The Effects of Hurricane David on the Benthic Macroalgae of a Coral Reef in La Parguera, Puerto Rico

Jaime L. Matta

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THE EFFECTS OF HURRICANE DAVID ON THE BENTHIC MACROALGAE
OF A CORAL REEF IN LA PARGUERA, PUERTO RICO

by

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RESUMEN

Observaciones de campo quantitativas y qualitativas fueron hechas en relación a los cambios acaecidos en las poblaciones macroalgales de un arrecife coralino seis meses antes de ser impactado por el Huracán David y siete meses luego del disturbio. Cinco transectos fijados permanentemente fueron muestreados por los menos mensualmente usando un cuadrante de 1 m^2 para obtener el porcentaje de aparición de especies.

Usando la prueba de chi-cuadrado, se encontraron diferencias estadísticamente significativas en las proporciones de presencia/ausencia de 14 especies algales perennes al estas ser comparadas durante el periodo de muestreo antes y luego del huracán. El Coeficiente de Concordancia de Kendall, W, mostró un valor promedio bajo durante el periodo previo al Huracán David lo que sugiere que diferentes poblaciones algales se encontraban presentes en varias áreas del arrecife. Las variaciones más pronunciadas en concordancia encontradas luego del Huracán David estuvieron relacionadas con el desarrollo de la sucesión algal.

Luego de las altas mortalidades causadas por este disturbio, la sucesión algal comenzó con un afloramiento durante dos meses de la especie oportunista *Trichosolen duchassaingii*. La sucesión al final del estudio representa una etapa sucesional intermedia pero no una comunidad climax. La periodicidad encontrada en la distribución de ciertas especies es discutida.

La influencia de sedimento, mareas, temperatura, oxigeno y salinidad en la flora algal es considerada. El Huracán David fue el factor ambiental mas importante que afectó las poblaciones algales durante este estudio.

ABSTRACT

Quantitative and qualitative field observations were made regarding the changes in the macroalgal populations of a coral reef six months before being struck by Hurricane David and seven months afterwards. Five permanently established transects were sampled at least monthly using a 1-m^2 quadrat to obtain the percent of appearance of species.

Using chi-square analysis, significant statistical differences were found in the proportions of presence/absence of 14 perennial algal species when compared for the sampling period before and after the hurricane. The Kendall Coefficient of Concordance, W, showed a low mean value for the period before Hurricane David, which suggests that different algal populations occurred in several reef areas during that period. The more pronounced variations in concordance found after Hurricane David were related to the successional development.

After the high mortalities caused by the disturbance, the algal succession began with a bloom of *Trichosolen duchassaingii*, lasting two months. The succession at the end of the study represented an in intermediate successional stage rather than a climax community. The periodicity shown by certain algal species is discussed.

The influence of sediment, tides, temperature, oxygen and salinity on the algal flora is considered. Hurricane David was the most important environmental factor affecting the algal populations during the period of this investigation.

DEDICATION

I wish to dedicate this investigation to the memory of my father, Antonio J. Matta, for the unfailing encouragement and generous support that he gave me, and for the enthusiasm shown until the very end.

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INTRODUCTION

This investigation was initially undertaken to study the occurrence of seasonality among benthic coral reef macroalgae and to determine to what extent physical and chemical parameters were limiting to such algal populations. In August 30, 1979, the study site was struck by a hurricane that passed 70 to 80 miles south of Puerto Rico with winds up to 130 knots (Mariner's Weather Log, Sept., 1979) which together with swells, gales, heavy rains and storm tides, caused considerable damage. Since data had been gathered for six months previous to the disturbance, this provided a valuable opportunity to study its effects on the benthic macroalgae and to observe the beginning of the algal succession.

Hurricanes and tropical storms are major modifying forces in the reef ecology (Stoddart, 1963, 1969). Several reports in the past have described some of the effects of these disturbances on coral reefs (Stoddart, 1963, 1969; Glynn, Almódovar and González, 1963; Verneer, 1963; Flood and Jell, 1977; Highsmith, Riggs and D'Antonio, 1980). However, none of the known published studies have established quantitative and qualitative comparisons of the changes in the benthic macro-algal populations in a coral reef after the high mortalities caused by a hurricane. That is the primary objective of this investigation.

Algae are important components of coral reefs. Species endowed with specialized rhizoidal systems function as sediment consolidants while others capture sediment particles in suspension. Algae also function as primary producers, carrying out biochemical processes such as photosynthesis and nitrogen fixation (Doty, 1962; Wanders, 1976). Calcium carbonate-producing algae serve as one of the primary components of many coral reefs (Boyd et al, 1963; Chapman, 1901) and as a source of sediment (Doty, 1962; Wiman and McKendree, 1975). Large numbers of herbivore reef fishes and invertebrates feed on algae (Randall, 1961). Certain reef algae are known to possess antibiotic substances with valuable pharmacological properties (Burkholder, Burkholder and Almodóvar, 1960). Finally, hernatypic or reef building corals owe their fast growth, relative to ahermatypic species, to the presence of endosymbiotic microscopic algae known as zooxanthellae (Muscatine, 1973).

LITERATURE REVIEW

The literature review revealed the existence of two reports regarding algal succession in coral reefs following disturbances. No information concerning variations in coral reef algal populations, before and after a hurricane has been published in Puerto Rico or in any other part of the world. Nevertheless, some reviews of related works will be briefly discussed. These reviews fall under two headings:

a) Studies concerning the general effects of hurricanes on coral reefs and other areas, and

b) Studies concerning Turrumote Reef, the site of this investigation.

I. Effects of hurricanes on coral reefs

Stoddart (1962) presents a pioneer study of the effects of a tropical storm on the coral reefs of British Honduras (Belize), following the path of Hurricane Hattie in 1961. These reefs had been surveyed during 1959-1961 and re-surveyed during 1962, thus allowing in many instances to obtain an accurate picture of the extent of the damage caused by the disturbance.

Stoddart found that the damage to living coral reefs was variable and in some places catastrophic. In general, survival of the massive, slower-growing species and the destruction of fragile, rapidly-growing ones, was significant.

