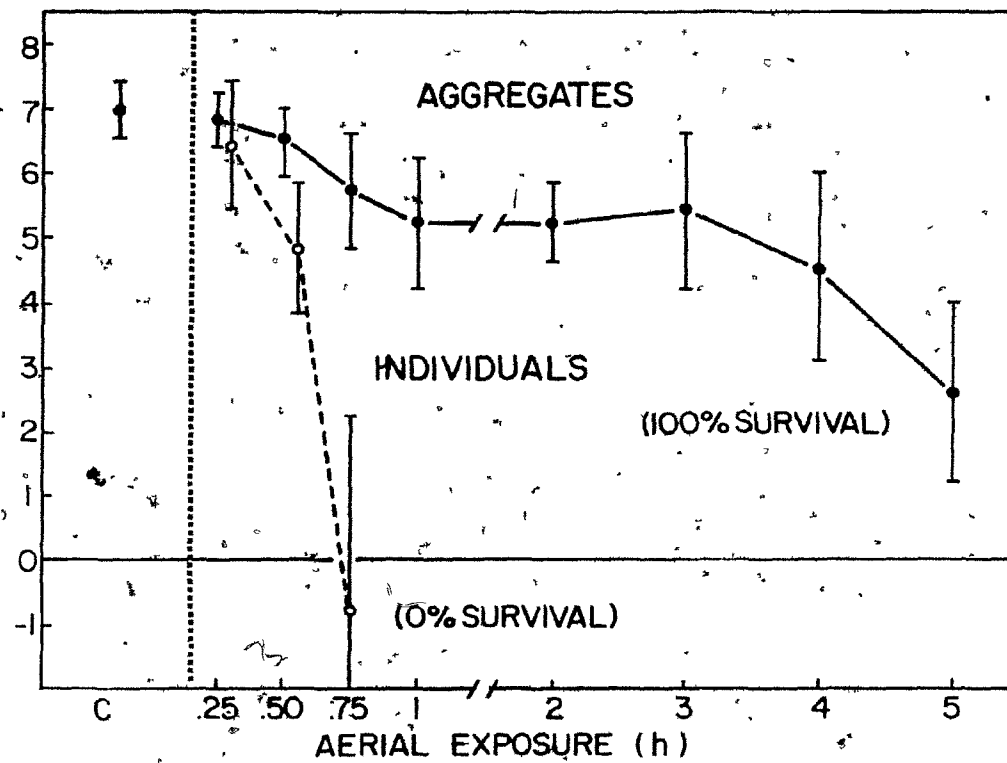


Figure 56. Changes in the mean rate of apparent photosynthesis of L. papillosa fronds growing as "individuals" (separated from "aggregates") or as "aggregates" when subject to different periods of aerial exposure. Fronds used as controls came from the same "aggregate" of L. papillosa but were not exposed in the air. Apparent photosynthesis was measured after a 24 hour recovery period. Vertical bars indicate $\pm$ the standard deviation. $n = 12$ for the control. $n = 6$ for each point in the experimental treatment.



to air and a 24-hour recovery period in a seawater tank, only a decrease of $1 \text{ mg O}_2 \text{ g (d wt)}^{-1} \text{ h}^{-1}$ in apparent photosynthesis was measured among fronds of an "aggregate", while a $6 \text{ mg O}_2 \text{ g (d wt)}^{-1} \text{ h}^{-1}$ decrease occurred among "individuals". After one hour of exposure, all "individuals" lost pigmentation and later disintegrated during the recovery period. In contrast, fronds that were part of an "aggregate" changed little in photosynthetic capacity. After five hours of aerial exposure, single fronds that were part of an "aggregate" continued to show net oxygen production.

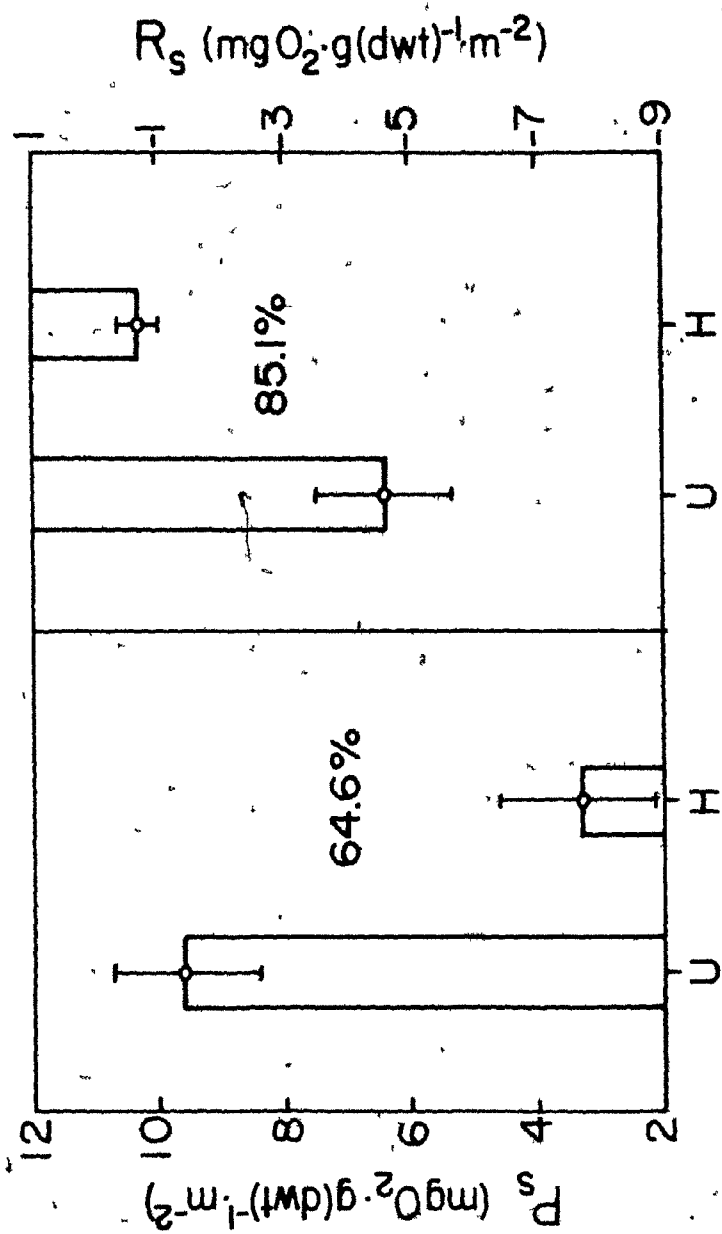
Photosynthetic Partitioning

Comparisons of uprights and holdfasts of A. spicifera revealed significant differences in rates of photosynthesis ($T = 11.35$, $df = 38$, $p < 0.001$) and respiration ($T = 7.59$, $df = 38$, $p < 0.001$). The rate of apparent photosynthesis in Acanthophora was higher in the uprights than in the holdfasts. Similarly, respiration rates were higher in the uprights than in the holdfasts (Fig. 57).

Holdfast versus Upright Tolerance

After 45 minutes of aerial exposure, all holdfasts of A. spicifera recovered to produce new branches, while only 9 of 99 uprights formed new branches. These differences were highly significant ($\chi^2 = 159.48$, $df = 2$, $p < 0.001$). Accordingly, the null hypothesis that survivorship to aerial exposures was independent of thallus location was rejected.

Figure 57. Mean rates of apparent photosynthesis and respiration of holdfasts and uprights of A. spicifera. Also shown, is the percentage decrease in apparent photosynthesis and respiration. Vertical bars indicate $\pm 95\%$ confidence intervals. $n = 12$ for each point. U = Uprights; H = Holdfasts.



Of the surviving uprights, the proximal ends gave rise to the new branches, suggesting that the pigmentation of the plant was not the best criterion for separating uprights from their holdfast.

Competitive Interactions

Fore-Reef Biomass

Biomass samples taken along transects perpendicular to the wave front defined the spatial distribution and the abundance of L. papillosa in the Laurencia Zone. The biomass and occurrence of L. papillosa increased with decreasing wave exposure (Fig. 58a), ranging from a maximum of 253 g (d wt) m^{-2} at the Sheltered Station to a minimum of 191 g (d wt) m^{-2} at the Exposed Station, while percent occurrence ranged from 13 % at the Exposed Station to 66 % at the Sheltered Station. Transects that were parallel to the wave front and taken through the area where A. spicifera was the most abundant defined the abundance of A. spicifera and L. papillosa at the "center of distribution" of A. spicifera; here, the biomass of A. spicifera and L. papillosa was inversely related among the wave-exposure stations ($y = 274 - 0.273 x$, $r^2 = 29.2$, $p < 0.001$ [Figs. 58c and 59]). In addition, the biomass of A. spicifera and L. papillosa was also inversely related at each of the wave-exposure stations (Table XX). At the Sheltered Station, L. papillosa biomass was at its lowest within the "center of distribution" of A. spicifera, but increased significantly proceeding in a landward and seaward direction (Table XXI).

Figure 58. Reef Biomass, Percent Occurrence, and Species Richness at the Wave-Exposure Stations: (a) biomass and percent occurrence of L. papillosa in the Laurencia Zone ($\bar{X} \pm 95\%$ CI); (b) species richness in the Laurencia Zone; and (c) A. spicifera and L. papillosa biomass in the "center of distribution" of A. spicifera ($\bar{X} \pm SE$). E = Exposed Station; ME = Moderately-Exposed Station; S = Sheltered Station.

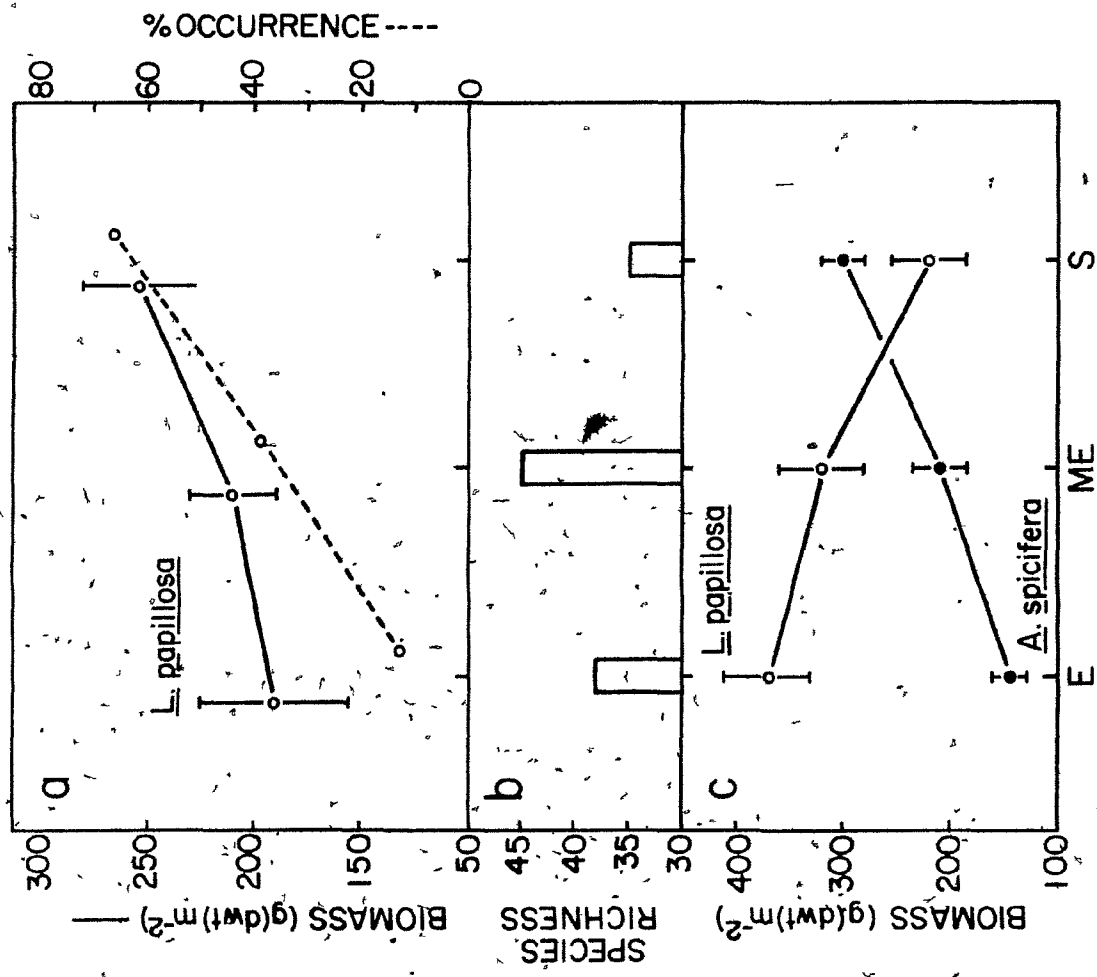


Figure 59. Biomass of A. spicifera and L. papillosa in the "center of distribution" of A. spicifera at the Exposed, Moderately-Exposed, and Sheltered Stations. Vertical bars indicate $\pm$ the standard deviation. $n = 20$ for each point. E = Exposed Station; ME = Moderately-Exposed Station; S = Sheltered Station.

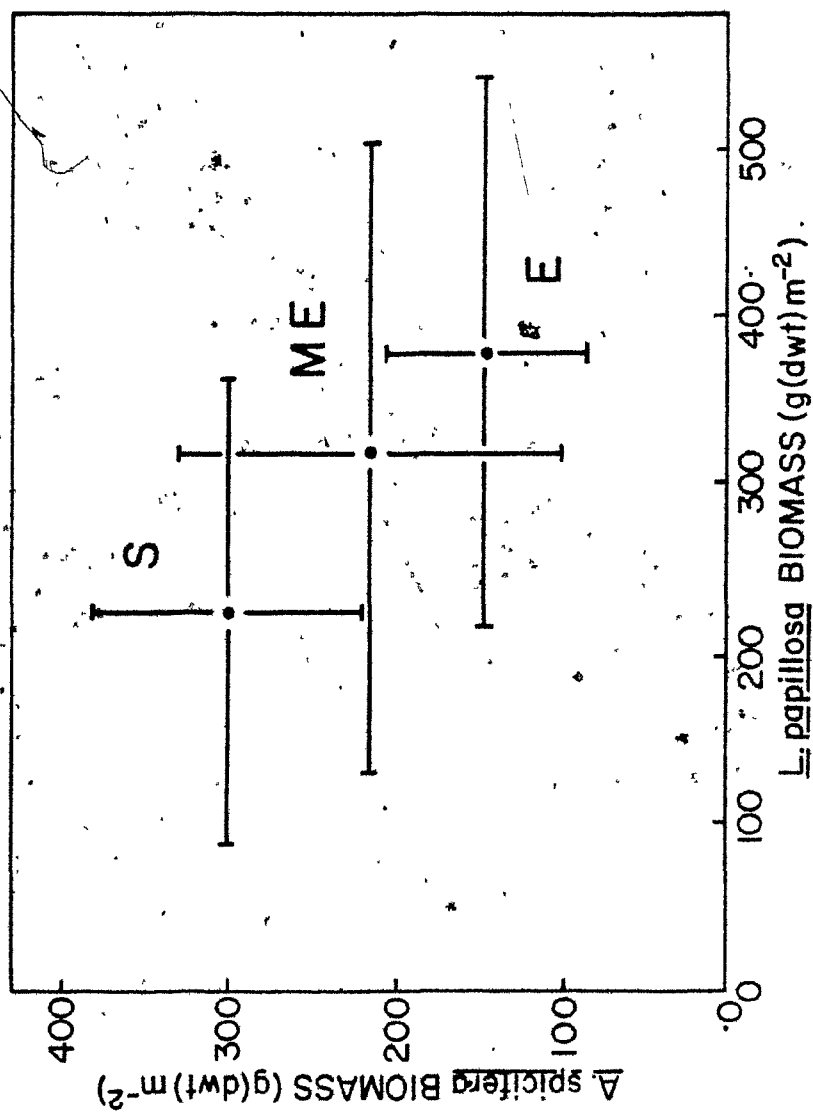


Table XX. Regression Analysis evaluating A. spicifera and L. papillosa biomass within the "center of distribution" of A. spicifera at the Wave Exposure Stations (October 1981). B_0 = Y intercept, B_1 = slope of the regression line, r^2 = regression coefficient

Station.	$Y = B_0 + B_1 X$	r^2	$F_{(1,18)}$	p
Sheltered	$y = 260 - 0.192x$	24.5	5.77	< 0.050
Moderately Exposed	$y = 321 - 0.537x$	30.5	7.91	< 0.050
Exposed	$y = 215 - 0.191x$	21.0	4.78	< 0.050

Table XXI. The biomass of L. papillosa at the Sheltered Station (October 1981). Negative distances were seaward of the "center of distribution of A. spicifera, while positive distances were in a landward direction.

Distance from the Center of Distribution of <u>A. spicifera</u>	<u>L. papillosa</u> Biomass ($\bar{X} \pm SD$)	t	df	p
-0.5 to -3.5	369.23 $\pm$ 218.00	4.77	28	< 0.001
0.0	144.07 $\pm$ 71.00	7.95	38	< 0.001
+0.5 to +3.5	418.83 $\pm$ 7.95			

Units = g (d wt) m⁻²

Biomass samples taken from the "center of distribution" of A. spicifera were further analysed by plotting the ratio of A. spicifera or L. papillosa biomass to total biomass against total biomass. It was observed that the proportion of A. spicifera biomass to total biomass decreased with increased total biomass and had its widest variation (i.e., scatter) at low total biomass (Fig. 60). Similarly, the proportion of L. papillosa biomass to total biomass increased in abundance with increased total biomass and showed its greatest variation at low total biomass (Fig. 61); Figures 60 and 61 are roughly inverse plots of each other.

The scatter of points represented by all the fore-reef stations clearly narrowed as total biomass increased (Figs. 60 and 61), suggesting that at low total biomass, when space was not limiting, a wide variation in A. spicifera and L. papillosa biomass occurred, and that when total biomass was high and space was at a premium, only a limited amount of biomass could be contained within the sample space, decreasing the scatter of points.

The scatter of points representing the Exposed and Sheltered Stations was clearly separated from each other, and those representing the Moderately-Exposed Station encompassed the points of both Exposed and Sheltered Stations. At the Sheltered Station, the proportion of total biomass contributed by A. spicifera was high, while at the Exposed Station, it was comparatively low; the biomass at the Exposed Stations was composed mostly of L. papillosa (Fig. 61). Presumably, the greater amounts of free space at the Exposed Station than at the Sheltered

Figure 60. The ratio of the biomass of A. spicifera to total biomass plotted against total biomass. Solid lines defined the scatter of point at the Exposed Station, while the dashed lines and shaded area defined the scatter of points at the Sheltered Station. $n = 20$ for each station. (O) Exposed Station; (●) Moderately-Exposed Station; (▲) Sheltered Station.

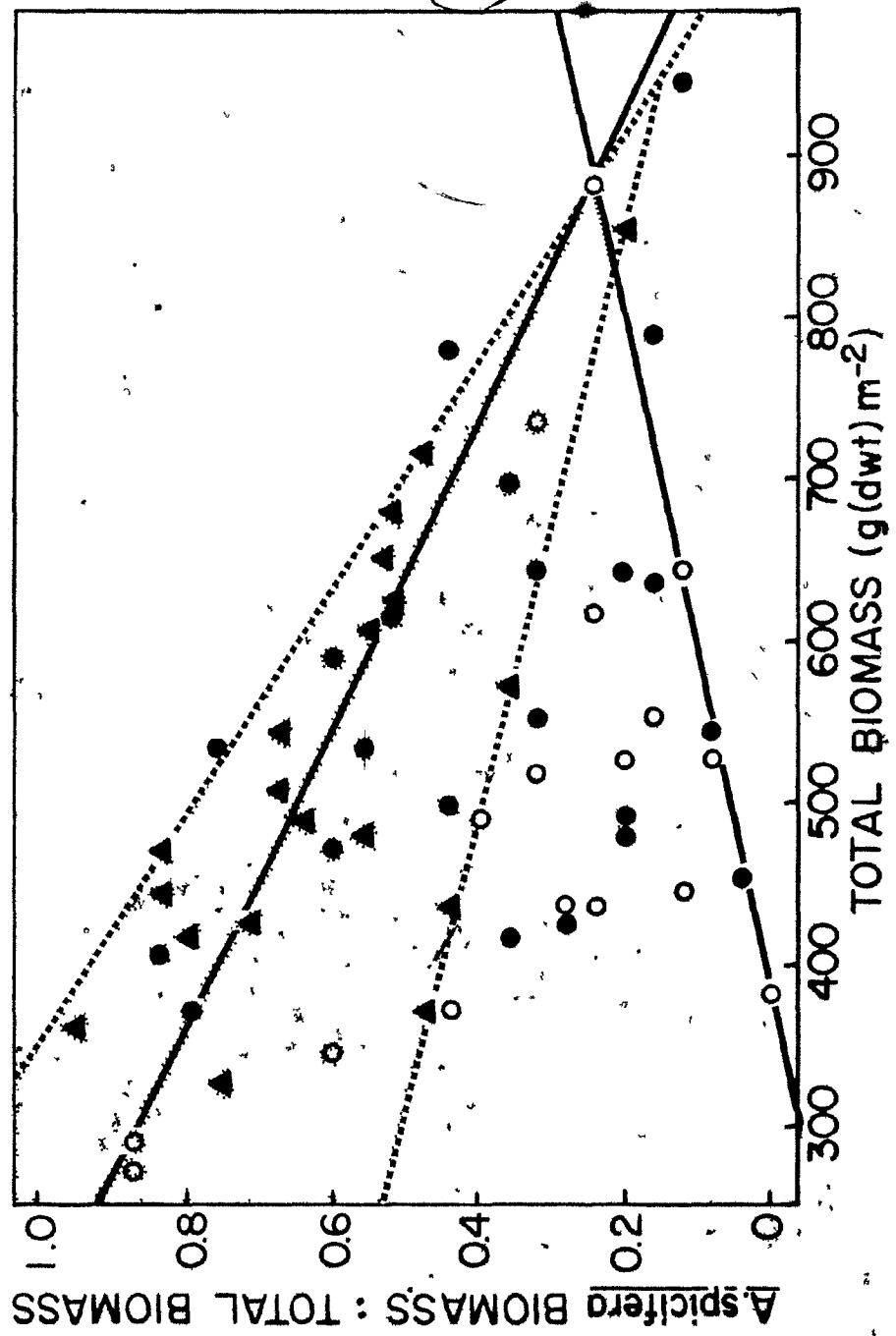
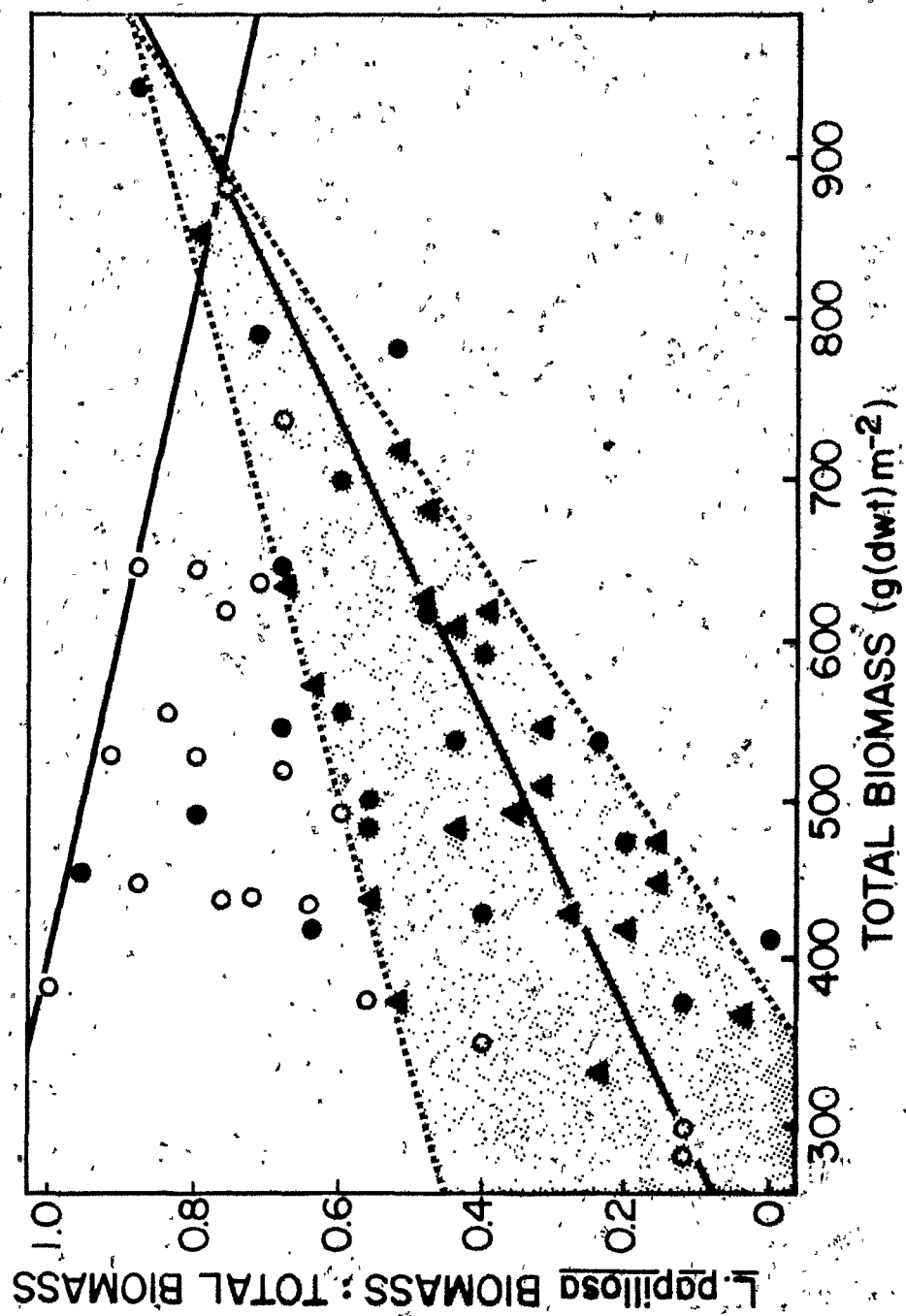


Figure 61. The ratio of the biomass of L. papillosa to total biomass plotted against total biomass. Solid lines defined the scatter of points at the Exposed Station, while the dashed lines and shaded area defined the scatter of points at the Sheltered Station. $n = 20$ for each station. (○) Exposed Station; (●) Moderately-Exposed Station; (▲) Sheltered Station.