For the Belize cays, four zones of damage were delineated. The degree of damage to a particular cay depended on: 1) its location relative to the storm track; 2) the type of cay, whether sand or mangrove; 3) the size of the island and 4) the nature of its vegetation and the extent of human interference. The latter factor appeared to have the highest damage correlation. It was estimated that a period of as much as 10 to 20 years might be necessary for reef recovery following hurricane damage.

Glynn, Almodóvar and González (1964) studied the effects of Hurricane Edith (1963) on the marine life and topography of the coral reefs in the vicinity of La Parguera, Puerto Rico. Weather and hydrographic observations such as winds, currents, wave action, atmospheric and water temperature, rainfall and salinity, were analyzed in relation to the observed faunal and floristic changes in that area.

The strong wave action caused by Edith appears to have been the most important of the factors studied. It caused extensive removal of benthic algae, the destruction of corals in shallow waters and the morphological alterations of some coral reef islands.

A taxonomic list of the benthic algae affected by the hurricane is included in this work. The authors report the bloom of a filamentous green alga, *Bryopsis hypnoides,* which dominated the shallow waters of the reef flat of many of the coral reefs of La Parguera after Hurricane Edith.

Flood and Jell (1977) reported the effects of Cyclone David (1975) on the sediment distribution patterns on Heron Reef, Great Barrier Reef, Australia. The sediments of this reef were analyzed six months prior to the cyclone and one month afterwards. Sediment comparisons were based on the distribution patterns of the parameters of grain mean size and their sorting. This disturbance caused marked changes in the distribution of grain sizes between -1 phi (2.0 mm) and 3 phi (0.125 mm). The windward side of the reef, which experienced the greatest impact of the cyclone, suffered the greatest alteration in the sedimentary distribution patterns.

Randall and Eldridge (1977) studied the effects of Typhoon Pamela on the coral reefs of Guam. These investigators found that the impact of Typhoon Pamela was greatest along the shoreline, where erosion removed several bands of beach deposits and the vegetation was defoliated. Relatively little damage occurred along the adjacent reef flat platforms and reef margins. Only the tips of some species of foliaceous corals were fragmented.

Ogg and Koslow (1978) also studied the effects of Typhoon Pamela (1976) on the coral reefs and beaches of Guam. This disturbance passed directly over the island, generating 8-meter swells with winds estimated between 220 to 270 km/hr. Their findings contrast with those of other studies that report large-scale reef destruction following the path of a typhoon but coincide with Randall and Eldridge's (1977) in that the coral reefs of Guam are well adapted to this type of disturbance. Pamela had little effect on Guam's coral reefs, even along the more exposed northern and eastern coasts.

Ogg and Koslow use their findings to support Newman's hypothesis (1974) that reefs struck infrequently by tropical storms develop morphological formations that are unable to withstand the impact of the surf and surge caused by such disturbances. The opposite appears to occur on reefs frequently struck by storms.

It was reported by Ogg and Koslow that within days after Typhoon Pamela, the development of a bright green mat of early colonizing algae composed of *Bryopsis* sp. and *Enteromorpha* sp. was noticed over the few reef areas that suffered extensive damage. During the course of the reef survey, this green algal mat was succeeded by the proliferation of an unidentified red alga. Within 18 months after Pamela struck, the algal community had been mostly replaced by newly recruited corals (Neudecker, personal commnication with Ogg and Koslow). Colonization by blue-green algae was not apparent in Guam's coral reefs after Pamela.

2. Previous studies in Turrumote Reef

Goreau et al (1960) briefly studied the community structure, standing crop and oxygen balance of the lagoon at Turrumote Reef. They estimated that two-thirds of the lagoon were covered by a dense growth of corals, anemones, algae and zoanthids. According to these authors, the oceanic waters enter the lagoon over the shallow eastern coral rampart and are discharged over the reefs on the western side. Circulation in the lagoon appeared to depend mostly on wind and less on tides. Turbulent mixing of water appeared to be complete except for a narrow inshore belt in the southwestern margin of the lagoon, where the water temperature was seen to rise above 34°C during mid-afternoon.

Goreau et al sampled the dominant faunal and floral components of the lagoon communities at Turrumote to establish total biomass as gm C/m^2, total protein as gm N/m^2, and total chlorophyll a in gm/m^2. Diurnal oxygen exchanges were observed at 3-hour intervals at two stations within the lagoon and one outside the eastern, windward end throughout a period of two days. The total balance was in favor of consumption during that period, the lagoonal communities appeared to utilize approximately 50% more oxygen than the amount they produced. It was concluded that the large standing crop of the lagoon was able to maintain itself only by importing suitable energy from the outside. Plankton and huge schools of the dwarf herring *Jenkinsia lamprotaenia* were cited as the most probable source of such outside energy to the lagoon.

Almy and Carrión-Torres (1963) used Turrumote Reef as a collecting site for their survey of the shallow water scleractinian corals of Puerto Rico. They found this reef to have the highest diversity of coral species among the reefs of La Parguera. In addition, they presented unpublished data from Glynn (1962) on daily variations in temperature, oxygen and tide levels for the forereef and lagoonal areas.

According to these authors, water circulation in the lagoon of Turrumote is sufficient to maintain salinities similar to that of neighboring oceanic waters, but restricted enough in some shallow waters so as to account for sharper oxygen and temperature variations.

Hernández-Avila, et al (1977) studied the effects of hurricane-generated waves and the formation of boulder ramparts along coasts. Studying the coral boulder rampart along the south coast of Grand Cayman, W.I., they found that coral communities as far as 3 km from shore and 10-12 m deep were the source of rampart rubble. Theoretical calculations of wave refraction analysis indicated that hurricanes have the required force to break and transport coral rubble from such depths. Turrumote Reef was used as a site for <u>in</u> <u>situ</u> breaking force tests using *Acropora palmata* colonies, to obtain data which supported theoretical calculations.

Goenaga and Cintrón (1979), as part of a survey of the coral reefs of Puerto Rico, briefly discussed the coral zonation, diversity and percent of cover for various coral zones on Turrumote. They found the mixed zone to be the highest in coral diversity and *Acropora palmata* to be the dominant species over *Millepora complanata* at the reef crest. A general profile of the coral zonation was drawn for this reef.