Station accounted for the wider scatter of points at the Exposed Station. At the Moderately-Exposed Station, where the widest scatter of points occurred, the biomass sample reflected the increased abundance of A. spicifera and L. papillosa and the increased numbers of species found in the samples (Fig. 58b).

To examine the interaction of Acanthophora and Laurencia further, association analysis (Pielou, 1974) was done with samples collected from the Reef Biomass Study Transects. At the Exposed and Sheltered Stations, A. spicifera and L. papillosa were not positively associated, while at the Moderately-Exposed Station, these species were positively associated (Table XXII). The greater amounts of free-space at the Exposed Station allowed A. spicifera to occur separately or in association with L. papillosa. The decrease in free-space at the Moderately-Exposed and Sheltered Stations was a result of the increase in A. spicifera and L. papillosa biomass (Figs. 58a,c). At the Moderately-Exposed Station, the increase in the biomasses of both species accounted for the positive association between them. At the Sheltered Station, however, a positive association between A. spicifera and L. papillosa was not observed, despite reduced free-space and increased biomass (Figs. 58a,c).

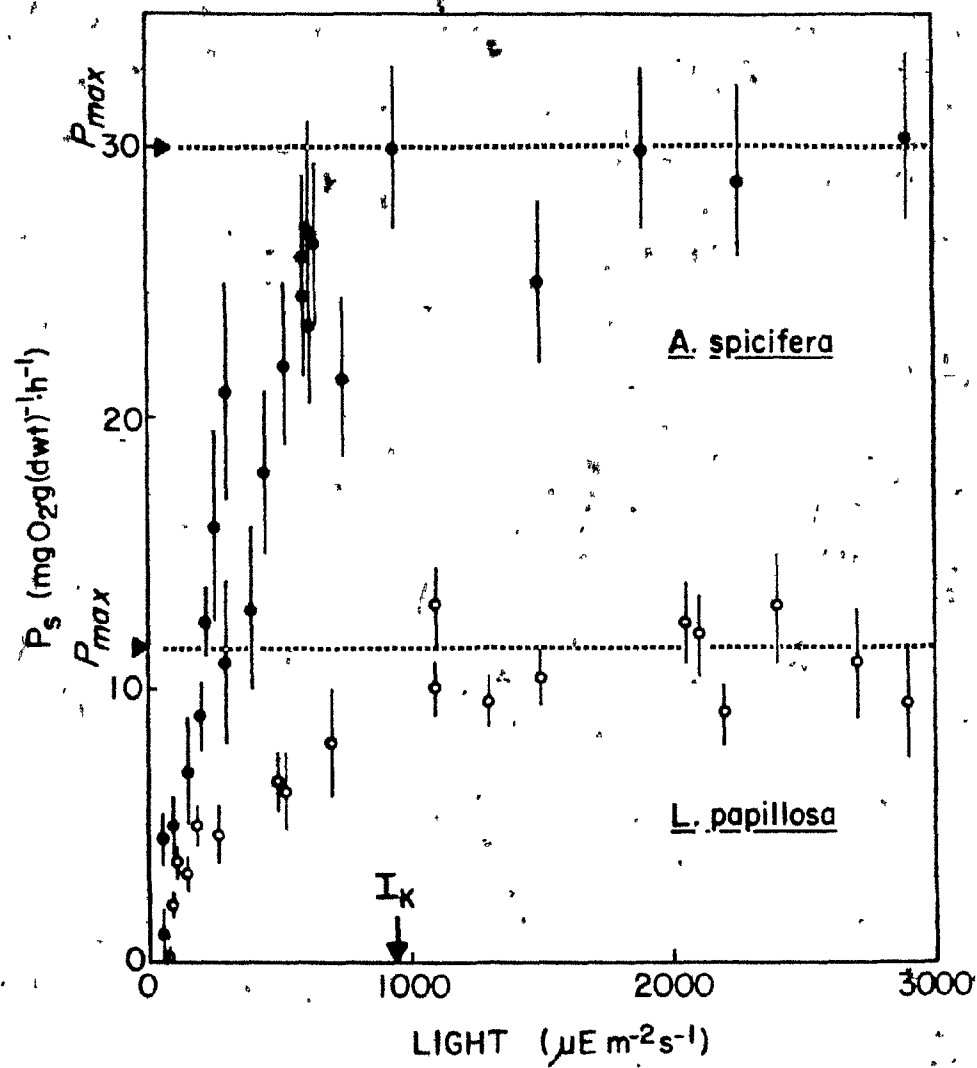
Apparent Photosynthesis

As shown in Figure 62, saturation constants (I_k) for A. spicifera and L. papillosa were at $1000 \mu E m^{-2} s^{-1}$. The maximum photosynthesis (P_{max}) of A. spicifera ($30 mg O_2 g (d wt)^{-1} h^{-1}$) was nearly three times

Table XXII. Association Analysis between A. spicifera and L. papillosa at three Wave-Exposure Stations. Displayed are the number of samples containing only A. spicifera, only L. papillosa, both species, or neither species (Reef Biomass Study; February 1979 to March 1980). (+) = present; (-) = absent

Station:	Sheltered		Moderately-Exposed		Exposed	
<u>L. papillosa:</u>	+	-	+	-	+	-
<u>A. spicifera:</u>						
+	23	1	50	1	12	7
-	122	203	83	210	61	203
χ^2	0.44		5.18		0.13	
p	> 0.05		< 0.025		> 0.05	
Association:	None		Positive		None	

Figure 62. Mean rate of apparent photosynthesis of A. spicifera and L. papillosa as a function of light intensity. Vertical bars indicate $\pm$ the standard deviation. $n = 6$ for each point. (O) L. papillosa; (●) A. spicifera.



the rate of L. papillosa ($11.5 \text{ mg O}_2 \text{ g (d wt)}^{-1} \text{ h}^{-1}$).

Between 20° and 40°C , the rate of apparent photosynthesis of A. spicifera was always higher than that of L. papillosa. The optimum temperature for apparent photosynthesis for both species was about 25°C , the lower end of the temperature range found at Galeta Point during 1979-80 (Figs. 13 and 63).

The rate of apparent photosynthesis of A. spicifera was always greater than that of L. papillosa when exposed to light and temperature combinations found on the reef flat (Fig. 64). In the morning hours, cooler temperatures probably enhanced the productivity of A. spicifera and L. papillosa with temperatures closer to the photosynthetic optimum of the algae (Fig. 63). Maximum photosynthesis occurred at 1100 h for A. spicifera and at 1200 h for L. papillosa. Throughout the day, quantum irradiance and seawater temperature were closely related to each other, with seawater temperature lagging about one hour behind irradiance. Temperature and light were maximum at midday (29°C and $3.2 \times 10^3 \mu\text{E m}^{-2} \text{ s}^{-1}$) and diminished throughout the day. In the afternoon the productivity of both species decreased; the change, however, was always more pronounced in A. spicifera than in L. papillosa. The rates of apparent photosynthesis of A. spicifera and L. papillosa, when exposed to light and temperature combinations found on the reef flat, closely followed the trends in the rates of apparent photosynthesis from light (Fig. 62) and temperature (Fig. 63) gradient measurements.

Figure 63. Apparent photosynthesis of A. spicifera and L. papillosa as a function of seawater temperature. Also shown, is the temperature range of seawater in shallow, reef-flat pools at Galeta Point, Panama. Vertical bars indicate $\pm$ the standard deviation. $n = 6$ for each point. (O) L. papillosa; (●) A. spicifera.

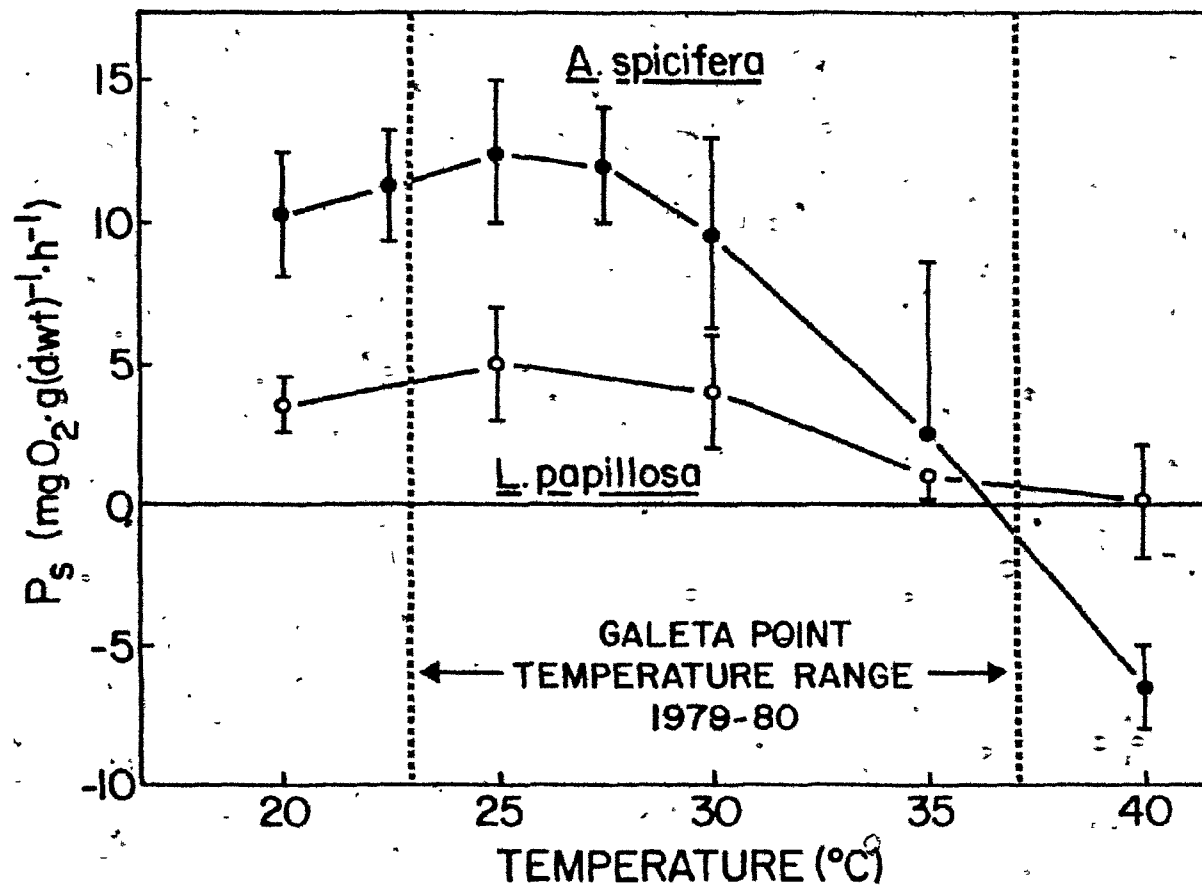
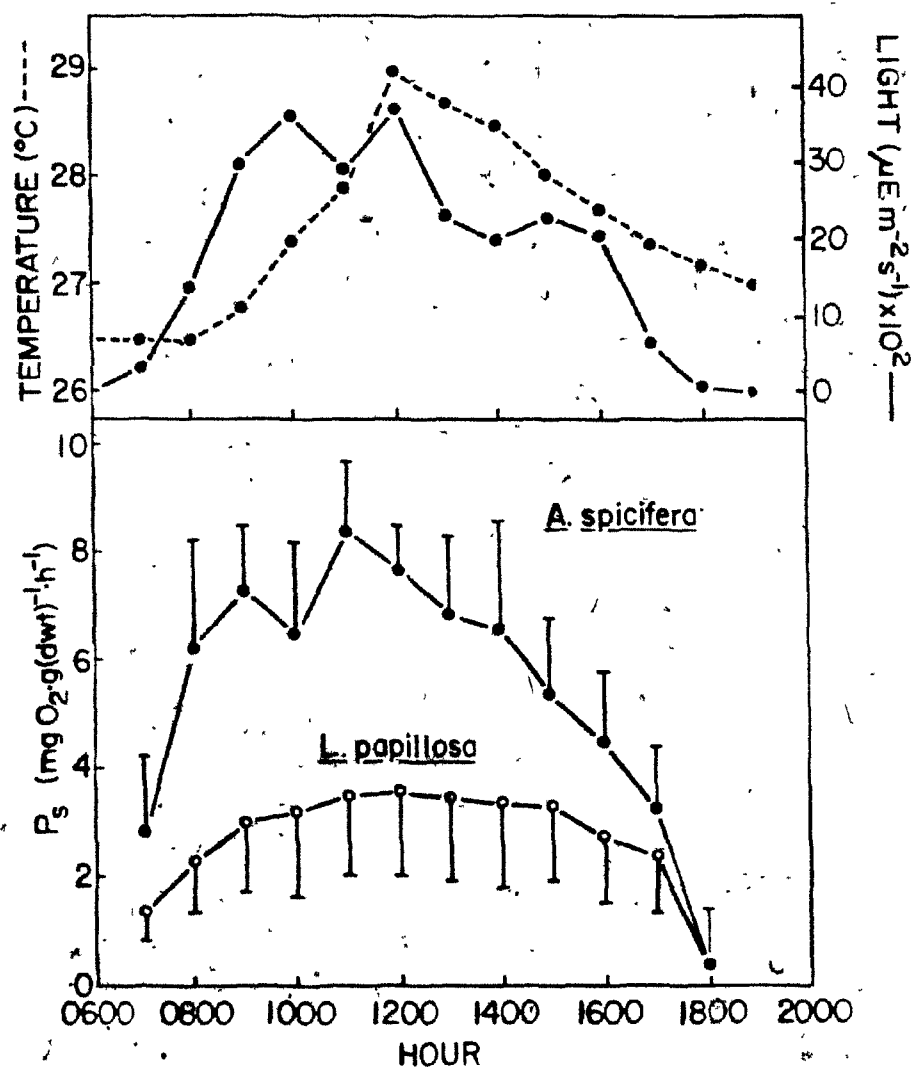


Figure 64. Mean rate of apparent photosynthesis of A. spicifera and L. papillosa at different combinations of reef-flat temperature and quantum irradiance. Vertical bars indicate $\pm$ or $-$ one standard deviation. $n = 6$ for each point.



Overgrowth

Algal Size

To demonstrate short-term changes in species abundance and possible competitive interactions, the heights of A. spicifera and L. papillosa at the Moderately-Exposed Station were examined after different stages in the recovery of the fore reef from an aerial exposure. After about one week, A. spicifera was more than twice the size of L. papillosa (Table XXIII). A. spicifera was visually the dominant Laurencia Zone alga, overgrowing adjacent L. papillosa. L. papillosa found beneath the canopy of A. spicifera was significantly shorter than plants which were nearby and not associated with A. spicifera ($T = 3.0$, $df = 184$, $p < 0.01$). Five weeks after the aerial exposure period, the height of A. spicifera was reduced from 77 to 33 mm, and was now significantly shorter than the surrounding L. papillosa ($T = 4.0$, $df = 400$, $p < 0.001$ [Table XXIII]).

Transmitted Light

Light penetration through the branches of L. papillosa and A. spicifera was greatly reduced. The larger plants of L. papillosa in the back reef filtered out more light than did the shorter plants of L. papillosa in the fore reef. Significantly more light penetrated the "aggregates" at the Exposed and Moderately-Exposed Stations than at the

Table XXIII. Size of A. spicifera and L. papillosa one and five weeks after an Aerial Exposure Period. n = number of plants

Period: One week after Aerial Exposure				
	<u>A. spicifera</u>	<u>L. papillosa</u> Covered by <u>A. spicifera</u>	t	p
Height (mm)	77.3 ± 21.6	27.4 ± 6.6	13.31	< 0.001
X ± S.D.				
n	88	87		
	<u>L. papillosa</u>	<u>L. papillosa</u> Covered by <u>A. spicifera</u>		
Height (mm)	29.5 ± 06.3	27.4 ± 6.6	3.02	< 0.010
X ± S.D.				
n	99	87		
t	12.00			
p	< 0.001			
Period: Five Weeks After Aerial Exposure				
	<u>A. spicifera</u>	<u>L. papillosa</u>	t	p
Height (mm)	32.6 ± 19.6	39.2 ± 23.4	4.02	< 0.001
X ± S.D.				
n	201	201		

Back-Reef and Sheltered Stations ($F = 60.0$; $p < 0.001$). Also, "aggregates" of L. papillosa from the Exposed and Moderately Exposed Stations transmitted about 0.39 % of the light, while at the Back-Reef and Sheltered Stations only about 0.03 % of the light penetrated the branches of L. papillosa. "Mats" of A. spicifera averaged 0.29 % transmittance at the Sheltered Station and Back-Reef Stations (Table XXIV). In full daylight, both "aggregates" and "mats" reduced light levels to well below saturation levels of A. spicifera and L. papillosa (Fig. 62).

Removal Experiment

After six months, four of six stations of L. papillosa that were cleared of A. spicifera showed significant increases in L. papillosa biomass when compared with adjacent areas that were not similarly treated ($T = 52.2$, $df = 6$, $p < 0.01$). The two stations were excluded from the analysis because they were severely disturbed by a late dry-season storm (Table XXV). In the Acanthophora Zone, "mats" of A. spicifera are shown to significantly restrict the growth of L. papillosa.

Holdfasts versus Uprights

The null hypothesis that the uprights and holdfasts of A. spicifera are equally tolerant of low light intensities was rejected. Holdfasts

Table XXIV. Percent Transmitted Light through L. papillosa "aggregates" and A. spicifera "mats" at Wave Exposure Stations (October-November 1981). N = number of photometer readings, min. = minimum, max. = maximum

Species:	Location:	Station:	N	Percent Transmitted Light		
<u>L. papillosa</u>				min.	max.	$\bar{X} \pm SD$
<u>Laurencia</u> Zone:						
		1. Exposed.	24	0.19	0.67	0.30 ± 0.19
		2. Moderately Exposed	24	0.16	1.21	0.47 ± 0.40
		3. Sheltered	24	0.01	0.18	0.01 ± 0.03
<u>Acanthophora</u> Zone:						
		1. Back-Reef	36	0.03	0.10	0.05 ± 0.02
<u>A. spicifera</u>						
<u>Laurencia</u> Zone:						
		1. Sheltered	36	0.05	0.68	0.28 ± 0.24
<u>Acanthophora</u> Zone:						
		1. Back-Reef	24	0.05	1.20	0.30 ± 0.27

Table XXV. Removal Experiment. Six plots were nonrandomly selected in the Acanthophora Zone in areas of a uniform cover of A. spicifera. One half of each plot was randomly selected by a toss of a coin and removed of all A. spicifera. For six months, any fragments of A. spicifera found in these cleared plots were removed. Both halves of the plot were then harvested and compared for differences in biomass. Data represent four of six stations. Two stations were destroyed by a late dry-season storm.

Species:	<u>L. papillosa</u> with <u>A. spicifera</u>	<u>L. papillosa</u> without <u>A. spicifera</u>	t	p
Biomass $\bar{X} \pm \text{S.D.}$	7.44 $\pm$ 1.72	20.66 $\pm$ 4.76	5.22	< 0.001

(1) units = g (d wt) quadrat⁻¹

survived longer periods of no light or reduced light conditions than did their upright counterparts (Table XXVI). In the first treatment, when fronds of A. spicifera were placed into darkened containers for one day, all holdfasts survived to produce branches, while all uprights lost pigmentation and disintegrated. The survivorship of A. spicifera improved when seawater was passed through the darkened containers, more than when fronds were placed under L. papillosa "aggregates" ($\chi^2 = 24.5$, $df = 92$, $p < 0.001$). No doubt the movement of water and the amount of available light were severely restricted in the "aggregates" of L. papillosa. Again, apical regions were more susceptible to low light conditions, with the fronds losing their pigments and breaking apart basipetally. Thus, during periods of low light, the holdfast of A. spicifera acted as a "resistant stage" when uprights could not be maintained.

Table XXVI. Survival of Uprights and Holdfasts in low light intensities (September-December 1981). Plants were subjected to: (i) total darkness in vessels filled with seawater, (ii) total darkness in vessels with seawater pumped through the vessels, and (iii) low light intensity beneath an "aggregate" of L. papillosa that was fitted to darken vessels, submerged in seawater, and sprayed with a jet of seawater. After 24 hours in treatment one and two weeks in treatment two and three, fronds were removed from vessels, sectioned into uprights and holdfasts, and noted for new branch formation after three weeks. (+ = production of new uprights, - = loss of pigmentation and thallus degeneration)

Treatment:	Treatment Duration (days)	Region of Thallus	Branch Production (+) (-)		X^2	p
(I) Dark Container	1	Holdfast	50	0	100.00	< 0.001
		Upright	0	50		
(II) Dark Container with flowing Seawater	47	Holdfast	29	1	15.03	< 0.001
		Upright	16	14		
(III) Dark Container with flowing Seawater with <u>L. papillosa</u>	47	Holdfast	36	4	45.10	< 0.001
		Upright	6	34		

Upright survival was significantly greater in Treatment II than in Treatment III ($X^2 = 24.46$, $df = 92$, $p < 0.001$).