DESCRIPTION OF THE STUDY AREA

Turrumote Reef was chosen as the site for this study. The location of this coral reef is approximately 17°56.1' North latitude and 67°05' West longitude (Fig. 1). The reef lies nearly 2.5 miles southeast of Magueyes Island, La Parguera, Puerto Rico. Turrumote belongs to the Outer Shelf Province which extends from the forereef of Media Luna to the insular shelf edge in the southwestern coast of Puerto Rico (Morelock, Schneidermann and Bryant, 1977). Considering its morphology, Turrumote can be classified as a fringing reef. The eastern part of the reef is composed of fragments of dead coral washed ashore, particularly *Acropora palmata, Millepora* sp. and occasional massive colonies of *Diploria* and *Montastrea,* known as a boulder rampart (Hernandez-Avila et al, 1977). The eastern part of the lagoon is the most protected site in the reef from wave action and where the finest sediments are found. The western half of the lagoon is dominated by corals such as *Acropora palmata*, *Millepora* sp., *Porites porites, Montastrea* sp., and particularly *Acropora cervicornis.* Coral colonies are widely dispersed within the lagoon thus allowing the establishment of dense benthic algal populations.

The sea anemones *Bartholomea annulata* and *Stoichactis helianthus* are abundant throughout the lagoon. Several species of herbivore reef fishes inhabit Turrumote Reef. Their presence is of importance in controlling the abundance and diversity of the algae upon which they prey (Randall, 1961). In the lagoon, damselfishes are numerous and widespread in their distribution. These fishes establish algal plots by bitting and eventually killing colonies of live coral to establish their territories (Kaufman, 1977) . Six species of the genus *Eupomacentrus* in addition to *Microspathodon* are known to inhabit this area (Waldner, , personal communication) .

On land, the mangrove *Laguncularia racemosa* is present besides plant species like *Sesuvium portulacastrum, Sporobolus virginicus* and *Surana maritima*. Migrations probably related to reproductive behavior were observed in populations of seagulls and the pelican *Pelecanus occidentalis*.

Climatic Conditions

La Parquera is a semi-arid zone. The annual rainfall from March, 1979, to March, 1980 was 59.8 inches (U.S. Dept. of Commerce, Climatological Data, 1979-80). During the study the highest precipitation occurred from June to September, 1979. The drier season occurred from December, 1979 to March, 1980. The highest monthly precipitation values gathered for

August, 1979, (20.15 inches) and September, 1979, (7.25 inches) correspond to the path of Hurricanes David and Frederick respectively. The annual evaporation average in La Parguera is of 2.068 mm (Smedley, 1961 as cited by Glynn, 1973a). Throughout most of the year (81.1%), wind velocities fluctuate between 10 to 25 km/h with an easterly-southeasterly direction (Glynn, 1973a).

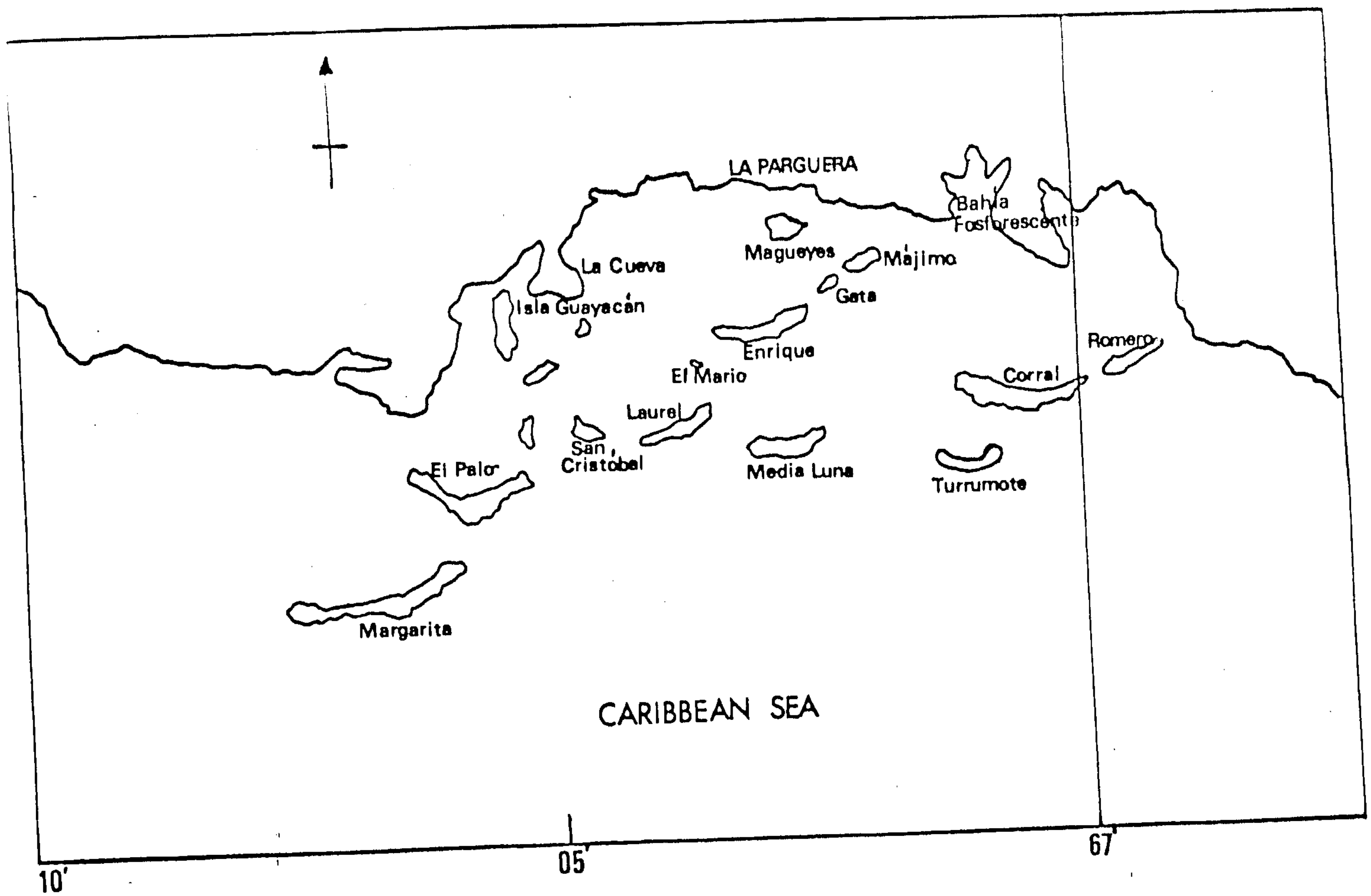


Fig. 1. Location of Turrumote Reef within the coral reef system of La Parguera, P.R.

METHODS AND MATERIALS

1. Field Measurements

a. Transect and line method

The transect and line method was chosen for this study. The location and length of the five transect sites are indicated in Figure 2. Transects were established by driving 50 cm steel stakes into the substrate beginning at the littoral zone and at 15-meter intervals extending into the lagoon area. At the forereef area the stakes were put at 6-meter intervals. A .65 cm (.25 inch) diameter nylon line, 25(?) meters long, marked at consecutive one-meter intervals with black paint, and with plastic tags every 5 meters, was fastened along the metal stakes.

Transects were sampled monthly for benthic macroscopic algae. The division Cyanophycophyta (blue-green algae) and crustose coralline species were not accounted for in the samples. Data was obtained on the basis of the presence/absence of algal species at consecutive 1 meter intervals. Sampling was done using a 1-square meter quadrat divided by steel rods into sixteen squares of equal size, thus allowing a quantitative assessment of the frequency of presence or absence of any given benthic algal species throughout the length of the transect. During the first three months after Hurricane David (September, October and November, 1979), it was necessary to sample twice every month so as to record the major successional changes in the macroalgal populations. Transect 4 was not sampled during the months of January and March, 1980, despite several attempts, due to the high wave action that prevailed at that site. Transects 3 and 4 had to be relocated after Hurricane David due to the extreme alteration in the morphology of the reef. The new sites of these two transects were in the same area where they were previously located.

Field notes were recorded using Polypaper underwater plastic sheets, slate and pencil, and mask and snorkel. In very shallow waters, particularly in the littoral zone, a wooden box (22 x 22 x 14 cm) with a transparent plexiglass bottom was used to observe the algae. b. Twenty-four hour experiments

b. Twenty-four hour experiments

Values for temperature, oxygen and salinity were obtained monthly for one year by registering their variations throughout continuous 24-hour measurements. Readings were taken at midwater at stations A, B and C (Fig. 2), at two-hour intervals during two months and at three-hour intervals during the next 10 months. Stations were permanently marked by driving 50-cm metal stakes into the substrate, a plastic orange flotation buoy was placed at each station to facilitate their location, particularly at night.

Fig. 2. Map of Turrumote Reef showing the major physiographic zones, the location and length of the five transects used for the study, and the location of stations A, B and C used for the monthly twenty-four hour experiments

Oxygen and temperature readings were obtained in situ with a calibrated temperature compensated oxygen meter manufactured by Yellow Springs Instruments (Model 57, accuracy of 0.1 ppm). Salinity measurements were taken in situ using a portable induction salinometer manufactured by Yellow Springs Instruments (Model 33, accuracy of 0.5%). During the months of February and March, 1980, salinity readings were obtained from water samples taken in the field and analyzed in the laboratory using a hand-held temperature compensated refractometer manufactured by American Optical (accuracy of 1.0%).

c. Sediment collection

Ten sediment samples were collected six months prior to Hurricane David, using seven-ounce plastic cups. Figure 3 shows the approximate site of each sediment collection. The exact position of each sample was obtained using a sextant and three known points of reference on the reef. Due to the extensive morphological alterations caused by Hurricane David, these marks were rendered useless for plotting the exact sites of the sediment collections.

2. Laboratory Procedures

a. Sediment analysis

Sediment analysis followed the procedures suggested by Folk (1968). The sediments were analyzed for particle size and biogenic constituents. In the laboratory, a 4 phi (.0625) screen was used to separate the fine from the coarse fractions in each of the samples. The fine fractions were collected in a pan and dried in an oven for 48 hours at 80°C and then weighed with an analytical balance. The coarse fractions were dried for at least four days and then weighed and separated using a RO-TAB with sieves at 1 phi intervals from -2θ (4.0 mm) to 4θ (.0625 mm). The sediment collected at each sieve was then weighed. Once, in sample 8, it was necessary to sieve to -3θ due to the presence of coarse coral fragments.

Samples 6 and 9 had greater than five percent fine material values and were separated for pipette analysis. For that analysis the fine material was placed in a 1000 ml graduated cylinder along with 5.5 g of Calgon to prevent flocculation. Since the recommended amount of fine material for pipette analysis is 15 grams, both samples were corrected for extra presence of fines by decanting their excess and adding distilled water.