4.0 Discussion

Numerous studies have documented the free-living existence of marine seaweeds (Austin, 1960; Burrows, 1958; Collins, 1914; Deacon, 1942; Dixon, 1965; Edwards & Kapraun, 1973; Gibb, 1957; Rosenvinge, 1905; Sauvageau, 1897; Segawa & Kamura, 1960; Wormersley & Norris, 1959); few researchers, however, have demonstrated that vegetative fragmentation is an effective means of reproduction, despite some obvious morphological and ecological evidence. For example, some species possess differentiated structures which can be attributed only to vegetative fragmentation: namely, the "propagules" of Sphacelaria (Fritsch, 1945; Zimmerman, 1923); the forked lateral branches of Polysiphonia furcellata (C. Ag.) Harv. in Hook. (Bornet, 1892); the leafy outgrowths of Dictyopteris propagulifera Troll. (Fritsch, 1945; Schussing, 1960); and the "crozier-hooks" of Hypnea musciformis (Wulf.) Lamour. (Taylor, 1967) and Bonnemaisonia hamifera Howe (Dixon, 1965; Taylor, 1962). Less conspicuous, but probably far more abundant, are species which release propagules but have no features that would otherwise identify them as species that reproduce by vegetative fragmentation. Among these algae, Audouinella purpureum (Lightf.) Woelk. (Pearlmutter & Vadas, 1978), Catenella caespitosa (Good. & Woodw.) Grev. (Prud'Homme Van Reine et al., 1983), Centroceras clavulatum (C. Ag.) Mont. (Lipkin, 1977), Codium fragile (Sur.) Hariot (Borden & Stein, 1969; Malinowski & Ramus, 1973; Meslin, 1939; Silva, 1957)

Ectocarpus sp. (Russell, 1967), Eucheuma isiforme (C. Ag.)

J. Ag. (Cheney, 1975; Cheney & Babbel, 1978; Dawes et al., 1974),

E. striatum Schmitz (Russell, 1981), and Pilayella littoralis

(Linn.) Kjell. (Wilce et al., 1982) are a few better-known examples.

There has been little field information gathered which demonstrates the successful use by marine algae of vegetative fragmentation. How this mode of reproduction may affect the autecology of a seaweed or community structure has not been addressed in any detail. Recently, Highsmith (1980a, 1980b, 1982) has shown fragmentation to be an extremely important mode of reproduction among reef-building corals, and has noted that fragmenting species avoid high juvenile mortality and reduce the risk of mortality for the genotype. His arguments are equally applicable to fragmenting seaweeds.

There are two main objectives in the ensuing discussion: first, to show that A. spicifera regularly produces fragments which are adapted to colonizing a variety of substrata; and second, to demonstrate the stability of the fragmentation process by examining A. spicifera populations in light of competition and major community disturbances.

4.1 The Fragmentation of Acanthephora spicifera

To demonstrate vegetative fragmentation, this thesis focusses on the fate of A. spicifera fragments on the reef platform of Galeta Point, Panama. It is shown that fragments are broken from plants by waves in the Laurencia Zone, transported by currents across the reef, and

established in the Acanthophora Zone. It is also demonstrated that spores play a minor role in the reef-flat ecology of A. spicifera. Fragments which were washed off the reef are not discussed in any detail.

Measurements of Thallus Breakage

Measurements of drift biomass and standing crop of A. spicifera provide the first evidence of fragmentation. As much as 171 kg (d wt) m^{-2} of L. papillosa and 61 kg (d wt) m^{-2} of A. spicifera were removed from the reef flat (Fig. 30). Over a 15-month period, L. papillosa averaged 38 kg (d wt) m^{-2} while A. spicifera averaged 23 kg (d wt) m^{-2} of drift biomass, demonstrating that significant amounts of algal materials were present in the reef-flat water. The difference in drift biomass between the two species was not surprising, as L. papillosa was more abundant (Fig. 52) and occupied a broader distribution on the reef flat than A. spicifera (Figs. 23 and 24). Also, A. spicifera was made up of 5 % more water than L. papillosa. If A. spicifera were more prone to losing uprights than L. papillosa, more biomass of A. spicifera should be lost from the reef platform when the drift biomass of A. spicifera and L. papillosa was standardized to a square meter of reef and expressed as wet weight. Such were the findings, and as shown in Figure 31, significantly more A. spicifera than L. papillosa was removed from the reef flat. Elsewhere, Eiseman & Benz (1975) and Benz et al. (1979) reported A. spicifera as a

major drift species in Florida, while Conover (1964) observed it in moderate amounts in Texas. The fragmentation of A. spicifera is probably not just confined to Galeta Reef.

In the Acanthophora Zone, three relationships relevant to drift biomass or to the standing crop of A. spicifera were observed: (i) periods of high A. spicifera biomass coincided with periods of increased solar irradiance and decreased aerial exposure and wave action; (ii) periods of maximum exported biomass were correlated with those of maximum biomass in the Acanthophora Zone; and (iii) periods of increasing biomass in the Laurencia Zone always preceded periods of increasing biomass in the Acanthophora Zone (Figs. 27 and 31).

Severe aerial exposure and wave action decreased the abundance and coverage of A. spicifera throughout the reef flat, especially in the Laurencia Zone (Figs. 27 and 45). The biomass of A. spicifera was most abundant when solar irradiance was at a maximum (Figs. 14 and 27) and wave exposure at a minimum. Parallel increases in the biomass of A. spicifera in the Acanthophora Zone, and in solar irradiance suggested that nutrients were not limiting the growth of A. spicifera in the Acanthophora Zone. When the biomass of A. spicifera was at a maximum, the largest quantities of drift biomass of A. spicifera were collected (Figs. 30 and 31). Because the Acanthophora Zone contained most of the reef biomass of A. spicifera, it was reasonable that increases in the biomass of A. spicifera in the Acanthophora Zone coincided with increases in the drift biomass of A. spicifera.

Increases of Acanthophora biomass in the Laurencia Zone always

preceded those in the Acanthophora Zone. Several explanations can account for the delayed increase in the biomass of A. spicifera in the Acanthophora Zone. Only a few, however, are plausible — namely, that A. spicifera in the Laurencia and Acanthophora Zones may experience differential (i) growth, (ii) water chemistry, (iii) predation, (iv) mortality, or (v) recruitment. The first scenario of differential growth is rejected outright because fronds of A. spicifera grow faster in the Acanthophora Zone than in the Laurencia Zone (Table VIII). As both reef zones receive the same seawater and are a relatively short distance apart (Fig. 23), it is unlikely that different water chemistries, the second scenario, exist between them. The third possibility of differential predation is rejected outright like the first, for all evidence shows predation intensity to be minimal on the reef flat (Appendix I; Hay, 1981a; 1983). Of the two remaining possibilities, both differential mortality and recruitment of A. spicifera offer the most likely explanation. That is, in the Laurencia Zone, A. spicifera tolerates aerial exposures by growing within the "aggregates" of L. papillosa, while in the Acanthophora Zone, A. spicifera has no similar refuge from aerial exposures. By growing as an epiphyte on L. papillosa and lacking a resistant holdfast, fronds of A. spicifera in the Acanthophora Zone are the first to succumb to desiccation and thermal effects. Only after the A. spicifera is removed, would the understorey of L. papillosa be affected. Thus, A. spicifera in the Laurencia Zone regenerates from its holdfast to increase its biomass, while in the Acanthophora Zone algal recruitment

is necessary before any major increase in biomass can take place. As shown in Figure 48, the recruitment of A. spicifera takes the form of vegetative fragments originating in the Laurencia Zone. Together, these observations explain the earlier increase of A. spicifera biomass in the Laurencia Zone and the subsequent increase in biomass of A. spicifera in the Acanthophora Zone. With the regrowth of A. spicifera proceeding rapidly after aerial exposures (Table XXIII), the fragments generated in the Laurencia Zone are not necessarily limiting A. spicifera recruitment into the Acanthophora Zone. Instead, the time lag is best explained with regard to the fragments' chief substratum, L. papillosa. Because L. papillosa grows slowly (Table XXIII), the settlement of A. spicifera fragments after periods of aerial exposure is delayed until sufficient biomass of L. papillosa has accumulated.

In the Acanthophora and Laurencia Zones the branching morphology of A. spicifera and L. papillosa share many similar characteristics; namely, plants in the Laurencia Zone are shorter, more compact, and have fewer branches than plants in the Acanthophora Zone (Figs. 33 to 37). The factors accounting for the shorter Laurencia Zone plants, however, are quite different, and this is reflected in their branching patterns. For example, if branches are not affected by any form of disturbance that removes or alters the number of branches, the distance from the holdfast to 1st-order branches should progressively increase. This observation was made for L. papillosa from both the Acanthophora and Laurencia Zones (Fig. 36) and of A. spicifera from the Acanthophora Zone (Fig. 33). In the case of L. papillosa, the small Laurencia Zone plants

were merely stunted plants, caused by the continual wave-pounding and repeated exposures in the air between successive waves. This conclusion was based on: (i) the branching pattern of L. papillosa in the Laurencia Zone reflecting that of a plant unaffected by environmental disturbance; (ii) the greater distances between 1st-order branches and the greater composition and number of branches in the Acanthophora Zone than in the Laurencia Zone; and (iii) the low mortality of fronds in both reef zones (Appendix I). Further support for this conclusion is offered in Appendix I; fronds of L. papillosa in the Laurencia Zone were identical in size and number of branches to the terminal regions of fronds of L. papillosa in the Acanthophora Zone.

An increase in the 1st-order branching distances from the holdfast did not occur with A. spicifera in the Laurencia Zone; the distance from the holdfast to all 1st-order branches remained about 5 mm (Fig. 33). With predation shown to have had little effect on reef-flat populations (Appendix I; Hay, 1981a; 1983), and with recent effects of aerial exposures on branching morphology minimized by the selected sampling period, wave action or past periods of aerial desiccation were the only other forms of disturbance which could account for the changes in branching structure. The effect of past periods of desiccation would be observed only in the subapical region of a frond. With wave action as the only remaining difference between the two zones, the prediction was that if the fronds of A. spicifera in the Laurencia Zone were unaffected by wave action, then they should be similar in numbers to the terminal fronds of A. spicifera in the Acanthophora Zone. When the ratios of

ordered branches in the Laurencia and Acanthophora Zones were examined (Strahler Method; Appendix I), fronds of A. spicifera in the Laurencia Zone showed significant decreases in the number of terminal branches. It is concluded, therefore, that wave action does significantly change the branching pattern of A. spicifera in the Laurencia Zone and is probably responsible for the lack of any increase in 1st-ordered branch distances (Botanical Method). As noted by Dahl (1971), studies of branching morphology provide an accurate record of the recent history of a seaweed. In contrast to the surf-swept populations of Lessonia nigrescens Bory that grows stiff and strong or to Durvillea antarctica (Cham.) Hariot that deforms under stress (Kohl, 1982), A. spicifera responds to wave forces by losing branches while L. papillosa remains small, exposing little surface area to the waves.

A. spicifera and L. papillosa exemplify two different types of growth common to plants: that which has been dominated in its evolution by selection pressure to attain height (i.e., A. spicifera); and that which has been dominated by pressures to remain small and expand laterally (i.e., L. papillosa). These growth categories are recognized in higher plants (Harper, 1977) and apply equally to their marine counterparts. During the October-November census of the Laurencia Zone, the mean length of 1st-order branches (Strahler Method; $\bar{X} \pm SD$) averaged $38 \text{ mm} \pm 14 \text{ mm}$ for A. spicifera and $26 \text{ mm} \pm 8 \text{ mm}$ for L. papillosa (Figs. 38 and 39). Fronds of A. spicifera were taller and varied more in size than those of L. papillosa, which were shorter and of more uniform size. The ability of A. spicifera to increase in vertical

height was best recognized directly after a period of aerial exposures when plants of A. spicifera and L. papillosa consisted only of their basal holdfasts. One week after the exposure period, A. spicifera was more than twice the size of L. papillosa (Table XXIII). Seasonal growth data confirmed the rapid growth of A. spicifera, which averaged 3 mm d^{-1} of new growth, while similar attempts to measure the growth of L. papillosa proved futile because growth was so slow. Increased growth rates in A. spicifera were attributed, in part, to the higher water content of its thallus (95 % water). This increased water content reduced the demand for structural resources and allowed A. spicifera to grow faster but form a structurally weaker thallus (Table X and Fig. 41). In contrast, L. papillosa (90 % water) grew slowly and was structurally more sound. In addition, the maximum branch diameter was also larger in L. papillosa than in A. spicifera, conferring more strength and utilizing more structural resources.

The horizontal growth strategy of L. papillosa was also recognized from the presence of specialized branches that were analogous to the runners of strawberries. These branches lacked papilli on their more distal ends and were usually found entangled or attached to adjacent fronds or hard substrata. Such a branching system provided additional anchorage and expanded the plant laterally along the substratum. Recently, Godin (1981) showed a similar sort of lateral expansion with Laurencia pinnatifida (Huds.) Lamour. Thus, with its shorter and uniform size and its added anchorage, L. papillosa was expected to lose fewer fronds to wave action than A. spicifera, which grew tall and was

weak structurally. These observations were verified from measurements of drift biomass (Fig. 31) and from survivorship data (Figs. 43 and 44; Appendix I).

With the recent introduction of Codium fragile on the northeast coast of North America (Ramus, 1972; Russell, 1981; Wood, 1962), numerous studies were done to account for its rapid dissemination and to measure its effects on local species assemblages. Several studies showed the propensity of this species to reproduce by several forms of vegetative fragmentation (Borden & Stein, 1969; Fralick & Mathieson, 1972). Noteworthy was the observation by Fralick & Mathieson (1972) of an abscission zone which predetermined the area of thallus breakage. Similarly, A. spicifera may have inherently weaker areas in its morphology. When examining the biomechanical strength of A. spicifera thallus, the main axis near the holdfast was the strongest region; the weakest region was at a branch node within the branch axil (Table X and Fig. 40). Having established a weakness in the thallus morphology, I attempted to determine (in situ) if the branch nodes represented an abscission site; this was not observed to be the case. From outplanted plants of known branching structure, breakage was approximately evenly divided between branching (node) and nonbranching (internode) areas of the thallus, suggesting that breakage was a function of drag forces caused by currents rather than predetermined by an abscission region. Other studies had shown that breakage location could be influenced by predators (Koehl, 1982; Koehl & Wainwright, 1977; North, 1971; Robertson & Mann, 1980; Wainwright et al., 1976) sand and ice abrasion

(Koehl & Wainwright, 1972; Mathieson et al., 1982; Neushul, 1965), or even fungal infections (Wilce et al., 1982). In the case of Sphacelaria and Centrocerus, liberation of fragments occurred at defined locations at the bases of "propagules" or branches (Hoek & Flinterman, 1968; Lipkin, 1977).

Wave-action is a critical factor that regulates the fragmentation of A. spicifera. When A. spicifera was outplanted into the Laurencia Zone, sea conditions greatly influenced the number and size of fragments produced (Fig. 42). During light seas, greater numbers of smaller-sized fragments were formed than during moderate seas, when fewer numbers of larger fragments were formed (Fig. 42). Similar results were observed in colonization studies in the Acanthophora Zone (Fig. 49). Also, the size distribution of fragments formed during the outplanting experiment and those captured during the colonization study were both heavily skewed toward the smaller-sized fragments with the majority of fragments ranging between 10 and 50 mm in length. This was probably a reflection of both the size distribution of A. spicifera in the Laurencia Zone (Fig. 38) and the gradual erosion of the larger fronds of A. spicifera. Recently, Bhattacharya (pers. comm.) found the highest losses of fronds in the larger size classes of Chondrus crispus Stackh. Higher mortality among the larger size classes of fronds seems logical from a biomechanical point of view (i.e., increased drag forces) and is probably operative in A. spicifera.

From tagging experiments, it was found that frond survivorship was greatly influenced by wave exposure and by the alga's growth form.

During the wet-season period (19 September to 31 October 1981), frond mortality was higher at the Sheltered Station than at the Exposed and Back-Reef Stations, with the Exposed and Back-Reef Stations showing similar frond losses (Table XI and Fig. 43). The higher mortality of fronds at the Sheltered Station was attributed to the development of "mats" of A. spicifera (Fig. 43). When sea conditions were light to moderate, the seawater of the reef flat became supersaturated with oxygen, which resulted in the accumulation of gas bubbles of oxygen within the "mat" and around the branches of A. spicifera. At times, sufficient oxygen was collected to rip sections of the "mat" from its substratum. Once this occurred, the structural integrity of the entire "mat" was weakened, allowing waves to systematically remove portions of the "mat" still present. Such a mechanism is not uncommon in the algae. For example, Wassman and Ramus (1973) reported oystermen becoming very annoyed when Codium fragile thalli fill with gas and float away, often still attached to their substratum, the oyster. Similar findings were reported much earlier by Sauvageau (1906) with Colpomenia sinuosa (Roth) Derb. & Sol. The reduction in percent cover at the Sheltered Station, which occurred on 18 October 1981 (day 24), was attributed to this mechanism (Fig. 46). In the Acanthophora Zone, "mats" of A. spicifera were similarly removed, but the looser construction of the "mats" (i.e., more space between branches), the continuous flow of seawater, and the colonization of new fragments, frequently prevented "mats" from being torn free.

During the dry-season period (4 November to 16 December 1981),

frond survivorship was related to wave exposure and tidal height. In general, tagged fronds were lost at a greater rate at the Exposed Station, followed by the Sheltered Station, and then by the Back-Reef Station (Fig. 44). A similar generalization can be made from Figure 46 which shows the decrease in the percent cover of A. spicifera at the Exposed and Sheltered Stations. When severe sea conditions increased the depth of water on the reef flat, however, or coincided with high tides (after day 17; Fig. 44), an increase in frond survivorship was observed at the Sheltered and Back-Reef Stations. The greater amount of water cover on the reef flat damped the wave forces exerted on the plants as it did on the force meters that were similarly located on the reef (Fig. 19).

Colonization by Fragments

The unidirectional flow of water over the reef surface transports fragments across the reef flat. Upon their release, fragments sink and tend to regularly contact the bottom as they are carried along in the current. The spiny nature of the determinate branchlets acts in combination with indeterminate branch or branches to catch or snag the drifting A. spicifera onto some substratum, usually L. papillosa or another frond of A. spicifera. Dawes et al. (1974) mention a similar mode of colonization with the spiny fragments of Eucheuma isiforme and E. nudum.

In traversing the reef flat, fragments of A. spicifera passed through different plant communities -- in particular, the Thalassia Zone, which contained areas of dense stands of T. testudinum and of scattered coral-rubble, and through the Acanthophora Zone, which contained a lush growth of A. spicifera and L. papillosa. Of the Acanthophora fragments released into these areas, those released in the Acanthophora Zone were the most successful when evaluating the percentage of snagged fronds, the distance required by the fragments to snag, and the percentage of snagged fragments that remained in position for 72 hours. When calculating the probability of fragment recruitment into these back-reef habitats, the Acanthophora Zone was again shown to be the most suitable habitat, with between 93 % and 49 % of the fragments successfully recruiting. These recruitment rates are too high to be attributed to chance alone and must be a reflection of the

adaptation of A. spicifera to reproduce by vegetative fragmentation.

Fragments of A. spicifera and L. papillosa released into the Acanthophora Zone showed no significant differences in their ability to snag, in remaining in position for 72 hours, or in their distance traveled before snagging (Table XIV). This was somewhat expected as A. spicifera fragments snagged well on L. papillosa; the converse situation had to be true. However, only A. spicifera was adapted to snagging and attaching itself to substrata. First, the success of A. spicifera to snag onto different substrata was attributed to its determinate branchlets which emerged from the thallus at a $1/4$ divergency (Børgesen, 1915-1920) and at about 45° to serve as grappling hooks (Fig. 4). The determinate branches of L. papillosa were too short and closely spaced to function effectively in the same capacity.

Secondly, A. spicifera attached to L. papillosa but not vice versa. The growth of L. papillosa was too slow to accommodate rapid attachment and few, if any, determinate branchlets of L. papillosa were capable of further growth. Similar results were obtained with A. spicifera and L. papillosa fragments that were released into the Acanthophora Zone because of a nearly complete cover of A. spicifera in this habitat.

Finally, L. papillosa was never observed as an epiphyte on A. spicifera in the Acanthophora Zone despite the rather large drift biomass of L. papillosa (Fig. 30). I attributed this to the growth form of L. papillosa, which resulted in plants being ripped from their substratum as an "aggregate" rather than as single fronds. On numerous occasions, "aggregates" of L. papillosa did not snag in the Acanthophora

Zone because their large surface areas, when exposed to reef currents, made it difficult for any single frond of the "aggregate" to secure a strong enough hold. Consequently, all L. papillosa removed from the fore reef was washed off the reef.

The colonization of fragments into the Acanthophora Zone was also facilitated by the surface topography of the zone. Much of the Acanthophora Zone consisted of large pieces of coral rubble (i.e., coral plates) dispersed within a sand plain. These plates of coral rubble were colonized primarily by L. papillosa, that was in return colonized by A. spicifera. If the mean heights of the two algae (Figs. 38 and 39) and the height of their coral substratum (about 0.15 m) are compared to the surrounding area of sand, the very irregular topography of the Acanthophora Zone becomes apparent. Undoubtedly, such a topography would impede the flow of water and establish many eddies and counter-currents. Fragments in the water column snagged when they impacted on the algal substratum on the upstream side of the coral plate or were slowed sufficiently to make contact with the algae growing on the coral plate's surface. Some fragments that passed over the coral plate were captured in eddies of water, which placed them in contact with overhanging A. spicifera or L. papillosa. On a finer scale, the variation in size of A. spicifera and L. papillosa fronds was much greater in the Acanthophora Zone than in the Laurencia Zone (Figs. 38 and 39). This wider variation in frond size increased the heterogeneity of the surface topography and thereby further increased the chances of a fragment snagging.

The colonization of the back reef by fragments was influenced by the availability of substrata and fragments. It was previously mentioned that A. spicifera snagged best in the back reef in the Acanthophora Zone, followed by the Thalassia-Rubble Area, and then by the Thalassia Zone. It was also shown that wave exposure altered the growth form of A. spicifera, and that the growth form may affect the quantity of fragments available to the back reef. To determine the substratum preference of fragments of A. spicifera and to examine how wave exposure influences the recruitment of fragments, five stations were established in the Thalassia Zone, each consisting of a square meter plot of T. testudinum, T. testudinum with coral rubble, and L. papillosa. At the end of four months, fragments of A. spicifera had settled primarily on L. papillosa, followed by Thalassia-rubble and by Thalassia. No fragments of A. spicifera colonized Thalassia blades, while all fragments that had settled into the plots of Thalassia-rubble were attached to the rubble substratum (Table XIII). This suggested that Acanthophora fragments were best suited for colonizing L. papillosa. Thalassia blades were only readily colonized by A. spicifera after an initial settlement of Centrocerus or Spyridea. As L. papillosa is found primarily in the Acanthophora Zone, the abundance of A. spicifera can be explained, in part, by the substratum of Laurencia.