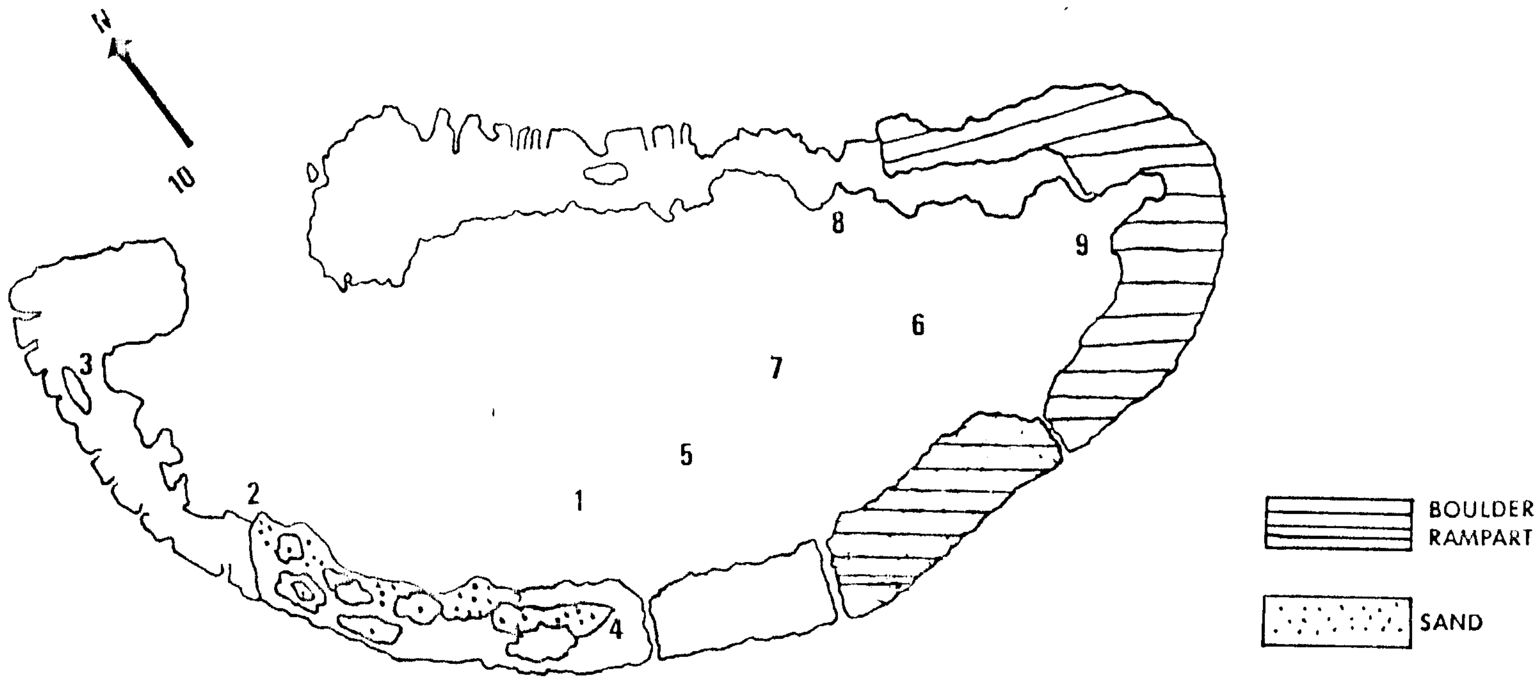


Figure 3. Map of Turrumote Reef showing the sediment collection sites of samples 1-10.

After the addition of Calgon, the samples were stirred vigorously and allowed to settle for a day. Since no obvious flocculation occurred, 20-ml aliqots were drawn off according to the schedule recommended by Folk (1968). The resultant fractions (5θ, 6θ, 7θ, 8θ, 9θ, 1θ) were dried in an oven and weighed. Individual and cumulative percents were calculated based on weight for the total samples. For each sample cumulative percents versus phi sizes were graphed. From these figures numerical values were obtained at the intersection of 5θ, 16θ, 50θ, 84θ and 95θ. The resulting values were entered into a programmed calculator to obtain mean and sorting values.

For the analysis of the biogenic constituents, a portion of the dried sand fraction of each sample was used. For each sample an approximate count of 125 grains chosen at random was made and constituent percentages were calculated based on the number of each constituent. Grains were analyzed on a Petri dish with a binocular microscope by means of comparison with standardized known fragments that existed on prepared slides. Grains were classified as: foraminiferan, spicules (gorgonian, sponge and tunicate), bryozoan, molluscan, coral and coralline algae, *Halimeda,* crustacean, echinoderm, calcareous worm tube, scaphopod, ostracod and pteropod.

b. Preservation and identification of specimens

A specimen of an unknown alga that could not be identified in the field, was collected and placed in a properly-labeled vial. After addition of 4% formaldehyde for preservation, the algal specimen was taken to the laboratory for identification as to species whenever possible. The taxonomic scheme proposed by Taylor (1960) and by Almodóvar, Blomquist, Ortiz and Ortiz (1972) for the Chlorophycophyta, was used in the laboratory for such purpose. The works of Taylor (1962 a, b and c; 1969, 1976) and Taylor and Rhyne (1970) were used as additional taxonomic references.

3. Statistical Analysis, Methods

a. Chi-square test

Chi-square analysis was applied to determine whether significant statistical differences occurred in the proportions of presence/absence of 15 algal species between the sampling periods before and after Hurricane David. The null hypothesis employed was: that the proportion of presence/absence for the algal species examined was not significantly different between the period before and after Hurricane David. The alternate hypothesis was: that the proportion of presence/absence of the algal species was significantly different for the period before Hurricane David (March-August, 1979) in relation with that after the hurricane (September, 1979 March, 1980). A 2 x 2 contingency table was prepared with the total number of times an algal species was present and absent within 16 parts of a 1 m^2 quadrat for the period before and after Hurricane David. Results were obtained by using a chi-square calculator program inserted in a Hewlett-Packard calculator.

b. Kendall Coefficient of Concordance test

The Kendall Coefficient of Concordance, W, was computed for each sampling period to obtain an index of the degree of concordance or association among the transects in terms of the presence/absence of each of the algal species present in than. W was obtained by the formula:

$$W = \frac{S}{1/12\, K^2\, (N^3 - N)}$$

where s = sum of the squares of the observed deviations from the mean of R_j. R_j is the sum of the ranks for each species in the different transects.

K = number of sets of rankings or the number of transects

N = number of entities ranked or number of algal species ranked

The method for determining whether the observed value of W is significantly different from zero depends on the size of N. If N is 7 or smaller, a table with a value of s associated with W values significant at the .05 and .01 levels is used (Siegel, 1956, page 286). If N is larger than 7, the formula $x^2 = K(N-1)W$ is used to compute a value of x^2 whose significance, for DF=N-1 was tested using a chi-square table.

RESULTS AND DISCUSSION

1. Visual and photographic observations

Aerial photographs of Turrumote Reef were taken five months before Hurricane David (Fig. 4) and one month afterwards (Fig. 5). Pronounced variations in the reef morphology can be observed as a result of this hurricane. The greenish areas present in the lagoon (Fig. 5) were caused by a bloom of the green filamentous alga *Trichosolen duchassaingii* which lasted from September until November, 1979.

Although no physical measurements were made, the photos indicate that the boulder rampart, which formerly enclosed only the eastern lagoonal area, increased in length, width and height due to the deposition of vast amounts of coral rubble transported from the forereef. This is evident in figures 4 and 5. On the eastern boulder rampart and in the southern windward shores the deposition of fragments of coral colonies torn by the impact of the strong wave action was very apparent. Fragments, and even entire coral colonies, were torn from their bases and washed ashore. A few colonies transported from the forereef into the lagoon were seen to initially survive. The eastern part of the reef also showed the formation of an additional small lagoon formerly inexistent (Fig. 5). Figures 6, 7 and 8 show some of the changes in Turrumote Reef and its algal populations before and after Hurricane David.

In Turrumote Reef the *Acropora palmata* zone appeared to be the most affected by the disturbance of the coral zones. Goenaga and Cintrón (1979) mention the relative barrenness and high depletion of *Acropora palmata* down to 4-5 meters in depth in the windward area where it was formerly luxuriant. In the lagoon, colonies of branching corals such as *Acropora cervicornis*, *Porites porites* and *Porites* sp. were the most adversely affected.

Before Hurricane David, the eastern lagoonal area was covered with dense patches of the zoanthid *Zoanthus sociatus,* which consolidated the abundant fine sediments present in that area. This species almost completely disappeared after the hurricane along with most of the fine sediments. Also, before Hurricane David, extensive burrowing activity, probably by *Callianasa,* was evident in the same area. According to Matthews (1974), this species greatly affects the sedimentary environment around their burrows by turning coarse sediment into fine.

Figure 4. Aerial photograph of Turrumote Reef taken five months before Hurricane David.