Significant differences in the number of colonizing fragments occurred between the five stations established in the Thalassia Zone (Table XIII). Stations II, III, and IV showed the highest numbers of

colonizing fragments of A. spicifera and were all located in close proximity to the Acanthophora Zone (Fig. 6). Station I, which was in the most wave-exposed region of the Thalassia Zone, did not capture any fragments. Station V, the most sheltered station, similarly did not capture any fragments. As observed in the Laurencia Zone, fragments at Station I did not establish because of strong wave action which frequently dislodged snagged fragments, forcing them downstream. Fragments of A. spicifera were recruited only into Stations II-IV. Two explanations are given for this pattern of recruitment: (i) stations II-IV received fragments from the more wave-exposed area of the fore reef —this area of the reef produces on an average more fragments (Figs. 43-45); and (ii) these stations were exposed to a greater concentration of fragments. As the water moves across the reef flat, it is funnelled into the back reef, thereby, increasing the concentration of fragments to these stations (Fig. 28). Station V, which received fragments from the more sheltered areas of the Laurencia Zone, was probably not colonized because of: (i) the reduced number of fragments released from the fore reef (Figs. 43 to 45); (ii) the proximity of the station to the Laurencia Zone (Fig. 6); and (iii) the "mat" growth form of A. spicifera that, like the "aggregate" growth form of L. papillosa, was washed off the reef platform. Accordingly, the Thalassia Zone lacked a suitable substratum for fragment recruitment adjacent to the Acanthophora Zone, but in the more exposed and sheltered regions of the Thalassia Zone, wave exposure and fragment availability limited the recruitment of A. spicifera.

Wave-action does not appear to act alone in determining colonization rates into the Acanthophora Zone. Previously, I had mentioned that the number and size of fragments settling into cleared plots corresponded with those of the outplanted algae which were used to examine thallus breakage (Figs. 42 and 49). That is, larger numbers of smaller fragments were produced during light sea conditions or during the wet season, and smaller numbers of larger fragments were produced in moderate seas or during the dry season, and the distributions of fragment sizes were skewed toward the smaller size classes. A closer examination of the colonization data indicated that other factors were involved. - In general, the number of colonizing fragments increased with increasing wave exposure over the wet-season period (9 September to 22 October 1979) and decreased with decreasing wave exposure during the dry-season period (23 January to 6 March 1980 [Fig. 48]). During both periods, the size of the colonizing fragments decreased (Fig. 49). With one exception, neither prediction of an increase in fragment size with increased wave action nor a decrease in the number of fragments with increased wave action appeared to have taken place. Only during the dry-season period did the size of fragments decrease with decreasing wave action (Fig. 49). It is believed that the abundance, size, and growth form of A. spicifera in the Laurencia Zone accounted for the observed variations.

A. spicifera attached more rapidly to fronds of A. spicifera and L. papillosa than to T. testudinum and Porites-rubble. By the end of the second day, 91 % of the Acanthophora fragments were secured to their

substratum of A. spicifera while 83 % of the Acanthophora fragments were secured to the substratum of L. papillosa. Four to five days were required by fragments of A. spicifera to establish similarly on Thalassia blades or Porites rubble (Fig. 51). Such differences in the rates of fragment attachment could explain the observed differences in settlement. The more time required by a fragment to become permanently established, the greater the likelihood that the fragment would be dislodged from its substratum. I suspect that the amount of contact made between the fragment and its host determined the rate of fragment attachment. The surface of Thalassia blades and Porites rubble, for example, permitted few points of contact with the fragment. In contrast, the substrata of L. papillosa and A. spicifera, had determinate branchlets which intermesh with those of the Acanthophora fragment, providing numerous points of contact between the fragment and its host. The branchlets of A. spicifera attached directly to the substrata of L. papillosa and A. spicifera, or developed into spineless branches that encircled them (Fig. 4). Spineless branches were less costly in time and resources (i.e., requiring less plant biomass) to produce than a secondary holdfast, insuring a faster rate of attachment.

When rates of fragment attachment were measured, it was found that A. spicifera fragments took longer to attach to Porites rubble than to Thalassia blades (Fig. 51). Field manipulations indicated the opposite situation (Table XIII). It is believed that opportunistic species (i.e., filamentous reds, greens, and browns) were responsible for these differences in attachment and assisted the establishment of a fragment

by entangling with it or by allowing the fragment to secure a better foothold on a now presumably different substratum. The Porites-rubble used to measure attachment rates were all sun-baked, lacking an epiflora, while rubble used in the colonization experiments had time for opportunistic species to establish. Previously, Harlin et al. (1977) observed the difficulty that species had colonizing smooth substrata, noting that only encrusting algae and "transient" species were colonizers. Such species may change the texture, shape, etc., of the surface, permitting further colonization by other species.

Fragment versus Tetraspore Dispersal

Tetraspores appear to play a minor role in the propagation of A. spicifera. Plants that possessed mature tetrasporangia were abundant throughout the year and comprised 96 % of the plants found in the Laurencia Zone (Fig. 47). Only four cystocarpic plants were found in October 1979 in the Laurencia Zone, while no cystocarpic plants were observed in the Acanthophora Zone. Cordeiro-Marino et al. (1974) had identified the tetrasporangium as the site of meiosis from populations of A. spicifera in Brazil. Their findings suggest: (i) that an obligate life history was probably operative in A. spicifera; and (ii) that the chances of an apomictic life history was unlikely (Sundene, 1962; Kim, 1976). If Russell's (1981) hypothesis is correct — that tetraspores are the major dispersal agents — it follows that the gametophytic plants would be well represented. This did not appear to be the case in Panama or Hawaii. Russell (1981) reported A. spicifera to be nearly always fertile with tetrasporangia and K. Schlech (pers. comm.) acknowledged that carposporic plants were rare but did occur in Hawaii. Prior to Russell (1981), Mshigini (1978) observed the colonization of A. spicifera onto artificial and natural substrata. On the bases of size and colonization rates (fronds exceeding 20 mm in length after only 1 week), Mshigini concluded that these fronds "could hardly have arisen from spores", and must have originated from vegetative fragments. Given the effectiveness of the fragmentation process in Panama, the similar reef-flat conditions described in Hawaii (Doty, 1969; Russell, 1981;

Santelices, 1977), and the colonization study of Mshigini (1978), fragments rather than spores are the most likely explanation for the rapid dissemination of A. spicifera throughout Hawaii, described by Doty (1961, 1973) and Russell (1981). Furthermore, Russell's (1981) observations, that A. spicifera is excluded from the most wave exposed coasts, can grow as an epiphyte, and occurs on a wide range of substrate (pebbles, worm tubes, buoys, etc.,) are in accordance with the fragmentation scenario. It appears that the spread of A. spicifera throughout Hawaii or tropical waters in general could be attributed to vegetative fragmentation. The rapid spread throughout wide geographic areas of the "invading species", Bonnemaisonia hamifera and Codium fragile is well known and has been similarly attributed to the dissemination of vegetative propagules (see review by Russell, 1981).

Studies on the phenology of A. spicifera have yielded a variety of results. Borgesen (1915-1920) reported A. spicifera from the Virgin Islands with tetrasporangia, antheridia, and cystocarps in the months of January through March. In Florida, Croley and Dawes (1970) noted tetrasporangia and cystocarps in April and June, while Mathieson and Dawes (1975) reported no reproductive plants throughout their year-long survey. In Panama, as in Hawaii, tetrasporic plants were abundant the year-round, while gametophytic plants were rare. Such differences in phenologies were usually explained in terms of geographic differences in temperature, light, etc. In this study, major quantitative differences in the phenology of A. spicifera were also observed between plants within the Acanthophora and Laurencia Zones. In general, similar

seasonal trends (*i.e.*, increases and decreases) in tetrasporic plants were observed, but the total numbers of reproductive plants were greatly reduced in the Acanthophora Zone (Fig. 47). Upon closer examination, the branchlets in the apical regions of fronds in the Acanthophora Zone (upper 20 to 40 mm) were found devoid of tetrasporangia, while those from the Laurencia Zone generally possessed them. The lower percentage of reproductive plants may be a response to adverse conditions in the Acanthophora Zone; however, the fewer periods of aerial exposures (Fig. 17 and 18), the larger and bushier plants (Figs. 33 to 37), and the faster growth rates of Acanthophora Zone fronds (Table VIII) suggested otherwise. Alternatively, the lower percentage of reproductivity may be attributed to the detachment of the fragment from its holdfast. Biebl (1962) noted that seaweeds held in a drift condition in calm, confined locations proliferate and grow into anomalous forms, often losing their ability to produce spores (see review by Norton & Mathieson, 1983). Although A. spicifera attached to substrata (via spineless branches, etc.), it did assume a more weedy appearance (*i.e.*, larger plants with a less compact branching morphology) and changed its pigmentation from a reddish-purple to a straw-yellow. Thus, tetrasporic plants that were present in the Acanthophora Zone could conceivably be residual materials transferred from the Laurencia Zone. So, this would explain why tetrasporangia were principally confined to the older, subapical regions of A. spicifera. A general reduction or loss of reproductive phase from fragment-derived communities had been observed by others.

(Chock & Mathieson, 1976; Gibb, 1957; Irvine et al., 1975; McLachlan & Edelstein, 1970-1; South & Hill, 1970; Womersley & Norris, 1959). For example, Prud'Homme Van Reine et al. (1980) suggested that the sexual potency of Bostrychia scorpiodes (Gmel.) Mont. had been lost or reduced during evolution, but this had not necessarily affected the survival of the species because a mechanism of comparable efficiency (i.e., fragmentation) may have developed.

4.2 The Maintenance and Persistence of A. spicifera

Connell (1961) was the first to demonstrate rigorously that intense competition for space, a limiting resource in the rocky intertidal zone, leads towards the competitive exclusion of an inferior competitor by the competitive dominant species and towards a spatial monopoly of the best competitor. As coastlines are not dominated by single monospecific stands of organisms, biotic and abiotic disturbances intervene to prevent the dominant competitor from monopolizing space, thus maintaining high diversity (Connell, 1970; Dayton, 1971; Janzen, 1970; Menge, 1976; Paine, 1966; 1971; 1976). On Galea Reef two species of seaweeds, A. spicifera and L. papillosa, make up the majority of algal biomass. The two species are closely related taxonomically, morphologically, and in their distribution throughout the reef platform; each species, however, is adapted quite differently to their surroundings. A. spicifera grows quickly and fragments easily, whereas L. papillosa grows slowly and is more resistant to physical disturbances. More importantly, the persistence of both species is dependent upon a fine balance between parasitic and mutualistic relationships which are closely regulated by environmental disturbance.

Aerial Reef-Flat Exposures

Aerial exposures of the reef flat figure predominantly in determining the seasonal abundance of algal species. In May and June 1979, prolonged periods of low water destroyed most of the algal biomass

on the reef platform (Figs. 15 and 18). The biomass of L. papillosa decreased from a previous high of 200 to 65 g (d wt) m⁻², and A. spicifera was reduced in biomass from 55 to 5 g (d wt) m⁻² (Figs. 27 and 52). Hendler (1977) observed that water temperatures on the reef flat were generally between 26° and 29°C and the salinity usually between 32 and 35 ‰, but extreme values of 39°C and 38 ‰ (25 ‰ during heavy rain) occurred during aerial exposures. Throughout the rest of the year, exposures of the reef surface were less frequent and confined to the higher elevations of the Laurencia Zone (Fig. 15). Accordingly, the Acanthophora Zone, because of its lower reef elevation, was subjected to fewer aerial exposures. Fewer exposures of the plants in the air accounted for their higher Acanthophora Zone biomass from October 1979 to February 1980 (Figs. 25 and 52). In the Laurencia Zone, differences in reef elevation (Fig. 21) and wave exposure (Fig. 20) influenced the timing and hence the amount of destruction caused by aerial exposures; thus, some of the difficulty in trying to establish a critical tidal elevation for an aerial exposures could be explained. Previously, Doty (1946), Druehl & Green (1982), and Lawson (1957) recognized the importance of wave exposure and tidal elevation in determining desiccation stress. Another factor that influenced the survival of plant and animal assemblages to aerial exposures was the presence of many small depressions and crevices in the Laurencia Zone. Substrate rugosity, a measure of actual distance to linear distance, was much greater in the Laurencia Zone than in the Acanthophora Zone. Thus, despite the greater frequency of aerial exposures in the Laurencia

Zones, some refuge from aerial exposure could be gained from the water that was trapped in the depressions, or from the shade that was found within crevices. In December, and extending into February 1980, aerial exposures of the reef surface were at a minimum, enabling A. spicifera and L. papillosa in the Laurencia Zone to increase in abundance to levels comparable with those found in the Acanthophora Zone. As noted by Glynn (1968), numerous atmospheric and marine conditions determined the extent of mass destruction of reef biota: the timing of the exposure; clear sky; low wind velocities; high atmospheric temperature; low relative humidity; and ascending sea-water temperatures.

Low tides that result in the exposure in the air of reef platforms occur throughout the Caribbean (Glynn, 1968; Stoddart, 1962). Keeping in mind the minor variations in tidal cycle that occur from year to year and the local differences in time and height, Glynn (1968) noted that the timing of low tides on the Caribbean coast of Costa Rica, Panama, the north shore of Columbia, Curacao and Aruba, and certain regions of Venezuela would occur in more or less an abrupt shift during the midday hours. He further showed that such aerial exposures usually commenced in February or March and continued into July. As shown in Figure 17, the frequency of aerial exposures of the Laurencia Zone exhibited a bimodal cycle of daytime and nighttime exposures. Periods of maximum daytime exposures occurred in May or June, with a second peak occurring in September or October. Daytime exposures began in March or April and continued into September or October. At night, aerial exposures occurred principally in October or November, with a second peak that

occurred in March 1979 and May 1980. Previously at Galeta, Hendler (1977) ascribed the reef emersion to be most serious during March-April from the coincidence of the lowest low tides with midday hours, and during September-October from low pressure calms generated by tropical storms and southerly winds. For 1979 and 1980, aerial-exposure data agreed more with the description given by Hendler (1977) than by Glynn (1968). As daytime exposures averaged about five hours (Fig. 16), the chance of a midday exposure occurring on the reef flat was quite good. In addition, when tidal elevation data were examined directly, a gradual and predictable increase in aerial exposures occurred during periods of the lowest low tides (Fig. 15). No evidence of an abrupt shift in tidal patterns was apparent in these data. In the terminology of Harper (1977) the aerial exposures of reef platforms in the Caribbean are classified as disasters. "A disaster recurs frequently enough for there to be reasonable expectation of occurrence within the life cycle of successive generations and the selective consequences may be expected to leave relevant genetic and evolutionary memories in succeeding generations."

Adaptations to aerial exposures are observed on the organismal and population levels of organization. For convenience sake, I will start by comparing the ability of single upright fronds of A. spicifera and L. papillosa to weather aerial exposures. It was observed that fronds of L. papillosa survived 30 minutes of aerial exposure to direct sunlight when placed onto a moistened piece of coral rubble (Fig. 56). In a separate experiment but under similar conditions, A. spicifera

tolerated only 15 minutes of aerial exposure (Fig. 53). In both cases, plants exposed in the air for longer periods did not recover when placed back into seawater, and soon disintegrated. Simultaneous comparisons in aerial exposure tolerance showed L. papillosa to lose 61.5 % of its photosynthetic capacity, compared with an 83.0 % loss for A. spicifera. These exposures in the air took place on a partly cloudy day and lasted for 30 minutes (Fig. 54). Fronds of L. papillosa were thus once again more resistant to aerial exposures than fronds of A. spicifera. Also, the ability of A. spicifera to withstand aerial exposures was greatly increased when exposures in the air took place on a partly cloudy rather than on a clear sunny day, confirming one of Glynn's (1968) previously mentioned observations. Upon inspection, fronds of A. spicifera were found to have a greater surface-to-volume ratio than did the fronds of L. papillosa. The diameter of Acanthophora's branches were smaller, and the determinate branches thinner and more acute than those of L. papillosa. Differences in surface-to-volume ratios probably accounted for the differential tolerances of A. spicifera and L. papillosa to aerial exposures. It has been shown by other investigators that surface-to-volume relationships can determine desiccation resistance in algae (Dring & Brown, 1982; Kristensen, 1968; Schonbeck & Norton, 1980; Dromgoole, 1980).

The resistance to aerial exposures by A. spicifera and L. papillosa is affected by their growth form. As fragments of A. spicifera that colonize the Acanthophora Zone come from the more wave-exposed regions of the reef flat, it is of interest to compare the aerial exposure

tolerances of A. spicifera, which has "individual" growth form, to L. papillosa, which has an "aggregate" growth form. Figure 56 shows that fronds of L. papillosa that were part of a Laurencia "aggregate" all survived five hours of aerial exposures in direct sunlight, while single fronds separated from the same "aggregate" survived for 30 minutes. With single fronds of A. spicifera being less tolerant to aerial exposures than those of L. papillosa, fronds of L. papillosa that grow as an "aggregate" are, by far, more tolerant to aerial exposures than any frond of A. spicifera. Similar conclusions have been reached by Hay (1981), noting "individuals" lose water and photosynthetic ability at a much faster rate than turfs (equals "aggregate"; Appendix I). The lower evaporation rate of water from the "aggregate" is probably related to: (i) increased contact between branches, which decrease the effective evaporation surface area; (ii) increased self-shading and the shading of substratum; and (iii) decreased air movement within the "aggregate", all of which discourage the formation of strong vapor-pressure gradients.

At the Back-Reef and Sheltered Stations, the "mat" growth form of A. spicifera provided limited resistance to aerial exposure. During periods of daytime exposures, "mats" of A. spicifera behaved similarly to "individuals" and succumbed quickly to desiccation and thermal effects. Because fronds in a "mat" are arranged on top of each other, an upper layer of dried algae forms over a lower layer of seemingly healthy plants when exposed in the air during low tides. When the reef water returns, which is within 18 hours (Fig. 16), the desiccated

portions of the "mat" degenerate and are washed from the reef. If repetitive aerial exposures occurred, the "mat" is eventually worn down to the underlying L. papillosa at the Back-Reef Station or to its holdfasts at the Sheltered Station. Continuous periods of daytime exposures up to 38 days have been recorded in the Laurencia Zone and up to nine days in the Acanthophora Zone. To demonstrate the ability of the "mat" growth form to resist aerial exposure injury, "mats" of

A. spicifera were exposed in the air at night. After 12 hours of aerial exposure, fronds sampled from the lower regions of the "mat" showed little change in photosynthetic capacity, while fronds from the upper surface showed decreases in photosynthetic capacity as much as 82 % (Fig. 55).

The effect of aerial exposures at night on algae has attracted little attention in the literature. Researchers generally agree that "the effect on seaweeds of emersion at night is negligible, as the drying power of the atmosphere is at its lowest and there can not be any direct injury from the sun" (from Lawson, 1957; also noted by Tsuda, 1974). The results in Figure 55 showed this to be an oversimplification. While all fronds survived the 12 hours of night exposure, a considerable though patchy reduction in photosynthetic capacity resulted. In the most severely desiccated regions, an 82 % reduction in photosynthetic capacity occurred, while fronds which showed no outward signs of desiccation exhibited a 22.4 % reduction in photosynthetic capacity. The surface areas of the exposed "mats" were roughly divided between partially and severely desiccated regions; the

higher elevations of the "mat" were always the more severely desiccated. From September through December, repetitive aerial exposures at night may further decrease the alga's photosynthetic ability, and may eventually result in the death of the plant. The steepness of the vapor-pressure gradient between the water on and within the alga and in the atmosphere was sufficient to cause considerable desiccation (i.e., via Henry's Law). Southerly winds which coincide with night exposures (Hendler, 1977) probably significantly enhance evaporation, as moving air enhances the rates of transpiration in higher plants" (Meyer et al., 1973).

The survival of A. spicifera through prolonged periods of daytime exposures is accomplished, in part, by its basal holdfast. Many researchers have noted that the survival of many seaweeds to wave exposure (Dawes et al., 1974; Dixon, 1978; Doty, 1971), sand burial (Daly & Mathieson, 1977; Fritsch, 1945; Mathieson, 1982), and low tides (Hay, 1981) depends upon a resistant holdfast. At Galeta Point, extended periods of daytime exposures often reduced plants of A. spicifera and L. papillosa to their basal holdfasts. Hay (1981a) found that turfs (i.e., "aggregates"), by concentrating photosynthesis in the upper portions of their thallus and reducing respiration in their lower portions, were better able to tolerate aerial exposures. He hypothesized that "the decreased respirative demand of the turf's basal portion lowers the energetic cost of the growth form and may allow this portion to act as a resting stage during periods of severe stress when uprights cannot be maintained". After examining photosynthesis and

respiration rates in the growth forms of A. spicifera, similar results to those of Hay (1981a) were found, suggesting that such partitioning of photosynthesis and respiration was not confined to the turf (i.e., "aggregate") morphology (Fig. 57). To test the hypothesis that the holdfasts of A. spicifera were able to act as resistant stages, entire plants were exposed in the air in direct sunlight for 45 minutes (a time previously determined to kill all uprights [Fig. 53]). The results indicated overwhelmingly that 100 % of basal holdfasts survived the exposure period (i.e., produced new upright branches when returned to water), compared with about 10 % of the uprights. Of the uprights that did recover, it was always their proximal portions that survived, suggesting that a clear separation between upright and holdfast regions was not accomplished on the basis of thallus pigmentation. Hay's (1981a) hypothesis that holdfasts of "aggregates" (namely L. papillosa) may act as a resting or resistant stage appears justified.

As A. spicifera and L. papillosa grow alongside each other, many benefits derived from one growth form are also shared with the other. For example, in the Laurencia Zone, A. spicifera can be as much a part of the "aggregate" of L. papillosa as any one frond of L. papillosa. Accordingly, the benefits of the "aggregate" growth form (i.e., desiccation, thermal, and wave-exposure resistance) are shared with A. spicifera and other species. Together with its resistant holdfast, A. spicifera that grows within the Laurencia "aggregate" is tolerant of most aerial exposures. Similarly in the Acanthophora Zone, L. papillosa is protected from aerial exposures by the overlying "mats" of

A. spicifera. Such interactions between species could explain Russell's (1981) observation of a "clear, consistent and intimate association" of A. spicifera with Laurencia nidifica J. Ag. in Hawaii, or as found in this study, with L. papillosa in Panama.

Predation

Herbivory has little effect on the reef-flat populations. In Appendix I, observations demonstrated that reef-flat populations of L. papillosa possessed few grazing scars on the apices of indeterminate branches. Some grazing of determinate branchlets was observed (probably crabs, amphipods, small fish, etc.), with no obvious effect on branching structure. These results were not surprising, as many researchers have noted that on tropical reefs dense stands of seaweeds are usually confined to shallow areas of wave-washed reef platforms or beachrock benches (Adey & Vassar, 1975; Hoek van den et al., 1978; Ogden, 1976; Odum & Odum, 1955; Randall, 1961). Such locations constitute a major refuge for algae from herbivorous fishes and urchins (Randall, 1964; 1967; Earle, 1972b; Hay, 1981a; 1981b; 1983).

Current velocity has been observed to influence herbivory. Odum and Odum (1955) observed at Eniwetok that many large fish were not capable of feeding at current velocities greater than 0.3 m s^{-1} . In Puerto Rico, Odum et al. (1959) reported that current velocities over several reef flats commonly fell into the range of 0.07 to 0.13 m s^{-1} , while Glynn (1968) (also in Puerto Rico) measured current velocities

over the range of 0.5 to 2.0 m³ min⁻¹. On the reef flat at Galeta Point, current velocities were typically between 0.06 to 0.24 m s⁻¹; however, during dry-season storms or in the wave-swept Laurencia Zone, current velocities usually exceeded these values (Figs. 20 and 21). When high current velocities combine with the shallow water of the wave zone (i.e., about 0 to 0.2 m deep in the Laurencia Zone), grazing becomes difficult at best, effectively eliminating many herbivorous fish from the Laurencia Zone or from the entire reef flat.