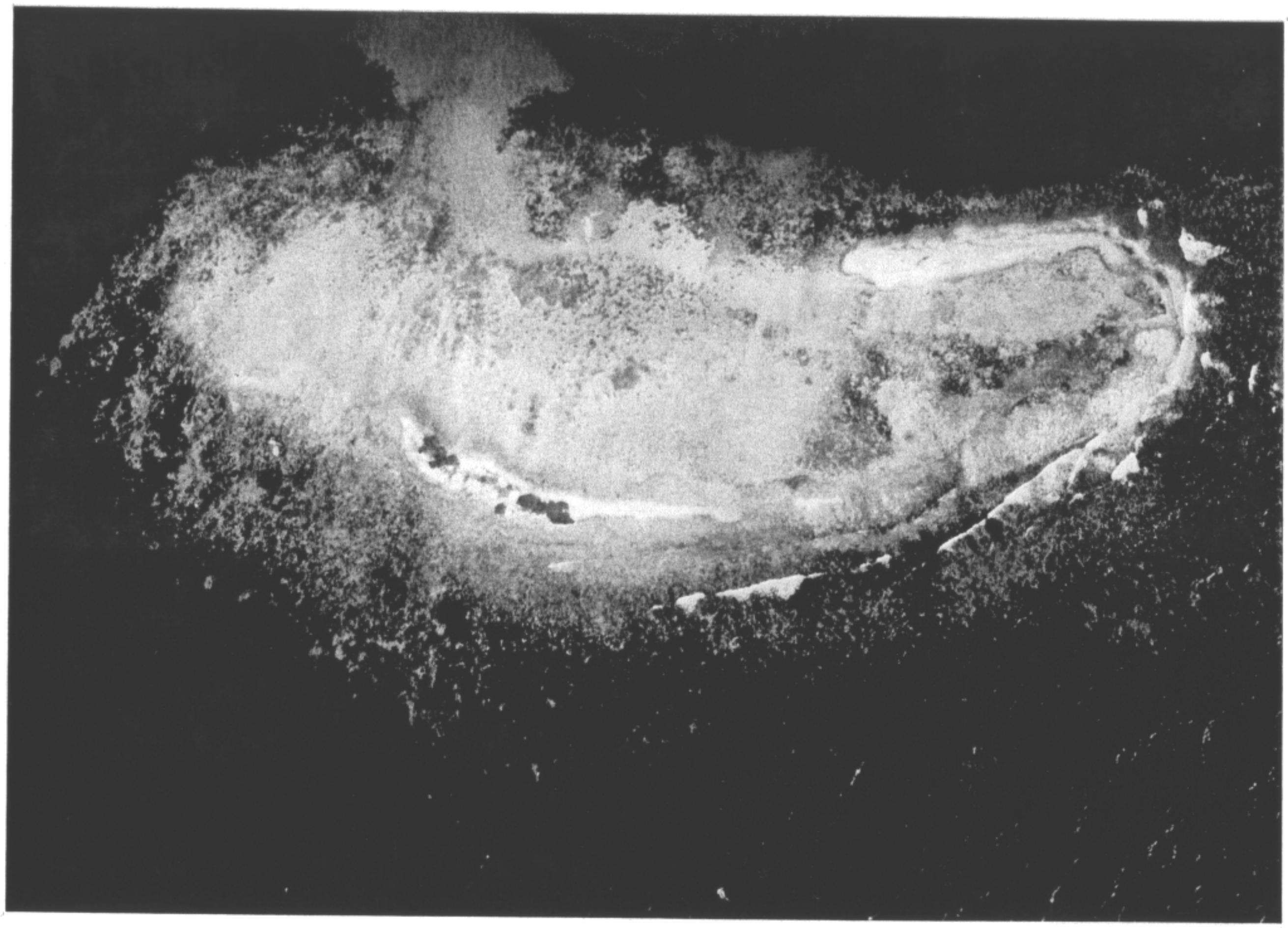


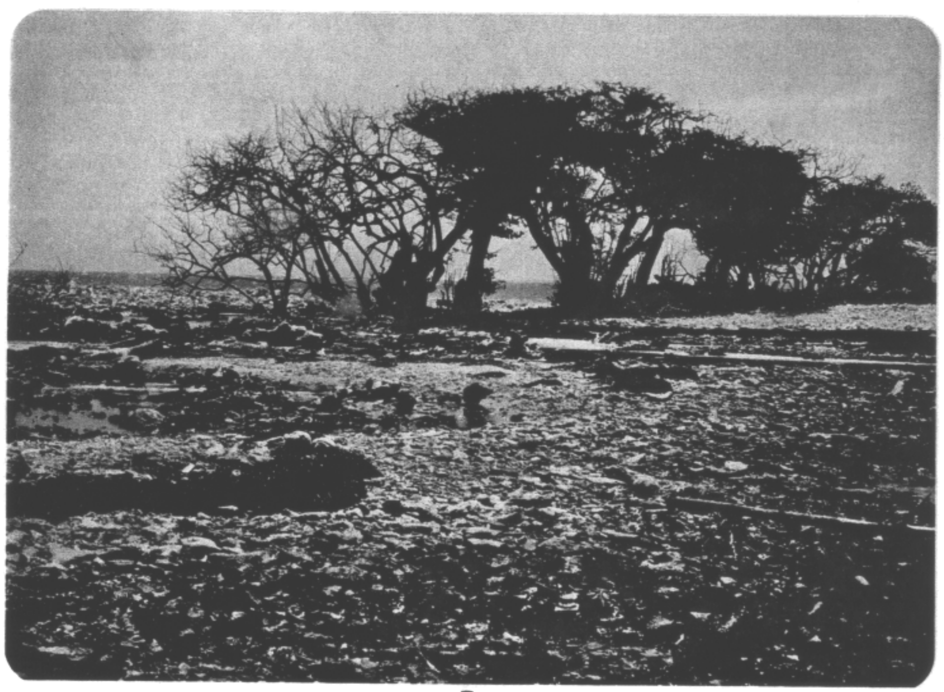
Figure 5. Aerial photograph of Turrumote Reef taken one month after Hurricane David.

Figure 6.

A. Turrumote Reef one month before Hurricane David

B. Turrumote Reef four days after Hurricane David.

A

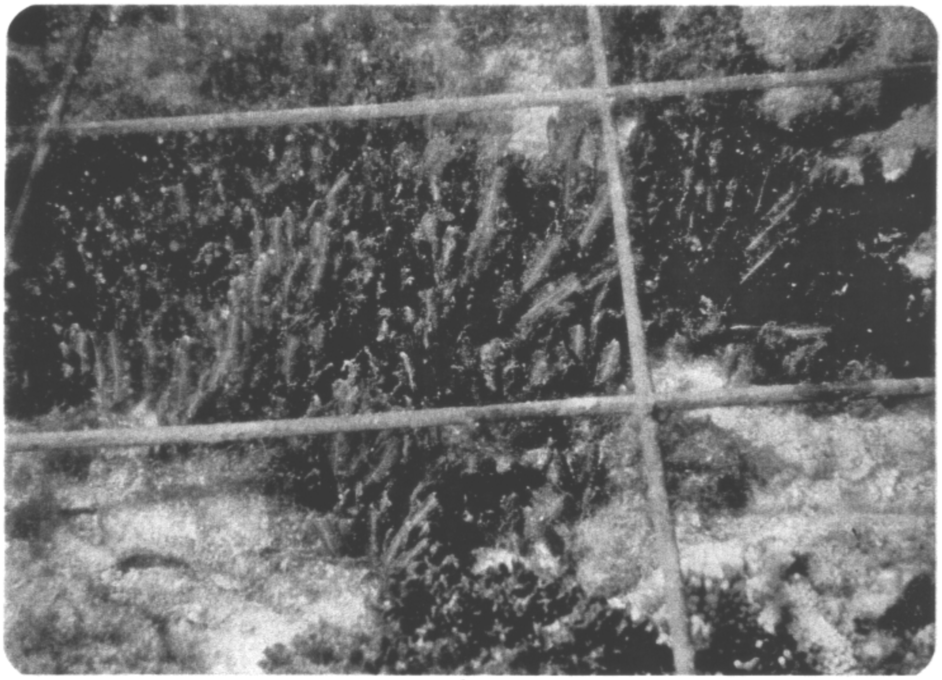


B

Figure 7.

A. **Portion of transect 1 of the study area with *Caulerpa sertularioides, C. racemosa* and *Halimeda opuntia* as they appeared before Hurricane David.**

B. **Portion of transect 1 of the study area with *Porites* rubble approximately six months after Hurricane David.**



A

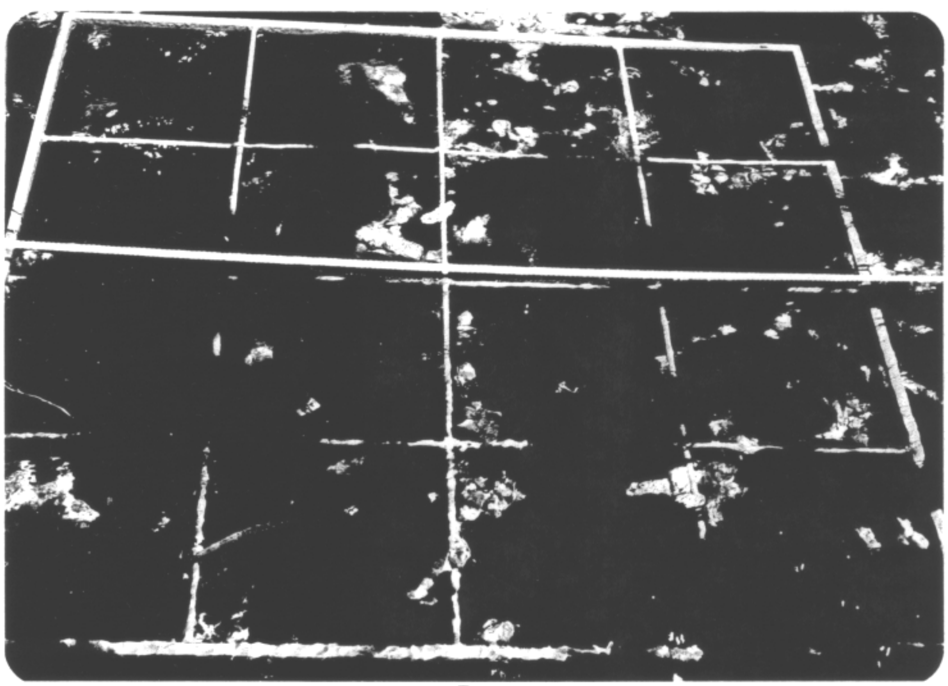
B

Figure 8.