Outside of the Laurencia Zone, predation is minimized because of:

- (i) periodic aerial exposures of the reef, which kill most slow moving herbivores (Hendler, 1976; 1977);
- (ii) predation by shore-birds during periods of low water and annual fall migration (Hendler, 1976); and
- (iii) low substrate heterogeneity, which provides herbivorous fish and urchins with little protective cover from their predators. The effects of aerial exposures on echinoid populations have been observed by: Hendler (1976, 1977) at Galeta Reef; Glynn (1968) in Puerto Rico; Hodgkin (1959) in western Australia; and Tokioka (1966) in Seto, Japan. The effects of aerial exposures on urchin populations are devastating. With the large frequency of aerial exposures on Galeta Reef (Fig. 15 and 18), predators who venture onto the reef flat run the risk of being trapped out of the water when it recedes. During the daytime this could be lethal, with water temperatures in pools approaching 38°C (Fig. 13). Temperatures of this magnitude are reported by Glynn (1968) to be lethal for most Caribbean urchins for periods of greater than one half hour. With the fall migration of many birds overlapping with periods of low

water, larger urchins that do not find protective cover are easy prey for some birds. Accordingly, most urchins on the reef flat occur under rubble, within crevices, or in the back-reef lagoon or channel where some protection from predatory birds is provided (Kilar, pers. obs.). Recently at Galeta Reef, Hay (1983) has observed that predation by herbivorous fish was highest in habitats that were most topographically complex, noting herbivory in the Thalassia Zone to be relatively low compared with the shallow reef slope. Extending these results to the entire reef flat, it can be said that the surface of Galeta Reef is rather uniform with its carpets of A. spicifera and L. papillosa and its beds of T. testudinum. Such habitats offer little refuge for larger fish and urchins. For the above reasons, small urchins and juvenile fishes occur on the reef flat. During periods of high water, juvenile lemon sharks (Negaprion brevirostris Poey) are frequent visitors and are probably feeding on the occasional larger fish that strays onto the reef flat.

Wave Exposure

In the Laurencia Zone, the spatial distributions and abundances of A. spicifera and L. papillosa increased as wave exposure decreased along the fore reef (Figs. 23 to 25). Changes in reef biomass reflected changes in survivorship and growth form of each species. At the Exposed Station, the biomasses of A. spicifera and L. papillosa were at their lowest (Fig. 58a). The stunted morphology of L. papillosa (i.e., short

and closely branched) and the fragmentation of A. spicifera by wave action probably accounted for their low abundances. Secondly, the large amount of free space between plants at this station allowed A. spicifera to grow independent of or in close association with L. papillosa (Table XXII and Figs. 60 and 61). This was important, for the highest mortalities of A. spicifera plants occurred among those individuals that were not found within the Laurencia "aggregates". Koehl (1982) offered a biomechanical explanation for this differential mortality - aggregates of organisms reduce the overall amounts of drag exerted on their thalli compared with an "individual" growing in the same habitat. This reduction in the coexistence of A. spicifera and L. papillosa increased the mortality of A. spicifera both to wave action and, as previously described, to aerial exposures (Table XXII).

With decreasing wave exposure, the biomass and coverage of L. papillosa increased (Fig. 58a), decreasing further the amounts of available space. At the Moderately-Exposed Station, the association of A. spicifera and L. papillosa increased, permitting the survival of more "individuals" of A. spicifera within the Laurencia "aggregates" (Table XXII). Other genera, such as Hypnea, Centrocerus, and Anadyomene, were able to survive within the Laurencia "aggregate" or on the existing substratum as suggested by their continual reoccurrence at the same locations. Previously, Hay (1981a) observed on Galeta Reef that the primary advantage of the turf growth form (i.e., "aggregate") appeared to be its ability to persist within areas affected by herbivores and physical stress that continuously or periodically

excluded the more productive algae (i.e., Hypnea, Centrocerus, Anadyomene, etc.). These results seem reasonable, as after more than two years plots cleared of all algae in the Laurencia Zone were not colonized by any species that normally occurred in abundance within the Laurencia "aggregates" (Kilar, pers. obs.). With the establishment of L. papillosa in the Laurencia Zone, the habitat supports a wider variety of species (Fig. 56b). Like A. spicifera, these species are protected from periods of severe aerial exposure and wave action by L. papillosa, and grow when conditions were favorable. Their survival depends upon frequent enough disturbances by wave action to open up free space or by aerial exposures to prevent their exclusion by L. papillosa.

Conversely, these species are competitively superior to L. papillosa and must be removed from the "aggregate" growth form for it to be maintained (Hay, 1981a). Overall, L. papillosa is best adapted to aerial exposures and wave action, tipping the balance of survivorship in its favor.

At the Sheltered Station, A. spicifera and L. papillosa biomass was at a maximum when compared with any other fore-reef area (Fig. 58a). Here, the growth and form of A. spicifera changed as a result of the decreased wave exposure (Figs. 20 and 21) and the increased survivorship of fronds. A. spicifera, instead of growing as an "individual" within and around L. papillosa, increased in number and formed dense "mats" (about 0.5 m^2). At the same time, L. papillosa continued to grow taller and bushier than at the previous stations and formed a lush algal carpet. When periods of calm seas coincided with periods of minimal aerial exposures of the reef platform, a mosaic of A. spicifera and

L. papillosa patches developed at the Sheltered Station.

Accompanying the development of A. spicifera and L. papillosa biomass at the wave-exposure stations, the species richness increased, from 38 species at the Exposed Station to 45 species at the Moderately-Exposed Station, then decreased to 35 species at the Sheltered Station (Fig. 58b). Species richness data conformed to Connell's (1978) "intermediate disturbance" hypothesis, which suggests that at intermediate disturbances there is a greater species richness. "At high, frequent disturbances only a few well-adapted species will persist while at low disturbances a few species become the climax community".

Competitive Interactions

Dayton (1971) has observed two corresponding levels of interactions among benthic organisms in competition for a potential limiting resource: they can compete for primary space and (or) they can grow above and then over their competitors and compete for physical resources and nutrients. Examples of the above strategies have been illustrated by Sousa et al. (1981) and by Kain (1975, 1976). Sousa et al. (1981) showed the ability of filamentous red algae to invade and occupy open space while Kain (1975, 1976) showed the stiffer stipe of Laminaria hyperborea (Gunn.) Fosl. to overgrow and exclude two other Laminaria species from mixed stands. At Saleta Reef, L. papillosa represents the first and A. spicifera the second of these competitive

strategies. The lateral expansion of L. papillosa fits the description of a primary space competitor well, while A. spicifera, which grows quickly and vertically, is more adapted to overgrowing a neighboring alga; these growth strategies, however, are not mutually exclusive.

Selection for competitive ability becomes increasingly important in habitats where physical disturbance is minimized. At the Exposed Station, neither A. spicifera nor L. papillosa could effectively exclude the other because of the continuous wave pounding which stunted the growth of L. papillosa and fragmented the thallus of A. spicifera (Figs. 33 and 37; Appendix I). At the Moderately-Exposed Station, the biomass of A. spicifera and L. papillosa increased in abundance, coinciding with a decreased wave action (Fig. 58a,c). Here, the first evidence of interference competition (Schoener, 1983) was suggested. After a period of severe aerial exposure, A. spicifera and L. papillosa were reduced to their holdfasts. When water returned to the reef, the faster growing A. spicifera increased in size (Table XXIII) and biomass (June-July; Fig. 27), becoming the most noticeable fore-reef seaweed. At this time, fronds of A. spicifera covered and slowed the growth of overgrown L. papillosa. This was shown by comparing the sizes of the overgrown plants of L. papillosa with plants growing nearby that were not covered by A. spicifera (Table XXIII). A. spicifera, however, was not able to maintain its large size and, by the end of the fifth week, was shorter than L. papillosa (Table XXIII). An increase in wave action and frond size (i.e., increased drag forces) decreased the size of fronds of A. spicifera. L. papillosa continued to grow slowly,

eventually completely covering A. spicifera. Fortunately, the holdfast of A. spicifera was able to tolerate prolonged periods of overgrowth (Table XXVI) and the frequency of aerial exposures were sufficient to remove the Laurencia overstorey, preventing the exclusion of A. spicifera from the Moderately-Exposed Station.

At the Sheltered Station, the biomass of A. spicifera and L. papillosa in the Laurencia Zone continued to increase over those of the Moderately-Exposed and Exposed Stations (Fig. 58a). Free substratum was now at a premium, with A. spicifera growing as a "mat". As previously stated, distinct mosaics of A. spicifera and L. papillosa patches developed at the Sheltered Station during periods of calm seas. Plotting the biomass of A. spicifera against the biomass of L. papillosa from the "center of distribution" of A. spicifera showed that both species were inversely related (Table XX and Fig. 58c); the biomass of A. spicifera increased from the Exposed to the Sheltered Station, while the biomass of L. papillosa decreased. Also at the Sheltered Station, the biomass of L. papillosa was significantly greater landward and seaward of the "center of distribution" of A. spicifera (Table XXI). These data suggest that "mats" of sufficient longevity develop that effectively remove L. papillosa from the "center of distribution" of A. spicifera. Further evidence suggesting the competitive exclusion of L. papillosa by A. spicifera was shown in an examination of the degree of association between these species in the Laurencia Zone. At the Exposed Station, open space was in large supply, allowing A. spicifera to grow independent of or in association with L. papillosa (Table XXII

and Figs. 60 and 61). As a result, the two species were not positively associated. At the Moderately-Exposed Station, the limited space and high algal biomass resulted in a positive association between A. spicifera and L. papillosa. At the Sheltered Station, plants of A. spicifera and L. papillosa were again not positively associated (Table XXII), despite further decreases in "free space" (Figs. 60 and 61) and overall increases in the biomasses of A. spicifera and L. papillosa (Figs. 58a,c). Again, these data suggest that A. spicifera is competitively excluding L. papillosa. As to a potential limiting resource, only about 0.29 % of the incident light was transmitted through the "mats" collected at the Sheltered and Back-Reef Stations (Table XXIV). However, it is difficult to separate other effects caused by the overlying "mat" of A. spicifera. For example, in the Acanthophora "mat", the flow of seawater was severely reduced, which could result in the build-up of waste products or the depletion of a vital nutrient. Such conditions probably accounted for the inability of A. spicifera uprights to grow when overgrown by L. papillosa (Table XXVI). Most likely, a combination of reduced light and nutrients and a build-up of waste products were all involved in limiting the growth and abundance of L. papillosa under the "mats" of A. spicifera. Conversely, the lack of a positive association between A. spicifera and L. papillosa at the Sheltered Station also suggested that L. papillosa could be excluding A. spicifera from areas outside its "center of distribution", where L. papillosa occurred in greater numbers than A. spicifera; little other supportive information is available.

"Mats" of A. spicifera are able to inhibit the growth of L. papillosa in the Acanthophora Zone. Here, dense "mats" of A. spicifera form from drifting fragments that accumulate on L. papillosa. These fronds quickly consolidate into a "mat" by entangling and attaching to each other. When understorey L. papillosa was cleared of the A. spicifera, the biomass of L. papillosa increased significantly compared with the L. papillosa that remained under the canopy of A. spicifera. Thus, the "mats" of A. spicifera severely limit the growth and abundance of L. papillosa in the Acanthophora Zone and probably do the same at the Sheltered Station.

In retrospect, competition appears most intense when disturbances are minimized, permitting the accumulation of large quantities of biomass (such as at the Back-Reef and Sheltered Stations) that allow competitors to interact on a more measurable, spatial scale (i.e., "mat" vs. "aggregate"). Equally intense but on a smaller spatial scale is the competition at the Moderately-Exposed Station (i.e., plant vs. plant), which makes measuring and detecting competition more difficult. These observations agree with the Lotka-Volterra Competition Model: competition is most intense in a fully saturated environment (Pianka, 1978).

It is possible that the competitive outcome between any two algae is dependent upon growth (Hay, 1981a; 1981b; 1983; Lubchenco, 1978; 1980) and the adaptation of the competitors to the level of disturbance within their habitats. For example, A. spicifera overgrew and inhibited L. papillosa at the Moderately-Exposed Station; however, it did not

exclude it because of increases in frond mortality that resulted from wave action. On the other hand, L. papillosa then proceeded to overgrow A. spicifera but did not exclude it because of the resistant holdfast of A. spicifera. In the former case, A. spicifera is not well-suited to tolerating wave exposure, giving L. papillosa the competitive advantage, while in the latter case, the holdfast of A. spicifera tolerates the overgrowth of the Laurencia canopy until the next aerial exposure. Faster growing species like A. spicifera are not always so fortunate. Paine (1979) showed that in the absence of an appropriate regime of space-clearing disturbance, dense stands of Postelsia palmaeformis Rupr. often went extinct. Their disappearance is caused by the continual encroachment of the slower growing, coralline alga Corallina vancouveriensis Yendo which preempt space, preventing local recruitment. A similar situation in New England was described by Lubchenco (1980) between Chondrus crispus and Fucus spp. A fine balance between adaptation and physical disturbance maintains P. palmaeformis and C. vancouveriensis, as it does A. spicifera and L. papillosa.

Where wave disturbance is reduced on the reef flat, the faster growing competitor is favored. Measurements of growth (Fig. 32), biomass (Figs. 27 and 53), and photosynthetic ability (Figs. 62 and 64) indicated A. spicifera grows faster than L. papillosa. The ability to grow fast allowed A. spicifera to form dense "mats" with sufficient longevity to overgrow and severely limit the growth of L. papillosa at the Sheltered (Fig. 58c) and the Back-Reef Stations (Table XXV). The potential of A. spicifera and L. papillosa to exclude faster growing

genera (i.e., Centrocerus and Spyridea) may result in: (i) their inability to tolerate existing levels of aerial exposure and wave disturbance;

(ii) their low probability of settlement during favorable reef conditions; and (iii) their low densities at the time of settlement.

For similar reasons, A. spicifera, like Centrocerus and Spyridea, is at a disadvantage outside its "center of distribution". The relatively short period of favorable growth conditions (2 to 3 months) is not sufficient to allow A. spicifera to expand beyond its "center of distribution"; thus, the population of L. papillosa is maintained.

Lubchenco (1978) showed that when predation pressure (biotic disturbance) was minimized by the removal of Littorina littorea L. from New England tide pools, the faster growing Enteromorpha sp. excluded the slower growing Chondrus crispus. Alternatively, when predation pressure was maximized by adding snails, the faster growing Enteromorpha was excluded by the snails, allowing C. crispus to persist. Thus, growth regulates the competitive outcome only when adaptations to habitat disturbances are minimized between competitors, giving no one species special survival advantages. These results are contrary to the work of Hutchinson (1951) who envisioned "fugitive" species which have a high instantaneous rate of increase as a predictably inferior competitor, being always excluded by a more K-selected (MacArthur & Wilson, 1967; Pianka, 1970) competitor. Connell and Slayter (1977) have shown in their "inhibition" model of succession that the fast-growing early successional species may dominate a resource and, in the absence of disturbance, prevent the recruitment of other species.

Sousa (1979) and Sousa et al. (1981) have shown in California that the intertidal alga, Ulva, and the subtidal filamentous red algae are such successional species (i.e., both fast growing taxa). Applying these results to Connell and Slayter's "tolerance" model of succession (later species are successful whether earlier species have preceded them or not), the faster growing species which settles first is not necessarily the best adapted to the habitat, so the slower growing species wins out (i.e., Postelsia-Corallina example; Paine, 1979). In their "facilitation" model of succession, the later species can only become established and grow after the earlier species have modified conditions. The very description of this model implies a kind of altruistic behavior by the early colonist — one species makes the habitat more suitable for another species. It is totally illogical for one species to devote its energies and resources for the benefit of other species without itself requiring something in the process. Instead, this model represents two possible situations: (i) where the early colonist depletes a resource (i.e., nutrients, etc.), thereby placing itself in stress (i.e., slowing its growth), and then is outcompeted by a superior competitor better able to tolerate the new conditions; or (ii) where the early colonist inadvertently changes the habitat, allowing a superior competitor to recruit, and then is outcompeted.

Grime (1974, 1977) proposed a model which predicts three basic kinds of life history strategies: low stress with low disturbance (competitive plants); high stress with low disturbance (stress-tolerant plants); and low stress with high disturbance (ruderal plants). The

utility of this model may have profound theoretical implications, but as an ecological tool its usefulness is questionable. To point out one of the problems, my use of the word disturbance in reference to wave exposure reflects that of Grime's (1974, 1977) with respect to

A. spicifera. That is, a disturbance consists of those mechanisms which limit the plant biomass by causing its destruction (i.e.,

fragmentation). With L. papillosa, the wave-exposure gradient is best characterized as a stress gradient. Stress is defined by Grime

(1974, 1977) "as the external constraints which limit the rate of dry-matter production of all or part of the vegetation" (i.e., the

stunted morphology of L. papillosa). What is a stressful environment for one species can be a high disturbance environment for another, and yet a competitive environment for others (Postelsia-Corallina example; Paine, 1979). Similar observations were made by Menges and Waller (1983) when working with herbs in a floodplain forest in Wisconsin.

Grime's three-strategy model appears too simplistic to be predictive.

While my conclusions about growth and adaptation to environmental disturbance superficially resemble those of Grime (1974, 1977), they differ in regards to approach and definition. From the above example, it seems reasonable that when attempting to understand community structure it is best to examine how the species utilizes its environment to promote its survival rather than to rigidly classify a species by how its environment affects it. Secondly, what is important in determining community structure is the fact that disturbance and stress limit biomass, and not the selective nature of the limitation. Thus, I prefer

to join Grime's (1974, 1977) definitions of stress and disturbance into a broader, ecologically more useful meaning of environmental disturbance when attempting to understand community structure.

4.3 Summary

A. spicifera is shown to be highly adapted both to dispersing fragments and to its reef-flat environment. Field data and experiments demonstrate that abiotic disturbances in the form of wave exposure and aerial desiccation control the abundance and distribution of

A. spicifera. The Acanthophora Zone, which receives A. spicifera fragments from the Exposed and Moderately-Exposed Stations, receives a continuous supply of fragments from plants adapted to breaking and colonizing new substrata and to tolerating wave action, aerial exposures, and the overgrowth of neighboring algae.

Aerial exposures prevent the competitive exclusion of A. spicifera in the Laurencia Zone by removing the canopy of L. papillosa, allowing overgrown A. spicifera the opportunity to grow and produce fragments when reef water returns. In the Acanthophora Zone, the situation is reversed. The canopy of A. spicifera is removed by aerial exposures, permitting L. papillosa, which is an essential substratum for colonizing A. spicifera fragments, to re-establish itself and to escape competitive exclusion. In both of the above situations, the overgrown species benefits during the aerial exposure period by having a protective layer of algae above it, reducing both desiccation and thermal effects of aerial exposures. Similarly, the Laurencia Zone plants of A. spicifera benefit by growing within "aggregates" of L. papillosa, increasing their resistance to wave and aerial exposures. Thus, the fragmentation strategy of A. spicifera is maintained by a fine balance between

adaptations to wave action, aerial exposures, and competitive interactions, that are all instrumental in allowing A. spicifera to persist.

APPENDICES

Appendix I. An Assessment of the Effects of Wave Action and
 Predation on the Branching Morphology of Acanthophora spicifera (Vahl)
 Borg. and Laurencia papillosa (Forsk.) Grey.

Introduction

Seaweeds are morphologically variable, often not conforming to categorized morphological schemes (Chapman and Chapman, 1976; Garbary, 1976). This characteristic of seaweeds has ecological significance as algal morphology is implicated in many survivorship strategies, such as in predatory defense mechanisms (Dethier, 1981; Hay, 1981a; Slocum, 1980; Littler and Littler, 1980; Lubchenco and Cubit, 1980; Steneck and Watling, 1982); competitive interactions (Kain, 1975; 1976); photosynthesis (King and Schramm, 1976; Littler and Murray, 1974; Littler, 1980; Raven and Glidewell, 1975); nutritive acquisition (Charters et al., 1972; Leyton, 1975; Odum et al., 1958; Raven, 1981); and reproductive adaptations (Coon et al., 1972; Neushul, 1975; Searles, 1980). No doubt there is much to learn in such studies of morphology despite the difficulties of clearly identifying "a given feature as an obvious adaptation to a given environmental factor" (Neushul, 1975).

Bifurcation ratios have been used to characterize tree architecture (Baker et al., 1973; McMahon, 1975; McMahon and Kronauer, 1976), but the results of such studies are often equivocal, as branching ratios represent a single basic property, are not predictive of tree development, and ignore information essential to tree design (Borchert and Slade, 1981). Fortunately, the rather simple structure of seaweeds alleviates many of the problems associated with higher plants. For

example, Dahl (1971) has noted that the morphology of many seaweeds is an accurate record of their recent history; algae can become shorter, more erect, and highly branched and compact in desiccated and grazed areas or in areas subject to wave action (Dahl, 1968; Gittins, 1975; Hay, 1981a,b; Liddle, 1975; Munda, 1972; Stewart, 1968). By using bifurcation ratios to quantify branching structure, questions as whether an alga is increasing or decreasing the number and length of its branches can be determined.

In this study, the two tropical red algae, Acanthophora spicifera (Vahl) Borg. and Laurencia papillosa (Forsk.) Grev. are evaluated for the number and segment length of branches. Two hypotheses are tested: (i) A. spicifera disperses by fragmenting; and (ii) L. papillosa is not affected by grazers on the reef flat. Both species are similar morphologically, possessing short determinate branchlets and large indeterminate branches, and ecologically, occurring in the same habitats on the reef platform. It will be shown that bifurcation ratios provide a practical means of detecting and displaying changes in algal branching design.

Methods

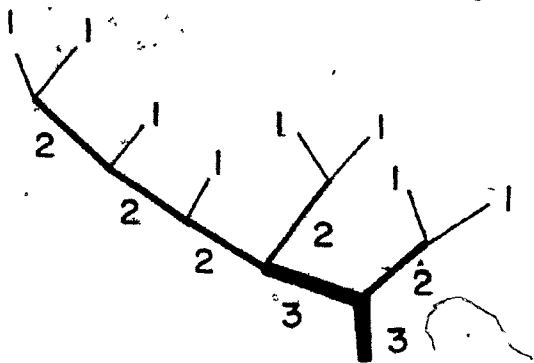
Sampling and Labelling of Branches

Randomly located quadrats (0.15 m X 0.30 m) at of. Galeta Point, Panama ($9^{\circ} 24' N$, $79^{\circ} 52' W$) were harvested for A. spicifera and L. papillosa from 26 September to 1 October 1981 in the Acanthophora Zone and from 29 October to 5 November 1981 in the Laurencia Zone (described by Meyer and Birkeland, 1974). The sampling period was chosen to maximize the regrowth of the two plant species from past periods of desiccation (i.e., about two months of regrowth). All fronds in the quadrat were collected, and quadrats were sampled until 100 fronds of each species were obtained both from the Acanthophora and Laurencia Zones (hereafter referred to as the fore and back reef, respectively). Samples were removed from the substratum with a razor, placed into trays, and returned to the laboratory. Individual fronds were separated and the number and length of different branch orders determined by the Strahler (1953) method of labelling branches. In this system (Fig. 1a), the end branches are of order 1, and two of these meet to form an order 2 branch; two order 2 branches meet to form an order 3 branch, and so on to the main axis. When two branches of different order meet, the conjoined branches take on the same order as the higher of the two branches. Finally, any two or more contiguous branches of the same order are considered to constitute only one branch (Fig. 1b).

Branches labelled in this fashion allow for a comparison of branching characteristics between individuals or populations of fronds. Such comparisons may consist of differences in: the number of branches,

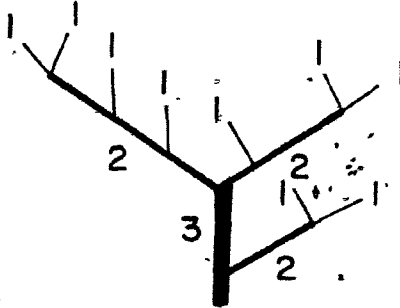
Figure 1. (a) Branching system ordered by Strahler method; (b) the same branching system redrawn to show how contiguous branches of the same order become one branch; and (c) an example of the modified Strahler method taking into account the loss of a branch.

Strahler Method

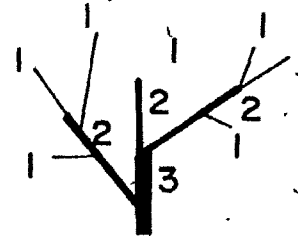


(a)

Modified Method



(b)



(c)

the length of branch segments, or any characteristic that can be ascribed to an order of branching. For example, when comparing two fronds, the procedure requires that the log of the variable in question — as the number of branches — be plotted as a function of branching order. In doing so, a linear relationship between the number of branches and the branching order is observed for each frond. The linear relationship serves as the basis for comparing the two fronds: in this instance, the antilog of the absolute value of the slope (R_b or the branching ratio) indicates that there are on an average R_b times as many branches in each order as in the next higher order (Barker *et al.*, 1973); the Y-intercept may serve as an index of the number of terminal branches; or the X-intercept may serve as an index of branching complexity (*i.e.*, the greatest number of ordered branches). When populations of fronds are compared, the mean number of branches for each individual frond is averaged over the entire sample and plotted in a similar manner.

In this study, comparisons are also made between the lengths of different orders of branches. The length of an ordered branch is defined as the sum of the lengths of all branches found between the holdfast and the terminal end of the ordered branch. The antilog of the absolute value of the slope when the log of the mean length is plotted against branching order is termed the length ratio (L_b).

To make the branching ratio more sensitive to losses in branches, the Strahler method of labelling branches was modified by scoring the broken ends of branches as 1st-order branches (Fig. 1c). In respect to the Strahler method, the modified scheme reduces the branching ratio

when broken ends of branches are encountered.

Disturbance and Branching Pattern

In an "ideal environment" where plants are free from external and internal constraints, each species has a characteristic branching ratio; this is best understood by expanding a branching-pattern progression.

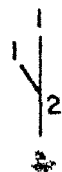
For example, given a plant that produces two lateral branches before the oldest lateral branch itself produces a branch, the growth of a frond would proceed as in Figure 2. As the number of branches increases, the range of the branching ratio narrows and approaches its characteristic value (R_b theoretical). As shown in Figure 2, the branching ratio of plants with only two orders of branching is either two or three, while the branching ratio of plants with three orders of branching is between 2.2 and 2.8. If the branching progression is further expanded, an R_b theoretical value of 2.5 is obtained.

As an alga grows, branches near its base often receive less light and fewer nutrients because of self-shading and reduced water flow around the branches. In effect, an alga inhibits its own development as it grows larger. Accordingly, a population of large-sized plants would naturally have a lower branching ratio than a population of small-sized plants with few branches.

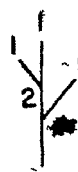
When the branching system of an alga is perturbed by a form of disturbance the alga will respond in one of two ways: (1) if the intensity of the disturbance is severe, the alga will continually lose branches faster than it can replace them, thereby decreasing the

Figure 2. Branching pattern progression with two branches as the maximum number of lateral branches produced before the oldest lateral produced its own branch. Also displayed, are the branching ratios and the number of ordered branches.

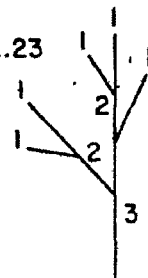
Rb=2



Rb=3

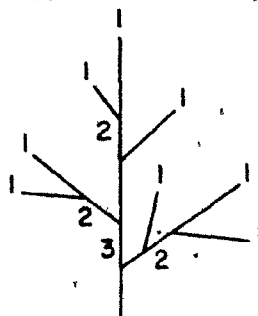


Rb=2.23

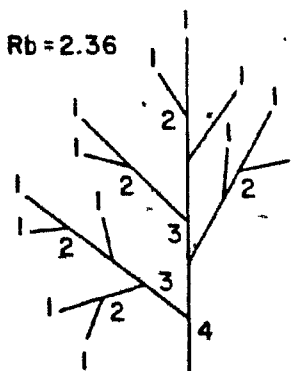


Order of Branching	(Number of branches)		
1.	2	3	5
2.	1	1	2
3.	0	0	1

Rb = 2.83



Rb = 2.36



Order of Branching	(Number of branches)	
1.	8	13
2.	3	5
3.	1	2
4.	0	1

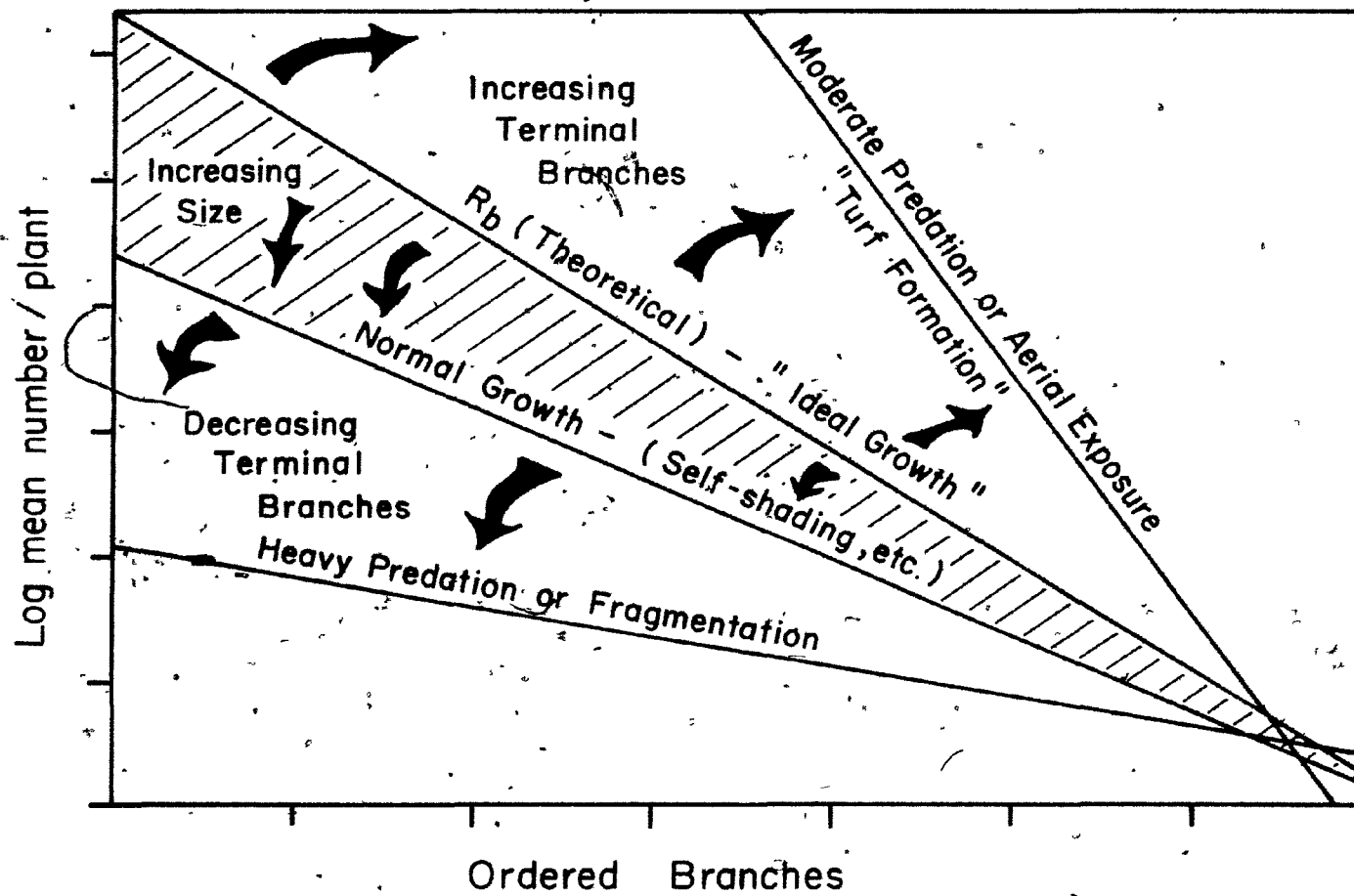
branching ratio; and (ii) if the intensity of the disturbance is moderate, the alga will have time to respond to its injury, thus resulting in further branch production and an increase in the branching ratio. It is generally accepted that a form of "apical dominance" is operating in most algae (Augier, 1972; Buggeln, 1981; Moss, 1965; 1966) and based on preliminary experiments, including A. spicifera and L. papillosa. By producing more terminal branches, the branching ratio would quickly exceed Rb theoretical. Conditions between moderate and severe disturbance would yield little change in the branching ratio. Such conditions, however, are easily distinguished from that of little to no disturbance by a direct examination of fronds for grazing or branching scars. Figure 3 summarizes the expected changes in the branching ratio in response to growth and environmental disturbance.

Hypothesis Testing

To address the hypotheses that A. spicifera releases fragments in the wave zone and that L. papillosa is unaffected by grazers, it is necessary to eliminate or minimize the effects of all forms of disturbance on the plants, other than the one in question. The major disturbances of algae on the reef flat are: exposure in the air, wave action, and predation.

In selecting an appropriate sampling period, aerial exposures of plants can be kept to a minimum. In this study, plants were collected in October-November when luxuriant stands of A. spicifera and L. papillosa could be collected. Sampling at this time provided

Figure 3. Changes in branching ratio from predation, fragmentation, growth, and exposures in the air.



seaweeds with about two months of regrowth without exposure in the air.

Predation pressure on the reef flat was examined by evaluating the branching structure and the number of branching scars on L. papillosa. During periods of minimum aerial exposures, conditions for predation by herbivorous fishes (mostly small Pomacentridae, Scaridae, and Labridae) are optimal because of the continuous cover of water over the reef flat and the reduced intensity of wave exposure. Other grazers, such as sea urchins, are few in number, small, or confined to the Thalassia meadows, coral rubble areas, or within crevices in the fore-reef (Meyer and Birkeland, 1974). Before scars on the thallus of L. papillosa could be attributed to grazing, the effects of wave action on L. papillosa had to be examined. To do so, 60 fronds were tagged in the fore and back reef with plastic "cable ties". From 20 September to 15 December 1981, tagged fronds were noted for their presence or absence every fortnight. If L. papillosa lost few fronds from wave action then scars that occurred on the thalli of L. papillosa must have resulted from predation. As the back-reef area of Galeta Reef (Hay, 1983) and other Caribbean reefs (Steneck, 1983) are effected little by grazers, grazing pressure can be further evaluated by comparing the number of grazing scars and the branching structure of fore- and back-reef plants. If grazing pressure is minimal in the fore reef, then the prediction would be that the smaller-sized plants of L. papillosa in the the fore reef will have a larger branching ratio than the larger-sized plants in the back reef and that little difference in the number of grazing scars will occur between the fore and back reef.

A. spicifera is believed to regularly fragment in the fore reef.

IF A. spicifera does fragment in the wave zone, it should exhibit a different branching structure to plants of A. spicifera found in the sheltered back reef. To test this hypothesis, it is necessary that grazing pressure in the fore reef is shown to be minimal; otherwise, it is no possible to distinguish between effects of predation and fragmentation on branching structure; the two forms of disturbance are confounded. The fragmentation hypothesis, however, can be tested if predation can be shown to play a minor role. Because L. papillosa is similar to A. spicifera in morphology and spatial distribution, it could serve as a control for predation, providing: (i) A. spicifera and L. papillosa are equally consumed by predators; and (ii) L. papillosa is unaffected by wave action. Because of the shallow depth of the wave zone and the high current velocities from breaking waves, it is unlikely that selective grazing of A. spicifera over L. papillosa could take place in these harsh conditions. Also, Hay (1981a) has shown both species to be readily consumed by herbivorous fish. We believe that L. papillosa can be used as a control for the amounts of predation on A. spicifera.

Providing that grazing does not influence the branching structure of fore-reef populations, the prediction is that the branching ratio in the fore-reef population will be smaller than in the back-reef population, if A. spicifera regularly fragments in the fore reef. As A. spicifera is smaller in the fore reef than in the back reef, the opposite prediction is expected if A. spicifera does not fragment or exhibits moderate levels of fragmentation.

Length ratios were not used to test for fragmentation because they

lacked the necessary sensitivity, but were useful as a descriptive measure.

Statistical tests were done utilizing the methods of Zar (1974) and Sokal and Rohlf (1969).

Results

Predation on L. papillosa

Predation and wave exposure had little effect on the branching structure of L. papillosa. Of the 120 tagged fronds of L. papillosa, four back-reef tags and ten fore-reef tags were lost at the end of nearly four months. Accordingly, L. papillosa was concluded to lose few fronds to wave exposure, and scars that occurred on its thallus were assumed to be grazing scars.

Few indeterminate branches of L. papillosa showed any signs of predation. Of the fronds examined, only 4.5 % (44 fore-reef and 53 back-reef branches) of the indeterminate branches had missing apices, and the numbers of grazed apices were not statistically different between the fore- and back-reef populations of L. papillosa (Test of Proportions, $p > 0.05$). Also, the grazing of indeterminate branches appeared to stimulate the growth of one to four determinate branches immediately adjacent to the grazing scar.

Most fronds of L. papillosa and A. spicifera showed some grazing of the small determinate branchlets. This grazing, however, did not affect branching structure. Field observations revealed the presence of many small herbivorous fish and amphipods that could account for the grazing of the determinate branches.

Branching and Length Ratios

Figure 4 shows the regression of log mean number and length against branching order for back and fore reef L. papillosa. All regressions were significant and high coefficients of determination were observed for each model; the simple linear models accounted for a minimum of 95% of the variance (Fig. 4). The slopes of the regression models were not significantly different between the fore and back reef when the plots of log mean length were compared, but they were significantly different when plots of log mean number of ordered branches were compared ($T = 2.58$, $p < 0.05$, $N = 7$). The branching ratio in the back reef ($R_b = 2.67$) was smaller than in the fore reef ($R_b = 3.35$). Y-intercepts were significantly different between fore and back reef in length ($T = 9.71$, $p < 0.001$, $N = 7$) and number ($T = 22.30$, $p < 0.001$, $N = 7$) of branches (Fig. 4), suggesting that back reef plants were taller and "bushier" (i.e., having a greater number of terminal branches) than fore reef plants. The height of fore- and back-reef L. papillosa averaged 26 mm and 75 mm, respectively.

Figure 5 shows similar regression models for A. spicifera. Like L. papillosa, taller ($T = 5.81$, $p < 0.005$, $N = 7$) and bushier ($T = 49.91$, $p < 0.001$, $N = 7$), plants occurred in the back reef. The length ratios (L_b) did not differ between the fore and back reef; however, the branching ratios were different ($T = 4.49$, $p < 0.002$, $N = 8$). The branching ratio of the fore reef ($R_b = 2.33$) was smaller than that of the back reef ($R_b = 2.74$). The average height of A. spicifera was 38 mm in the fore reef and 110 mm in the back reef.

Figure 4. Log mean length and number of Strahler labelled branches for L. papillosa. (▲ = fore reef; ● = back reef.)

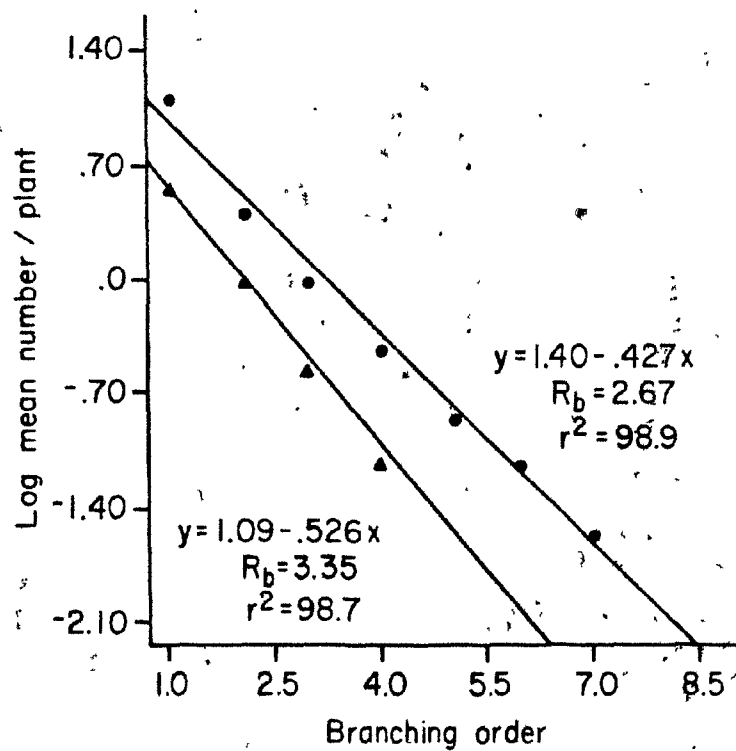
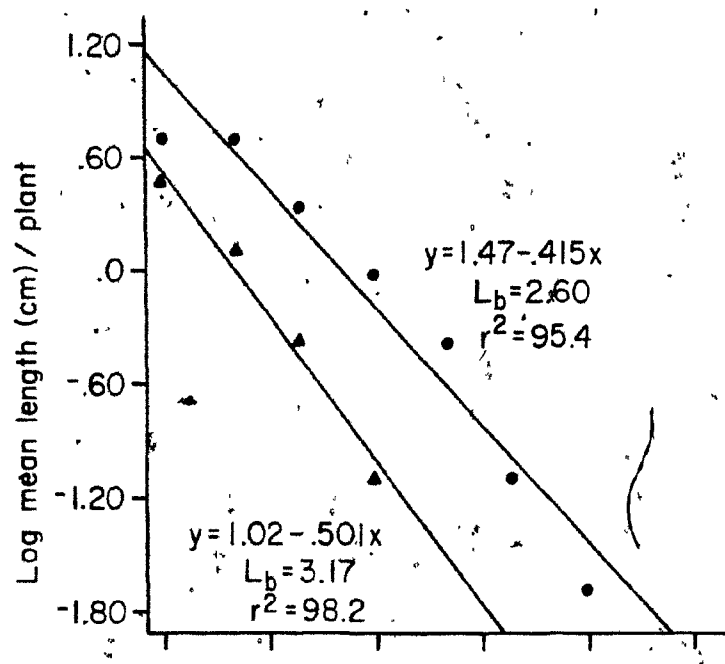
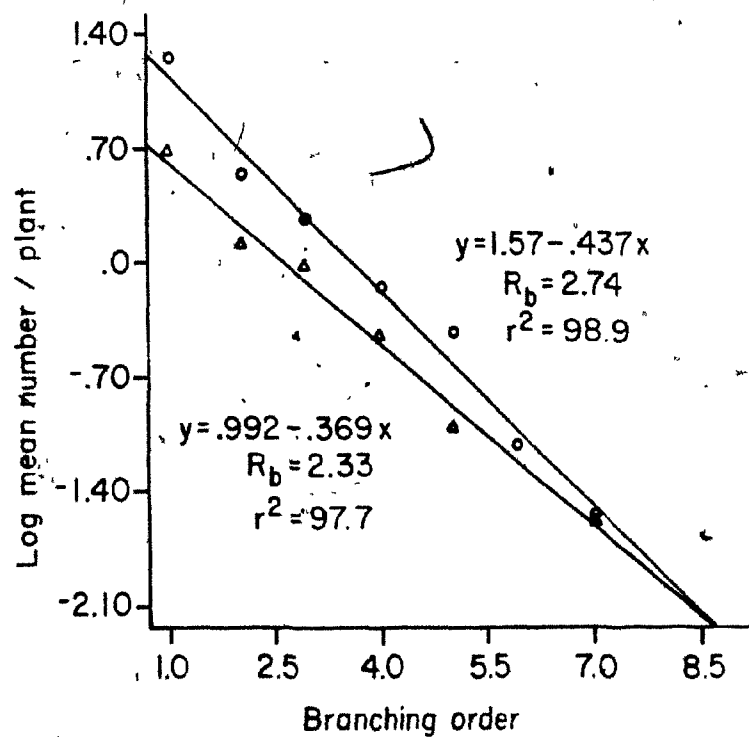
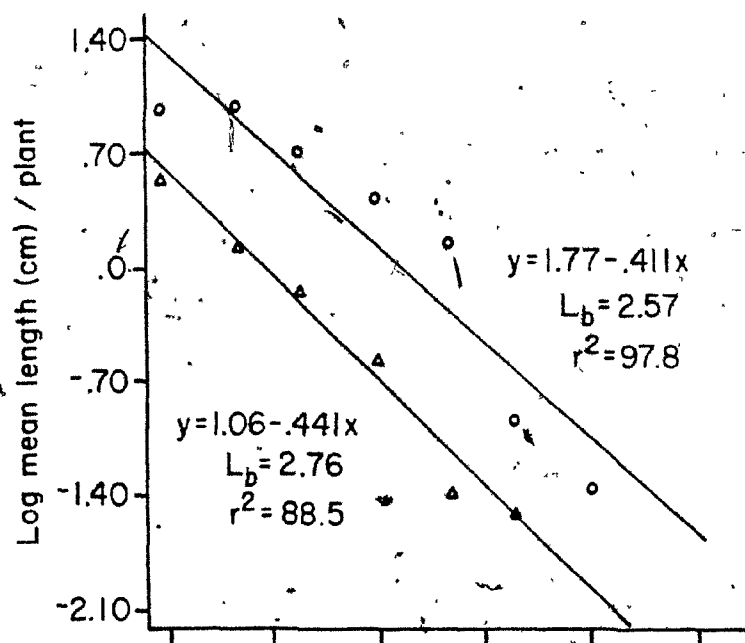


Figure 5. Log mean length and number of Strahler labelled branches for A. spicifera. (Δ = fore reef; $\circ$ = back reef.)



Numerous scars (fragmenting or grazing) were observed on A. spicifera collected in the fore and back reef.

Discussion

Branching ratios provide a convenient method for analyzing plant morphology. We are aware only of one previous study (Carbary et al., 1980) that showed quantitative differences in branching pattern. In the present instance, we have shown that in certain circumstances, branching ratios and length ratios can be correlated with ecological events.

Previously Mshigeni (1978) concluded from colonization studies in Hawaii that A. spicifera reproduced by vegetative fragmentation, which could account for its rapid spread throughout Hawaii (Doty, 1961; 1973) and other tropical areas (Russell, 1981). Russell (1981) noted that the distribution of A. spicifera was limited by wave exposure to moderate-to-sheltered coasts. These results seem reasonable, as A. spicifera easily loses branches upon handling. At Galeta Point, it was postulated that the fore-reef population on the reef flat, because of wave exposure, produced fragments that colonized the back reef; the aim was to test whether, on the bases of bifurcation ratios, A. spicifera disperses fragments. To do so, it was necessary to determine if grazing had a significant effect on the branching structure of fore-reef seaweeds. By finding few grazing scars and the expected difference in the branching ratios of L. papillosa in the fore and back reef, grazing pressure within the wave-swept populations of the fore reef and in the sheltered back reef is concluded to be minimal. Also,

the observed differences in the branching structure of L. papillosa imply that little predation has occurred over the last few months of growth. Accordingly, it is concluded that there is little chance of grazing affecting the branching structure of A. spicifera. These findings are in agreement with those of Hay (1981a, 1983) for the reef flat at Galeta Point and those of Steneck (1983) who showed grazing pressure to be less in the back reef than on the reef slope at St. Croix. Other researchers have similarly noted that dense stands of seaweeds on tropical reefs were usually confined to shallow areas of wave-washed reef platforms or benchrock benches (Adey & Vassar, 1975; Earle, 1972b; Hoek van den et al., 1978; Ogden, 1976; Randall, 1961).

To demonstrating that A. spicifera disperses fragments, the prediction was that fronds in the sheltered habitat of the back reef would have a larger branching ratio than those in the fore reef or wave zone. As there is little apparent fragmentation and grazing of L. papillosa on the fore reef, this species too should have a larger Rb than the fore-reef population of A. spicifera. Indeed, both predictions were substantiated, as significant t-tests were shown for both comparisons (Table I). Despite the smaller size of A. spicifera in the fore reef than in the back reef, a smaller rather than a larger branching ratio was observed, indicating a severe form of disturbance, wave action, was affecting the branching structure. (i.e., fragmentation).

The branching ratio of L. papillosa was significantly greater in the fore reef than in the back reef. With predation shown to have had little effect on reef-flat populations and with effects of aerial

exposure minimized, the higher branching ratio of L. papillosa in the fore reef than in the back reef suggested that the fore-reef population of L. papillosa was the least affected by elements that alter branching structure. In addition, there were no statistical differences between fore-reef and back-reef length ratios which suggested that the fore-reef fronds were identical to the terminal area of the larger back-reef fronds. When examining L. papillosa in the fore reef, Hay (1981a) defined the alga as a "turf", which refers to situations where upright branches are more than 5-mm tall and are packed so that each is in contact with its neighbors. In addition, Hay implied that "turfs" were a specialized morphology whose configuration was affected by (i) the number of uprights per length of prostrate, (ii) their degree of branching, and (iii) the extent to which lateral connections form between uprights. The branching data collected in this study suggested that the vast majority of L. papillosa in the fore reef were stunted plants rather than a reflection of modified morphology as suggested by Hay (1981a). No evidence of a "turf" morphology was obtained. Repeated exposures to air and water in the shallow wave zone and wave pounding are believed responsible for the stunted morphology. While densities of fronds may be greater in the fore reef, they are not sufficient to alter the branching pattern; however, we do not rule out that a few scattered clumps of L. papillosa at the seaward edge of the fore reef could conform to Hay's criteria mentioned above. Desiccation periods which result from the exposure of the reef in the air could potentially increase the branching ratio to form "turfs", but as a mechanism of maintaining a "turf" morphology, the frequency and intensity of moderate

Table I. Branching ratios of A. spicifera and L. papillosa.

Displayed are comparisons between adjacent branching ratios. All other comparisons were highly significant.

	Area	Rb	T	p	df
<u>L. papillosa</u>	fore-reef	3.35			
			6.74	< 0.001	9
<u>A. spicifera</u>	back-reef	2.74			
			0.74	> 0.05	12
<u>L. papillosa</u>	back-reef	2.67			
			3.64	< 0.005	9
<u>A. papillosa</u>	fore-reef	2.33			

exposures required to kill only apical cells would deem this unlikely.

Instead, long periods of aerial exposures in May and June were observed to reduce A. spicifera and L. papillosa to their holdfasts, destroying all of their branching structures. We conclude that the fore-reef

L. papillosa does not represent a modified morphology and that the water retention properties, photosynthetic partitioning, and predator avoidance strategies attributed to the fore reef Laurencia "turfs" by Hay (1981a) are by-products and not the cause of the stunted growth morphology.



Appendices II - IV

Appendix II. Distances along transect of the Reef Biomass Study which defined the sampling area of drift nets.

Transect no.	Distance (Negative to Positive) (Y coordinate) (X coordinate)
1-7	No Samples
8	All locations up to 0.0 m
9	All locations up to 20.0 m
10	All locations up to 41.0 m
11	All locations up to 69.0 m
12	All locations up to 110.0 m
13	All locations up to 119.0 m
14	All locations up to 134.0 m
15	All locations up to 146.0 m
16	All locations up to 156.0 m
17	All locations up to 159.0 m
18	All locations up to 127.0 m
19-25	All locations
26	All locations up to 180.0 m
27	All locations up to 177.0 m
28	All locations up to 176.5 m
29	All locations up to 170.5 m
30	All locations up to 163.5 m
31	All locations up to 162.5 m
32	No Samples

Appendix III. Area occupied by A. spicifera and L. papillosa in the Drift Sampling Area (February 1979 to March 1980). Percent occurrence data were obtained from the Reef Biomass Study and multiplied by the total area sampled by the Drift Nets (1.32 ha) to estimate the area occupied by A. spicifera and L. papillosa.

Date	Percent Occurrence		Reef Area (m ²)	
	Species: <u>A. spicifera</u>	<u>L. papillosa</u>	<u>A. spicifera</u>	<u>L. papillosa</u>
2/79	17.5	32.9	2313	4348
3/79	10.5	33.6	1388	4440
4/79	14.8	35.2	1956	4652
5/79	10.7	30.0	1414	3965
6/79	4.9	20.4	648	2696
7/79	4.9	21.5	648	2841
8/79	9.1	26.6	1203	3515
9/79	7.7	19.7	1018	2603
10/79	13.0	34.2	1718	4520
11/79	14.2	31.1	1877	4110
12/79	16.6	37.4	2154	4943
1/80	16.2	37.2	2141	4916
2/80	9.3	31.4	1229	4150
3/79	17.0	36.2	2247	4784

Appendix IV. The Branching Structure of Acanthophora and Laurencia Zones fronds of A. spicifera (Botanical Method; October-November 1981). N = number of fronds

	<u>Laurencia</u> Zone		<u>Acanthophora</u> Zone			
	$\bar{X} \pm SD$	N	$\bar{X} \pm SD$	N	t	p
Height of Plant	4.68 $\pm$ 1.37	104	9.98 $\pm$ 6.08	102	39.33	< 0.001
Height of Main Axis	1.07 $\pm$ 1.05	104	6.28 $\pm$ 3.70	102	50.63	< 0.001
No. of 1st-order branches	2.38 $\pm$ 1.98	104	3.20 $\pm$ 2.73	102	4.37	< 0.001
No. of 2nd-order branches	1.54 $\pm$ 2.01	104	2.40 $\pm$ 3.13	102	4.35	< 0.001
No. of 3rd-order branches	0.29 $\pm$ 1.09	104	1.61 $\pm$ 4.32	102	12.43	< 0.001
No. of 4th-order branches	0.0	104	0.82 $\pm$ 3.35	102	2.48	< 0.010
No. of 5th-order branches	0.0	104	0.14 $\pm$ 1.29	102	1.08	< 0.050
No. of ordered branches	3		5			
No. of 2nd-order branches on the first 1st-order branch	0.55 $\pm$ 1.13	104	1.26 $\pm$ 2.06	102	6.42	< 0.001
No. of 2nd-order branches on the second 1st-order branch	0.50 $\pm$ 1.07	104	0.71 $\pm$ 1.33	102	2.00	< 0.050
No. of 2nd-order branches on the third 1st-order branch	0.19 $\pm$ 0.70	104	0.34 $\pm$.84	102	2.16	< 0.050
No. of 3rd-order branches on the first 2nd-order branch on the first 1st-order branch	0.14 $\pm$ 0.31	104	0.44 $\pm$ 1.57	102	13.24	< 0.001
No. of 3rd-order branches on the first 2nd-order branch on the second 1st-order branch	0.14 $\pm$ 0.81	104	0.23 $\pm$ 1.21	102	10.00	< 0.001

Appendix IV.(cont'd)

	<u>Laurencia</u> Zone		<u>Acanthophora</u> Zone		t	p
	$\bar{X} \pm SD$	N	$\bar{X} \pm SD$	N		
Distance from Holdfast to:						
first 1st-order branch	0.56 $\pm$ 0.68	91	2.92 $\pm$ 3.46	86	33.29	< 0.001
second 1st-order branch	0.74 $\pm$ 1.31	69	3.84 $\pm$ 1.74	66	19.67	< 0.001
Distance from the Main Axis of the first 2nd-order Branch on the:						
first 1st-order branch	1.02 $\pm$ 1.11	29	2.78 $\pm$ 1.25	38	8.57	< 0.001
second 1st-order branch	0.95 $\pm$ 1.03	28	2.67 $\pm$ 1.02	27	8.85	< 0.001

Appendix V. The Branching Structure of Acanthophora and Laurencia Zones fronds of L. papillosa (Botanical Method, October-November 1981). N = number of fronds

	<u>Laurencia</u> Zone		<u>Acanthophora</u> Zone		t	p
	$\bar{X} \pm SD$	N	$\bar{X} \pm SD$	N		
Height of Plant	2.95 $\pm$ 0.63	99	7.15 $\pm$ 1.92	99	21.75	< 0.001
Height of Main Axis	2.20 $\pm$ 0.90	99	3.33 $\pm$ 2.24	99	4.99	< 0.001
No. of 1st-order branches	2.00 $\pm$ 1.45	99	4.23 $\pm$ 2.88	99	7.69	< 0.001
No. of 2nd-order branches	0.49 $\pm$ 1.12	99	6.29 $\pm$ 5.81	99	9.92	< 0.001
No. of 3rd-order branches	0.02 $\pm$ 0.14	99	4.31 $\pm$ 7.11	99	6.01	< 0.001
No. of 4th-order branches	0.0	99	1.21 $\pm$ 4.30	99	2.80	< 0.010
No. of fifth order branches	0.0	99	0.22 $\pm$ 1.01	99	2.19	< 0.050
No. of ordered branches	3		5			
No. of 2nd-order branches on the first 1st-order branch	0.24 $\pm$ 0.59	99	1.86 $\pm$ 2.87	99	5.59	< 0.001
No. of 2nd-order branches on the second 1st-order branch	0.18 $\pm$ 0.52	99	1.63 $\pm$ 2.59	99	5.54	< 0.001
No. of 2nd-order branches on the third 1st-order branch	0.04 $\pm$ 0.28	99	1.03 $\pm$ 2.15	99	4.59	< 0.001
No. of 2nd-order branches on the fourth 1st-order branch	0.0	99	0.42 $\pm$ 1.06	99	3.98	< 0.001
No. of 2nd-order branches on the fifth 1st-order branch	0.0	99	0.33 $\pm$ 1.12	99	2.97	< 0.010
No. of 3rd-order branches on the first 2nd-order branch on the first 1st-order branch	0.0	99	0.51 $\pm$ 1.55	99	3.24	< 0.010

Appendix V.(cont'd)

	Laurencia Zone		Acanthophora Zone		t	p
	$\bar{X} \pm SD$	N	$\bar{X} \pm SD$	N		
No. of 3rd-order branches on the second 2nd-order branch on the first 1st-order branch	0.0	99	0.79 $\pm$ 2.10	99	3.74	< 0.001
No. of 3rd-order branches on the first 2nd-order branch on the second 1st-order branch	0.0	99	0.35 $\pm$ 1.11	99	3.17	< 0.010
No. of 3rd-order branches on the second 2nd-order branch on the second 1st-order branch	0.0	99	0.24 $\pm$ 0.93	99	2.60	< 0.050
No. of 3rd-order branches on the first 2nd-order branch on the third 1st-order branch	0.0	99	0.16 $\pm$ 0.77	99	2.10	< 0.050
Distance from Holdfast to:						
first 1st-order branch	0.79 $\pm$ 0.58	86	1.17 $\pm$ 0.88	98	4.16	< 0.001
second 1st-order branch	1.08 $\pm$ 0.61	60	1.65 $\pm$ 1.01	83	5.21	< 0.001
third 1st-order branch	1.39 $\pm$ 0.68	29	2.11 $\pm$ 1.12	65	5.17	< 0.001
fourth 1st-order branch	0.0		2.77 $\pm$ 1.29			
Length of (cm):						
first 1st-order branch	1.47 $\pm$ 0.62	86	2.68 $\pm$ 1.61	98	7.43	< 0.001
second 1st-order branch	1.45 $\pm$ 0.68	60	2.67 $\pm$ 1.58	83	7.05	< 0.001
third 1st-order branch	1.44 $\pm$ 0.52	29	2.81 $\pm$ 1.47	65	7.47	< 0.001
fourth 1st-order branch	0.0		2.29 $\pm$ 1.10			

Appendix V. (cont'd)

	Laurencia Zone		Acanthophora Zone		t	p
	$\bar{X} \pm SD$	N	$\bar{X} \pm SD$	N		
Distance from the Main Axis to:						
first 2nd-order branch	0.0		1.50 $\pm$ 0.72			
second 2nd-order branch	0.0		1.95 $\pm$ 0.66			
on the first 1st-order branch						
first 2nd-order branch	0.0		1.26 $\pm$ 0.80			
on the second 1st-order branch						
second 2nd-order branch	0.0		1.69 $\pm$ 0.85			
on the second 1st-order branch						
first 2nd-order branch	0.0		1.27 $\pm$ 0.63			
on the third 1st-order branch						
Length from Main Axis of:						
first 2nd-order branch	0.0		2.60 $\pm$ 1.57			
on the first 1st-order branch						
second 2nd-order branch	0.0		2.79 $\pm$ 1.86			
on the first 1st-order branch						
first 2nd-order branch	0.0		2.20 $\pm$ 1.19			
on the second 1st-order branch						
second 2nd-order branch	0.0		2.11 $\pm$ 1.04			
on the second 1st-order branch						
first 2nd-order branch	0.0		2.32 $\pm$ 1.14			
on the third 1st-order branch						

Appendix V.(cont'd)

	<u>Laurencia Zone</u>		<u>Acanthophora Zone</u>		t	p
	$\bar{X} \pm SD$	N	$\bar{X} \pm SD$	N		
Distance from the first 1st-order Branch to the:						
first 3rd-order branch on the first 2nd-order branch	0.0		1.35 ± 0.54			
first 3rd-order branch on the second 2nd-order branch	0.0		1.43 ± 0.57			
Length of first 3rd-order Branch on:						
the first 2nd-order branch	0.0		1.73 ± 1.10			
the second 2nd-order branch	0.0		1.45 ± 0.76			

REFERENCES

- Adey, W.H., and J.M. Vassar. (1975) Colonization, succession, and growth rates of tropical crustose coralline algae (Rhodophyta, Cryptonemiales) *Phycologia* 14: 55-69.
- Almodovar, L.R., and F.A. Pagan. (1971) Notes on a mangrove lagoon and mangrove channels La Parguera, Puerto Rico. *Nova Hedwigia* 21: 241-253.
- Anonymous. (1981) B.M.D.P. Statistical Software 1981. W.D. Dixon (ed). pp 555-594. Univ. Calif. Press, Los Angeles.
- Augier, H. (1972) Contribution à l'étude biochimique et physiologique des substances de croissance chez les algues. These Doct. d'Etat, Marseille. 323 p.
- Austin, A.P. (1960) Observations on Furcellaria fastigata (L.) Lam. forma aegagropila Reinke in Danish waters, together with a note on other unattached forms. *Hydrobiologia* 14: 235-277.
- Barker, S.B., G. Cumming and K. Horsfield. (1973) Quantitative morphology of the branching structure of trees. *J. Theor. Biol.* 40: 33-43.
- Benz, M.C., N.J. Eiseman, and E.E. Gallaher. (1979) Seasonal occurrence and variation in standing crop of a drift algal community in the Indian River, Florida. *Botanica mar.* 22: 413-420.

- Biebl, R. (1962) Seaweeds. In: Physiology and Biochemistry of Algae. pp. 799-815. R.A. Lewin (ed). Academic Press, New York.
- Birkeland, C., A.A. Reimer, and J.R. Young. (1973) Effects of oil on tropical shore natural communities in Panama: Federal Water Quality Administration, Environmental Protection Agency, unpub. Project Report. 18050 EFV.
- Borchert, R., and N.A. Slade. (1981) Bifurcation ratios and the adaptive geometry of trees. Bot. Gaz. 142: 394-410.
- Borden, G.A., and J.R. Stein. (1969) Reproduction and early development in Codium fragile (Suringar) Hariot: Chlorophyceae. Phycologia 8: 91-99.
- Børgeesen, F. (1915-20) The marine algae of the Danish West Indies: Vol II, Rhodophyceae. Bianco Luno, Copenhagen. 504 p.
- Bornet, E. (1892) Les algues de P. -K. -A. Schousboe, récoltées au Maroc dans la Méditerranée de 1815 à 1829. Mem. Soc. natn. Sci. nat. math. Cherbourg 28: 165-376.
- Buggelen, R.G. (1981) Morphogenesis and growth regulators. In: The Biology of Seaweeds. pp. 627-660, C.S. Lobban and M.J. Wynne (eds). Blackwell Scient. Publ., Oxford.
- Burrow, E.M. (1958) Sublittoral algal populations in Port Erin Bay, Isle of Man. J. mar. biol. Ass., U.K. 37: 687-703.

Chapman, V.J., and D.J. Chapman. (1976) Life forms in the algae.

Botanica mar. 21: 65-74.

Charters, A.C., M. Neushul and D.A. Coon. (1972) Effect of water motion on algal spore attachment. In: Proceedings Seventh International Seaweed Symposium. pp. 243-247. K. Nisizawa (ed). Sapporo, Japan.

Cheney, D.P. (1975) A biosystematic investigation of the red alga genus Eucheuma (Solieriaceae) in Florida. Ph.D. Thesis, Univ. South Florida, Tampa, U.S.A. 208 p.

-----, and G.R. Babbel. (1978) Biosystematic studies of the red algal genus Eucheuma. I. Electrophoretic variation among Florida populations. Mar. Biol. 47: 251-264.

Chock, J.S., and A.C. Mathieson. (1976) Ecological studies of the salt marsh ecad Scorpiodes (Hornemann) Hauck of Ascophyllum nodosum (L.) Le Jolis. J. Exp. Mar. Biol. & Ecol. 23: 171-190.

Collins, F.S. (1914) Drift algae. Rhodora 16: 1-5.

Connell, J.H. (1961) The influence of interspecific competition and other factors on the distribution of the barnacle Chthamalus stellatus. Ecology 42: 710-723.

----- (1970) A predator-prey system in the marine intertidal region. I. Balanus glandula and several predatory species of Thais. Ecol. Monogr. 40: 49-78.

_____ (1978) Diversity in tropical rain forests and coral reefs.

Science 199: 1302-1310.

_____, and R.O. Slatyer. (1977) Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. 111: 1119-1144.

Connor, J.L., and W.H. Adey. (1977) The benthic algal composition, standing crop, and productivity of a Caribbean algal ridge. Atoll Res. Bull. 211: 1-15.

Conover, J.T. (1964) The ecology, seasonal periodicity, and distribution of benthic plants in some Texas lagoons. Botanica mar. 7: 4-41.

Coon, D.A., M. Neushul, and A.C. Charters. (1972) The settling behavior of marine algal spores. In: Proceedings Seventh International Seaweed Symposium. pp. 237-242. K. Nisizawa (ed). Sapporo, Japan.

Cordeiro-Marino, M., N. Yamaguishi-Tomita, and H. Yabu. (1974) Nuclear division in the tetresporangia of Acanthophora spicifera (Vahl) Boergesen and Laurencia papillosa (Forsk.) Greville. J. Fac. Fish. Hokkaido Univ. 25: 79-81.

Cowper, S.W. (1978) The drift algal community of seagrass beds in Redfish Bay, Texas. Contr. Mar. Sci. Univ. Tex. 21: 125-132.

- Croley, F.C., and C.J. Dawes. (1970) Ecology of the algae of a Florida Key. I. A preliminary checklist, zonation, and seasonality. Bull. Mar. Sci. 20: 165-185.
- Dahl, A.L. (1968) The effects of environment on growth and development of Zonaria farlowii. In: Proceedings of the Sixth International Seaweed Symposium. pp. 151-159. R. Margalef (ed). Madrid, Spain.
- _____. (1971) Development, form, and environment in the brown alga, Zonaria farlowii (Dictyotales). Botanica mar. 14: 76-112.
- _____. (1973) Benthic algal ecology in a deep reef and sand habitat of Puerto Rico. Botanica mar. 6: 71-175.
- _____. (1974) Algal zonation on the Belize barrier reef. In: Proceedings Eighth International Seaweed Symposium. pp. 303-306. G.E. Fogg and W. Eifion Jones (eds). Bangor, North Wales.
- Daly, M.A., and A.C. Mathieson. (1977) The effects of sand movement on intertidal seaweeds and selected invertebrates at Bound Rock, New Hampshire, U.S.A. Mar. Biol. 43: 45-55.
- Dawes, C.J., A.C. Mathieson, and D.P. Cheney. (1974) Ecological studies of Floridian Eucheuma (Rhodophyta, Gigartinales) I. Seasonal growth and reproduction. Bull. Mar. Sci. 24: 235-273.
- Dawson, E.Y. (1954) Marine plants in the vicinity of the Institut Oceanographique de Nha Trang, Viet Nam. Pacif. Sci. 8: 372-481.

Dayton, P.K. (1971) Competition, disturbance, and community organization: The provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* 41: 351-389.

Deacon, G.E. (1942) The Sargasso Sea. *Geogr. J.* 99: 16-28.

Denny, M.W. (1983) A simple device for recording the maximum force exerted on intertidal organisms. *Limnol. Oceanogr.* 28: 1269-1274.

Dethier, M.N. (1981) Heteromorphic algal life histories: The seasonal pattern and response to herbivory of the brown crust, Ralfsia californica. *Oecologia* 49: 333-339

Dixon, P.S. (1965) Perennation, vegetative propagation, and algal life histories, with special reference to Asparagopsis and other Rhodophyta. *Bot. Gothoburg* 3: 67-74.

_____. (1978) *Biology of the Rhodophyta*. Hafner Press, New York. 285 p.

Doty, M.S. (1946) Critical tidal factors that are correlated with the vertical distribution of marine algae and other organisms along the Pacific coast. *Ecology* 27: 315-327.

_____. (1961) Acanthophora, a possible invader of the marine flora of Hawaii. *Pacif. Sci.* 15: 547-552.

_____. (1967) Pioneer intertidal population and the related general vertical distribution of marine algae in Hawaii. *Blumea* 5: 95-105.

- _____. (1969) The standing crop of benthic frondose algae at Waikiki Beach 1966-69. Univ. Hawaii Bot. Sci. Paper 11: 1-22.
- _____. (1971) Physical factors in the production of tropical benthic marine algae. In: Fertility of the Sea, Vol II. pp. 99-121. J.D. Costlow (ed). Gordon and Breach, New York.
- _____. (1973) Marine organisms-tropical algal ecology and conservation. In: Proceedings Symposium Nature Conservation in the Pacific. pp. 183-195. A.B. Costin and R.H. Groves (eds). Canberra, 1971.
- Dring, M.J., and F.A. Brown. (1982) Photosynthesis of intertidal brown algae during and after periods of emersion: A renewed search for physiological causes of zonation. Mar. Ecol. Prog. Ser. 8: 301-308.
- Dromgoole, F.I. (1980) Desiccation resistance of intertidal and subtidal algae. Botanica mar. 23: 149-159.
- Druehl, L.D., and J.M. Green. (1982) Vertical distribution of intertidal seaweeds as related to patterns of submersion and emersion. Mar. Ecol. Prog. Ser. 9: 163-170.
- Earle, S.A. (1972a) The influences of herbivores on marine plants of Great Lameshur Bay, with an annotated list of plants. In: Results of the Tektite Program: Ecology of Coral Reef Fishes. B.B. Collette and S.A. Earle (eds). Nat. Mus. L.A. Co., Sci. Bull. 14: 17-44.

_____. (1972b) A review of the marine plants of Panama.

Bull. Biol. Soc. Wash. 2: 69-87.

Edwards, P., and D.F. Kapraun. (1973) Benthic marine algal ecology in Port Aransas, Texas Area. Contr. Mar. Sci. Univ. Tex. 17: 15-57.

Eiseman, N.J., and M.C. Benz. (1975) Marine algae of the Indian River, I. Species of the algal drift community collected from April 1974 to April 1975. Tech. Rpt. No.1, Harbor Branch Foundation. 17 p.

Fralick, R.A., and A.C. Mathieson. (1972) Winter fragmentation of Codium fragile (Suringar) Hariot ssp. tomentosoides (Van Goor) Silva (Chlorophyceae, Siphonales) in New England. Phycologia 11: 67-70.

Feldmann, J. (1937) Recherches sur la végétation marine de la Méditerranée. La côte des Albères. Thèses Présentées à la Faculté des Sciences de l'Université de Paris, Série A, No. 1757, Order No. 2623, 10: 1-339.

Fritsch, F.E. (1945) The Structure and Reproduction of the Algae. Vol. I. The University Press, Cambridge. 791 p.

Garbary, D. (1976) Life-forms of algae and their distribution. Botanica mar. 19, 97-106.

_____, D.W. Grund, and J. McLachlan. (1980) Branching patterns and life history stages in Ceramium rubrum (Huds.) C. Ag. Nova Hedwigia 33: 249-260.

Gibb, D.C. (1957) The free-living forms of Ascophyllum nodosum (L.) Le Jol. J. Ecol. 45: 49-83.

Gilbert, S.S. (1976) Seasonal variations in standing crop of benthic vegetation in the north Indian River. M.S. Thesis, Fla. Inst. Tech., Melbourne, Fla. 62 p.

Gittins, B.T. (1975) The biology of Lithothrix aspergillum. Ph. D. Dissertation. University of California, Irvine, California, U.S.A. 201 p.

Glynn, P.W. (1968) Mass mortality of echinoids and other reef flat organisms coincident with muddy low water exposures in Puerto Rico. Mar. Biol. 1: 226-243.

_____. (1972) Observations on the ecology of the Caribbean and Pacific coasts of Panama. Biol. Soc. Wash. Bull. 2: 13-20.

_____. (1982). Coral communities and their modifications relative to past and prospective Central American seaways. Adv. Mar. Biol. 19: 91-132.

Godin, J. (1981) Modalités de la fixation et de la dispersion du
Laurencia pinnatifida (Hudson) Lamouroux (Rhodophyceae, Ceramiales)
sur les substrats rocheux de mode battu. Botanica
mar. 24: 245-249.

Grime, J.P. (1974) Vegetation classification by reference to strategies.
Nature 250: 26-31.

_____. (1977) Evidence for the existence of three primary
strategies in plants and its relevance to ecological and
evolutionary theory. Am. Nat. 111: 1169-1194.

Harlin, M.M., and J.M. Lindbergh. (1977) Selection of substrata by
seaweeds: Optimal surface relief. Mar. Biol. 40: 33-40.

Harper, J.L. (1977) The Population Biology of Plants. Academic Press,
New York. 892 p.

Hay, M.E. (1981a) The functional morphology of turf-forming seaweeds:
Persistence in stressful marine habitats. Ecology 62: 739-750.

_____. (1981b) Spatial patterns of grazing intensity on a Caribbean
Barrier reef: Herbivory and algal distribution.
Aquat. Bot. 11: 97-109.

_____, T. Colburn, and D. Downing. (1983) Spatial and temporal
patterns in herbivory on a Caribbean fringing reef: The effects on
plant distribution. Oecologia 58: 299-308.

Hendler, G.L. (1976) Marine studies-Galeta Piont. In: 1975 Environmental Monitoring and Baseline Data compiled under the Smithsonian Institution Environmental Science Program: Tropical Studies. pp. 131-249. D.M. Windsor (ed). Smithsonian Institution, Washington, D. C. U.S.A.

_____. (1977) The differential effects of seasonal stress and predation on the stability of reef-flat echinoid populations. In: Proceedings Third International Coral Reef Symposium. pp. 217-223. D.L. Taylor (ed). Rosensteil School of Marine and Atmospheric Sciences, Univ. Miami Fl. U.S.A.

Highsmith, R.C. (1980a) Passive colonizations and asexual colony multiplication in massive coral Porites lutea Milne, Edwards, and Haime. J. Exp. Mar. Biol. & Ecol. 47: 55-67.

_____. (1980b) Survival of hurricane generated coral fragments and a disturbance model of reef calcification growth rates. Oecologia 46: 322-329.

_____. (1982) Reproduction by fragmentation in corals. Mar. Ecol. Prog. Ser. 7: 207-226.

Hodgkin, E.P. (1959) Catastrophic destruction of the littoral fauna and flora near Fremantle, January 1959. West Aust. Nat. 7: 6-11.

Hoek, C. van den. (1978) Marine algae from the coral reef of Curacao, Netherlands Antilles. I. Three new and one rarely observed species from the steep fore-reef slope. Aquat. Bot. 5: 47-61.

_____, and A. Flinterman. (1968) The life-history of Sphacelaria furcigera Kutz (Phaeophyceae). Blumea 16: 193-242.

Hutchinson, G.E. (1951) Copepodology for the ornithologist. Ecology 32: 571-577.

Irvine, D.E.G., M.D. Guiry, I. Tittley, and G. Russell. (1975) New and interesting marine algae from the Shetland Isles. Br. Phycol. J. 10: 57-71.

Janzen, D.H. (1970) Herbivores and the number of trees species in tropical forest. Am. Nat. 104: 501-528.

Joly, A.B. (1957) Contribuição ao conhecimento da flora ficológica marinha da Baía de Santos e Arredores. Thesis. São Paulo. 196 p.

Kain, J.M. (1975) Algal recolonization of some cleared subtidal areas. J. Ecol. 63: 739-765.

_____. (1976) The biology of Laminaria hyperborea. VIII. Growth on cleared areas. J. mar. biol. Ass. U.K. 56: 267-290.

- Kilar, J.A., and R. Lou. (1983) Ecological and behavioral studies of the decorator crab, Microphrys bicornutus Latreille (Decapoda, Brachyura): A test of optimum foraging theory. J. Exp. Mar Biol. & Ecol. 74, 157-167.
- Kim, Chun Su. (1964) Marine algae of Alacian Reef, Southern Gulf of Mexico. Ph.D. Dissertation. Duke Univ., Durham, N.C. U.S.A.
- Kim, D.H. (1976) A study of the development of cystocarps and tetrasporangial sori in Gigartinaceae (Rhodophyta, Gigartinales). Nova Hedwigia 54: 1-146.
- King, R.J., and W. Schramm. (1976) Photosynthetic rates of benthic marine algae in relation to light intensity and seasonal variations. Mar. Biol. 37: 215-222.
- Koehl, M.A.R. (1982) The interaction of moving water and sessile organisms. Scient. Am. 247: 124-134.
- _____, and S.A. Wainwright. (1977) Mechanical adaptations of the giant kelp. Limnol. Oceanogr. 22: 1067-1071.
- Kristensen, I. (1968) Surf influences on the thallus of fucoids and the rate of desiccation. Sarsia 34: 69-82.
- Lawson, G.W. (1957) Seasonal variation of intertidal zonation on the coast of Ghana in relation to tidal factors. J. Ecol. 45: 831-860.

- Leyton, L. (1975) Fluid behaviour in biological systems. Clarendon Press, Oxford. 235 p.
- Liddle, L.B. (1975) The effects of intertidal stress on Padina sanctaerueis (Phaeophyta). J. Phycol. 11: 327-330.
- Lipkin, V. (1977) Centroceras, the 'missile' launching marine red alga. Nature 270: 48-49.
- Littler, M.M. (1979) The effects of bottle volume, thallus weight, oxygen saturation levels, and water movement on apparent photosynthetic rates in marine algae. Aquat. Bot. 7: 21-34.
- _____, (1980) Morphological form and photosynthetic performance of marine macroalgae: Test of functional / form hypothesis. Botanica mar. 22: 161-165.
- _____, and D.S. Littler. (1980) The evolution of thallus form and survival strategies in benthic marine macroalgae: Field and laboratory test of a functional form model. Am. Nat. 116, 25-44.
- _____, and S.N. Murray. (1974) The primary productivity of marine macrophytes from a rocky intertidal community. Mar. Biol. 27, 131-135.
- Lubchenco, J. (1978) Plant species diversity in a marine intertidal community: Importance of herbivore food preference and algal competitive abilities. Am. Nat. 112: 23-39.

- _____. (1980) Algal zonation in New England rocky intertidal communities: An experimental analysis. *Ecology* 61: 333-344.
- _____, and J. Cubitt. (1980) Heteromorphic life histories of certain marine algae as adaptations to variations in herbivory. *Ecology* 61: 617-687.
- Luckhurst, B.E., and K.I. Luckhurst. (1978) Analysis of the influences of substrate variables on coral reef fish communities. *Mar. Biol.* 49: 317-323.
- MacArthur, R.H., and E.O. Wilson. (1967) *Theory of Island Biogeography*. Princeton Univ. Press, Princeton. 203 p.
- MacIntyre, I.G., and P.W. Glynn. (1976) Evolution of modern Caribbean fringing reef, Galeta Point, Panama. *Am. Ass. Petr. Geo. Bull.* 60: 1054-1072.
- Malinowski, K.C. and J. Ramus. (1973) Growth of the green alga, Codium fragile in the Connecticut estuary. *J. Phycol.* 9: 102-110.
- Mantel, N. (1966) Evaluation of survival data and new rank order statistics arising in its consideration. *Cancer Chemother. Rep.* 50: 163-170.
- Mathieson, A.C. (1982) Field ecology of the brown alga Phaeostrophion irregulare Setchell and Gardner. *Botanica mar.* 25: 67-85.

_____, and C.J. Dawes. (1975) Seasonal studies of Florida sublittoral marine algae. Bull. Mar. Sci. 25: 46-65.

_____, R.A. Fralick, R. Burns, and W. Flashive. (1975) Phycological studies during Tektite II, at St. John, U.S. V.I. In: Results of the Tektite Program: Coral Reef Invertebrates and Plants. S.A. Earle and R.J. Lavenberg (eds). Nat. His. Mus. L.A. Co. Sci. Bull. 20: 77-103.

_____, C.A. Penniman, P.K. Busse, and E. Tveter, ~~Callagher~~. (1982) Effects of ice on Ascophyllum nodosum within the Great Bay Estuary system of New Hampshire. J. Phycol. 18: 331-336.

McLachlan, J., and T. Edelstein. (1970-1) Investigations of the marine algae of Nova Scotia: IX. A preliminary survey of the flora of Bras d'Or Lake Cape Breton Island. Proc. Nova Scotian Inst. Sci. 27: 11-22.

McMahon, T.A. (1975) The mechanical design of trees. Scient. Am. 233: 92-102.

_____, and R.E. Krnauer. (1976) Tree structures: Deducing the principle of mechanical design. J. Theor. Biol. 59: 433-466.

Menge, B.A. (1976) Organization of the New England rocky intertidal community: Role of predation, competition, and environmental heterogeneity. Ecol. Monogr. 46: 355-391.

Menges, E.S. and D.M. Waller. (1983) Plant strategies in relation to elevation and light in floodplain herbs. Am. Nat. 122: 454-473.

Meslin, R. (1939) De l'apparition d'une algue nouvelle sur les côtes de Bretagne et de Normandie. Bull. Soc. linn. Normandie : 73-75.

Meyer, B.S., D.B. Anderson, R.H. Bohning, and D.G. Fratianne. (1973) Introduction to Plant Physiology. D. Van Nostrand Co., New York. 565, p.

Meyer, D.L., and C. Birkeland. (1974) Environmental science program marine studies-Gelata Point. In: 1973 Environmental Monitoring and Baseline Data. pp. 131-252. R.W. Robinooff (ed). Smithsonian Institution: Washington D.C. U.S.A.

_____, _____, and G.L. Hendler. (1975) Environmental science program marine studies-Gelata Point. In: 1973 Environmental Monitoring and Baseline Data. pp. 223-409. D.M. Windsor (ed). Smithsonian Institution, Washington, D.C. U.S.A.

Moss, B. (1965) Apical dominance in Fucus vesiculosus. New Phytol. 64: 387-392.

_____. (1966) Polarity and apical dominance in Fucus vesiculosus. Br. Phycol. Bull. 3: 31-35.

- Mshigeni, K.E. (1978) Field observations on the colonization of new substrata and denuded intertidal surfaces by benthic macrophytic algae. *Botanica mar.* 21: 49-57.
- Munda, I. (1972) On the chemical composition, distribution, and ecology of some common benthic marine algae from Iceland. *Botanica mar.* 15: 1-45.
- Neushul, M. (1965) Diving-observations of sub-tidal antarctic marine vegetation. *Botanica mar.* 8: 234-243.
- _____. (1975) Functional interpretation of benthic marine algal morphology. In: Contributions to the systematics of benthic marine algae of the north Pacific. pp. 47-73. I.A. Abbott and M. Kurogi (eds). *Jap. Soc. Phycol.*, Kobe. 279 p.
- North, W.J. (1971) Introduction and background. In: The Biology of the Giant Kelp Beds (*Macrocystis*) in California, W.J. North (ed). *Nova Hedwigia* 32: 1-96.
- Norton, T.A. and A.C. Mathieson. (1983) The biology of unattached seaweeds. In: Progress in Phycological Research. pp. 333-386. F.E. Round and D.J. Chapman (eds) Elsevier Science Publishers B.V., New York.
- Odum, E.P., E.J. Kuenzler, and M.X. Blunt. (1958) Uptake of P^{32} and primary productivity in marine benthic algae. *Limnol. Oceanogr.* 3: 340-345.

Odum, H.T., P.R. Burkholder, and J. Rivero. (1959) Measurements of productivity of turtle grass flats, reefs, and the Bahía Fosforescente of southern Puerto Rico. Publs. Inst. Mar. Sci. Univ. Tex. 6: 159-170.

_____, and E.P. Odum. (1955) Tropic structure and productivity of a windward coral reef community on Eniwetok. Ecol. Monogr. 25: 291-320.

Ogden, J.C. (1976) Some aspects of herbivore-plant relationships on Caribbean reefs and seagrass beds. Aquat. Bot. 2: 103-116.

Paine, R.T. (1966) Food web complexity and species diversity. Am. Nat. 100: 65-75.

_____. (1971) A short-term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat. Ecology 52: 1096-1106.

_____. (1974) Intertidal community structure: Experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia 15: 93-120.

_____. (1976) Size-limited predation: An observational and experimental approach with the Mytilus-Piaster interaction. Ecology 57: 858-873.

_____. (1979) Diaster, catastrophe, and local persistence of the sea palm, Postelsia palmaeformis. Science 205: 685-686.

Pearlmutter, N.L., and R.L. Vadas. (1978) Regeneration of thallus fragments of Rhodochorton purpureum (Rhodophyceae, Nemalionales). Phycologia 17: 186-190.

Pianka, E.R. (1970) On r- and k- selection. Am. Nat. 104: 592-597.

_____. (1978) Evolutionary Ecology. Harper and Row, New York, U.S.A. 397 p.

Pielou, E.C. (1974) Population and Community Ecology: Principles and Methods. Gordon and Breach, New York. 424 p.

Prud'Homme Van Reine, W.F., and H.J. Sluiman. (1980) Red algae found on european salt-marshes. I. Bostrychia scorpioides (Rhodomelaceae) Aquat. Bot. 9: 323-342.

_____, H.J. Sluiman, and R.P. Marchand. (1983) Red algae found on european salt-marshes. II. Catenella caespitosa (Rhabdoniaceae) Aquat. Bot. 15: 287-298.

Ramus, J. (1972) Differentiation of the green alga Codium fragile. Am. J. Bot. 59: 478-482.

Randall, J.E. (1961) Overgrazing of algae by herbivorous marine fish. Ecology 42: 812.

_____. (1964) Contributions to the biology of the queen conch, Strombus gigas. Bull. Mar. Sci. Gulf. Carib. 14: 246-295.

_____. (1967) Food habits of reef fishes of the West Indies.

Stud. Trop. Oceanogr. Miami 5: 665-847.

Ravin, J.A. (1981) Nutritional strategies of submerged benthic plants:

the acquisition of C, N, and P by rhizophytes and haptophytes. New
Phytol. 88: 1-30.

_____. and S.M. Glidewell. (1975) Photosynthesis, respiration, and
growth in the shade alga Hydrodictyon africanum. Photosynthetica
9: 361-371.

Rao, M.U., and T. Steeramalu. (1974) Observations on changes in the
growth of four intertidal algae at Visakkapatram. Botanica
mar. 17: 52-54.

Robertson, A.I., and K.H. Mann. (1980) The rôle of isopods and amphipods
in the initial fragmentation of eelgrass detritus in Nova Scotia,
Canada. Mar. Biol. 59: 63-69.

Rosenvinge, C. (1905) Om fremmede Alger ilanddrevne paa Jyllands
Vestkyst. Bot. Tidsskrift 27: 83.

Russell, D.J. (1981) The introduction and establishment of
Acanthophora spicifera (Vahl) Boerg. and Eucheuma striatum Schmitz
in Hawaii. Ph.D. Dissertation, Univ. Hawaii, 508 p.

Russell, G. (1967) The genus Ectocarpus in Britain II. The free-living
forms. J. mar. biol. Ass. U.K. 47: 233-250.

_____. (1974) Report on marine vegetation of Egmont Is., Chagos Bank (Indian Ocean). In: Proceedings Eighth International Seaweed Symposium. pp. 464-468. G.E. Fogg and W. Eifion Jones (eds). Bangor, North Wales.

Santelices, B. (1977) Water movement and seasonal algal growth in Hawaii. Mar. Biol. 43: 225-235.

Sauvageau, C. (1897) Note preliminaire sur les algues marines du golfe de Gascogne. J. Bot. Paris 11: 3.

_____. (1906) 'A propos du Colpomenia sinuosa signalé dans les huîtres de la rivière de Vannes. Bull. Stat. Biol. Arcachon 9: 35-48.

Schbener, T.W. (1983) Field experiments on interspecific competition. Am. Nat. 122: 240-285.

Schonbeck, M.W., and T.A. Norton. (1980) The effects on intertidal furoid algae of exposure to air under various conditions. Botanica mar. 23: 141-147.

Schussing, B. (1960) Handbuch der Protophytenkunde, Vol. 2. Fischer, Jena, 1-x; 1144 p.

Sebens, K.P. (1977) Autotrophic and Heterotrophic Nutrition of coral reef zonathids. In: Proceedings Third International Coral reef Symposium. pp. 397-404. D.L. Taylor (ed). Rosentiel School of Marine and Atmospheric Science. Univ. Miami, Miami, Fl.

- Searles, R.B. (1980) The strategies of the red algal life history.
Am. Nat. 115: 113-120.
- Segawa, S., and S. Kamura. (1960) Marine flora of Ryukyu Island.
Biological Institute of Ryukyus. 72 p.
- Silva, P.C. (1957) Codium in scandinavian waters. Svensk bot. Tidskr
51: 117-134.
- Slocum, C.J. (1980) Differential susceptibility to grazers in two phases
of an intertidal alga: Advantages of heteromorphic generations.
J. Exp. Mar. Biol. & Ecol. 46, 99-110.
- Sokal, R.R., and F.J. Rohlf. (1969) Biometry. W.H. Freeman, San
Francisco. 776 p.
- Sousa, W.P. (1979) Experimental investigations of disturbance and
ecological succession in a rocky intertidal algal community.
Ecol. Monogr. 49: 227-254.
- _____, S.C. Schroeter, and S.D. Gaines. (1981) Latitudinal
variation in intertidal algal community structure: The influence of
grazing and vegetative propagation. Oecologia 48: 297-307.
- South, G.R., and R.D. Hill. (1970) Studies on the marine algae of
Newfoundland. I. Occurrence and distribution of free-living
Ascophyllum nodosum in Newfoundland. Can. J. Bot. 48: 1697-1701.

Steneck, R.B. (1983) Quantifying herbivory on coral reefs: just scratching the surface and biting off more than we can chew. In: The Ecology of Deep and Shallow Coral Reefs. M.I. Reaka (ed). U.S. Dept. Commerce 1: 103-111.

Steneck, R.B., and L. Watling. (1982) Feeding capabilities and limitations of herbivorous molluscs: A functional group approach. Mar. Biol. 68, 299-319.

Stewart, J.G. (1968) Morphological variation in Pterocladia pyramidale. J. Phycol. 4: 76-84.

Stoddart, D. (1969) Ecology and morphology of recent coral reefs. Biol. Rev. 44: 433-498.

Strahler, A.N. (1953) Revision of Horton's quantitative factors in erosional terrain. Trans. Am. geophys. Un. 34: 345.

Sundene, O. (1962) Reproduction and morphology in strains of Antithamnion boreale originating from Spitsbergen and Scandinavia. K. norske Vidensk. Skr. Mat. Nat. K1, 5, 1-19.

Tabb, D.C., and R.B. Manning. (1961) A checklist of the flora and fauna of northern Florida Bay, and adjacent brackish water of Florida mainland, collected during the period, July 1957 through September 1960. Bull. Mar. Sci. Gulf. Caribbean 11: 552-649.

Taylor, W.R. (1962) Marine Algae of Northeastern Coast of North America. Univ. of Michigan Press, Ann Arbor. 509 p.

_____. (1967) Marine Algae on the Eastern Tropical and Subtropical Coasts of the Americas. Univ. of Michigan Press, Ann Arbor. 870 p.

_____, and A.J. Bernatowicz. (1969) Distribution of the marine algae about Bermuda. Bermuda Biol. St. Res. sp. Publ. 1: 1-42.

Tokioka, T. (1966) Recovery of the Echinometra populations in the intertidal zone in the vicinity of Seto, with a preliminary note on the mass mortality of some urchins in the summer season. Publs. Seto. mar. biol. Lab. 14: 7-16.

Trono, G.C. (1968) The taxonomy and ecology of the marine benthic algae of the Caroline Islands. Ph.D. dissertation, Univ. Hawaii, Hawaii 387 p.

Tsuda, R.T. (1974) Seasonal aspects of the Guam Phaeophyta (Brown Algae). In: Proceedings Third International Coral Reef Symposium. pp. 43-47. D.L. Taylor (ed). Roentiel School of Marine and Atmospheric Science, Univ. Miami, Fl.

Uylings, H.B.M., G.J. Smith, and W.A.J. Veltman. (1975) Ordering methods in quantitative analysis of branching structures in dendritic trees. Advance. Neurol. 12: 247-254.

Vadas, R.L., T. Fenchel, and J.C. Ogden. (1982) Ecological studies on the sea urchin, Lytechinus variegatus, and the algal-seagrass communities of the Miskito Cays, Nicaragua. Aquat. Bot. 14: 109-126.

Varma, R.P. (1959) Studies on the succession of marine algae on a fresh substratum in Palk Bay. Proc. Indian Acad. Sci. B, 49: 245-263.

Wainwright, S.A., W.D. Briggs, J.D. Curry and J.M. Gosline. (1976)
Mechanical Design in Organisms. John Wiley and Sons Inc, New York,
U.S.A. 423 p.

Wassman, E.R., and J. Ramus. (1973) Primary-production measurements for the green seaweed Codium fragile in Long Island Sound. Mar. Biol. 21: 289-297.

Wetzel, R.G. (1975) Limnology. W.B. Saunders Co., Philadelphia.

Wilce, R.T., C.W. Schneider, A.V. Quinlan, and K. vanden Bosch. (1982)
The life history and morphology of free-living Pilayella littoralis (L.) Kjellm. (Ectocarpaceae, Ectocarpales) in Nahant Bay, Massachusetts. Phycologia 21: 336-354.

Willison, M.J.H. (1982) Assessment of rock topographical features and their effects on intertidal macroalgae. M.S. thesis, Dalhousie Univ., Halifax, N.S. Canada. 92p.

Wilson, B.F. (1966) Development of the shoot system of Acer rubrum L.
Harvard Forest Paper 14: 21.

Womersley, H.B.S., and A. Bailey. (1969) The marine algae of Solomon Islands and their place in biotic reefs.
Phil. Trans. Roy. Soc., London, B, 255: 433-442.

_____, and R.E. Norris. (1959) A free-floating marine red
alga. Nature 184: 828-829.

Wood, R.D. (1962) Codium is carried to Cape Cod. Bull. Torrey bot. Club
89: 78-80.

Zar, J.H. (1974) Biostatistical Analysis. Prentice-Hall, New Jersey.
619 p.

Zimmerman, W. (1923) Zytologische Untersuchungen an Sphacelaria fusca
Ag.: ein Beitrag zur Entwicklungsphysiologie der zelle. Zeitschr.
Jena. Z. Bot 14: 113-175.