A. **Erosion and coral rubble piled around mangrove roots four days after Hurricane David in Turrumote Reef.**

B. ***Trichosolen duchassaingii*** **in the littoral zone of transect 2 approximately one month after Hurricane David.**

A



B

The dry land part of Turrumote, which has the mangrove *Laguncularia racemosa* in addition to the terrestrial vegetation, suffered considerably from the impact of the southern swells that broke over this area.

Laguncularia racemosa trees died due to the erosion of the substrate which often exposed the root system of the plant (Fig. 8a). Within days of the hurricane, the leaves of this species turned dark brown as if being burned by the combination of high winds and salt spray. The terrestrial vegetation of Turrumote composed primarily of *Sesuvium portulacastrum, Sporobolus virginicus* and *Suriana maritima,* was washed away by breaking waves.

High siltation was a condition that prevailed for several days after Hurricane David, thus adversely affecting the algal, coral and other populations not adapted to such conditions. Many organisms were seen immersed in sediment that settled after the hurricane. This was particularly noticeable in the portions of the lagoon that received sediment from land due to the impact of swells. However, in the eastern part of the lagoon, fine sediment was removed without any apparent deposition of coarser sediment. In other lagoonal areas the capitulum of the green alga *Penicillus capitatus* was often found immersed in sediment. In addition, several of the 50 cm steel stakes that marked portions of the transects were found almost completely covered with sediment. Thus, some of the species that survived the initial impact of the hurricane, were killed by the subsequent deposition of sediment. Furthermore, unconsolidated sediment is likely a barrier for algal recolonization due to the difficulty it causes for the adhesion of spores.

Mathieson (1967) demonstrated the effects of algal burial by sand in a study of the biology of *Phaeostrophion irregularis*. This species is often found adhered to rocky substrates where sand movement is abundant and usually fluctuates annually in a cyclic manner. The thallus of this species is eroded as sand is deposited around it. Only the basal part persists and has been found to survive for four to six months buried in one meter of sediment. However, the survival of species not adapted to burial can sharply decrease after having been buried. Markham and Newroth (1972) found that *Gymnogongrus platyphyllus*, a species not adapted to sand burial, died within a month after being buried in experiments where water and sand movements were manipulated. Also, burial by sand for considerable periods apparently diminishes the resistance of certain benthic algal species to normal light intensities. Dahl (1969) found that plants of *Zonaria farlowii* that had been buried for a month, suffered heavy damage or even died when exposed to direct sunlight.

2. Summary of the taxa examined

Table 1 shows a taxonomic list of the 34 genera and 41 species that were either observed or collected during the thirteen months of this study. Of the taxa examined, 16 genera and 19 species belonged to the division Chlorophycophyta or 46.3% of all the species. One species of the Chlorophycophyta, *Rhizoclonium riparium,* was collected outside the transect area. This was closely followed by the division Rhodophycophyta with 17 genera and 18 species which accounted for 43.9% of the species. The least represented division was the Phaeophycophyta with three genera and four species, or 9.8% of the species present during the investigation.

Four orders of the Chlorophycophyta were represented in the samples. These were the order Siphonales, 8 species; order Siphocladiales, 6 species; order Cladophorales, 3 species; and order Ulotrichales, with 1 species. The division Rhodophycophyta was represented by 5 orders: order Ceramiales, 10 species; order Nemalionales, 2 species; order Rhodymeniales, 2 species; order Cryptonemiales, 1 species and the order Gigartinales with 1 species.

Table 1

Annotated systematic list of the benthic algal species present in the study area at Turrumote Reef from March, 1979, to March, 1980.

Division Chlorophycophyta

Order Cladophorales

Cladophora fascicularis (Mertens) Kutzing
Cladophora sp.
Chaetomorpha linum (Muller) Kutzing
Rhizoclonium riparium (Roth) Harvey

Order Siphonales

Caulerpa cupressoides (West) C. Agardh
Caulerpa racemosa (Forsskål) J. Agardh
Caulerpa sertularioides (Gmelin) Howe
Codium sp.
Halimeda opuntia (Linnaeus) Lamouroux
Halimeda tuna (Ellis and Solander) Lamouroux
Penicillus capitatus Lamarck
Trichosolen duchassaingii (J. Agardh) Taylor

Order Siphonocladiales

Cladophoropsis membranacea (C. Agardh) Børgesen
Dictyosphaeria cavernosa (Forsskål) Børgesen
Ernodesmis verticillata (Kutzing) Børgesen
Neomeris annulata Dickie
Struvea anastomosans (Harvey) Piccone
Valonia macrophysa Kutzing
Valonia ventricosa J. Agardh

Order Ulotrichales

Enteromorpha flexuosa (Wulfen) J. Agardh
Entenomorpha sp.

Division Rhodophycophyta

Order Ceramiales

Acanthophora spicifera (Vahl) Børgesen
Centroceras clavulatum (C. Agardh) Montagne
Ceramium nitens (C. Agardh) J. Agardh
Crouania attenuata (Bonnemaison) J. Agardh
Digenea simplex (Wulfen) C. Agardh
Herposiphonia tenella (C. Agardh) Ambronn

Table 1 (contd.)

Laurencia obtusa (Hudson) Lamouroux
Laurencia papillosa (Forsskål) Greville
Polysiphonia ferulacea Suhr
Wrangelia argus Montagne

Division Rhodophycophyta
Order Criptonemiales
Amphiroa fragilissima (Linnaeus) Lamouroux
Amphiroa rigida (Lamouroux) Børgesen
Order Gelidiales
Gelidiella acerosa (Forsskål) Feldmann and Hamel
Gelidium corneum (Hudson) Lamouroux
Order Gigartinales
Hypnea spinella (C. Agardh) Kutzing
Order Nemalionales
Galaxaura sp. *Lamouroux*
Liagora ceranoides Lamouroux
Liagora sp.
Order Rhodymeniales
Lomentaria baileyana (Harvey) Farlow

Division Phaeophycophyta
Order Dictyotales
Dictyota bartayresii Lamouroux
Dictyota divaricata Lamouroux
Padina vickerseae Hoyt
Padina sp.
Order Ectocarpales
Ectocarpus breviarticulatus J. Agardh

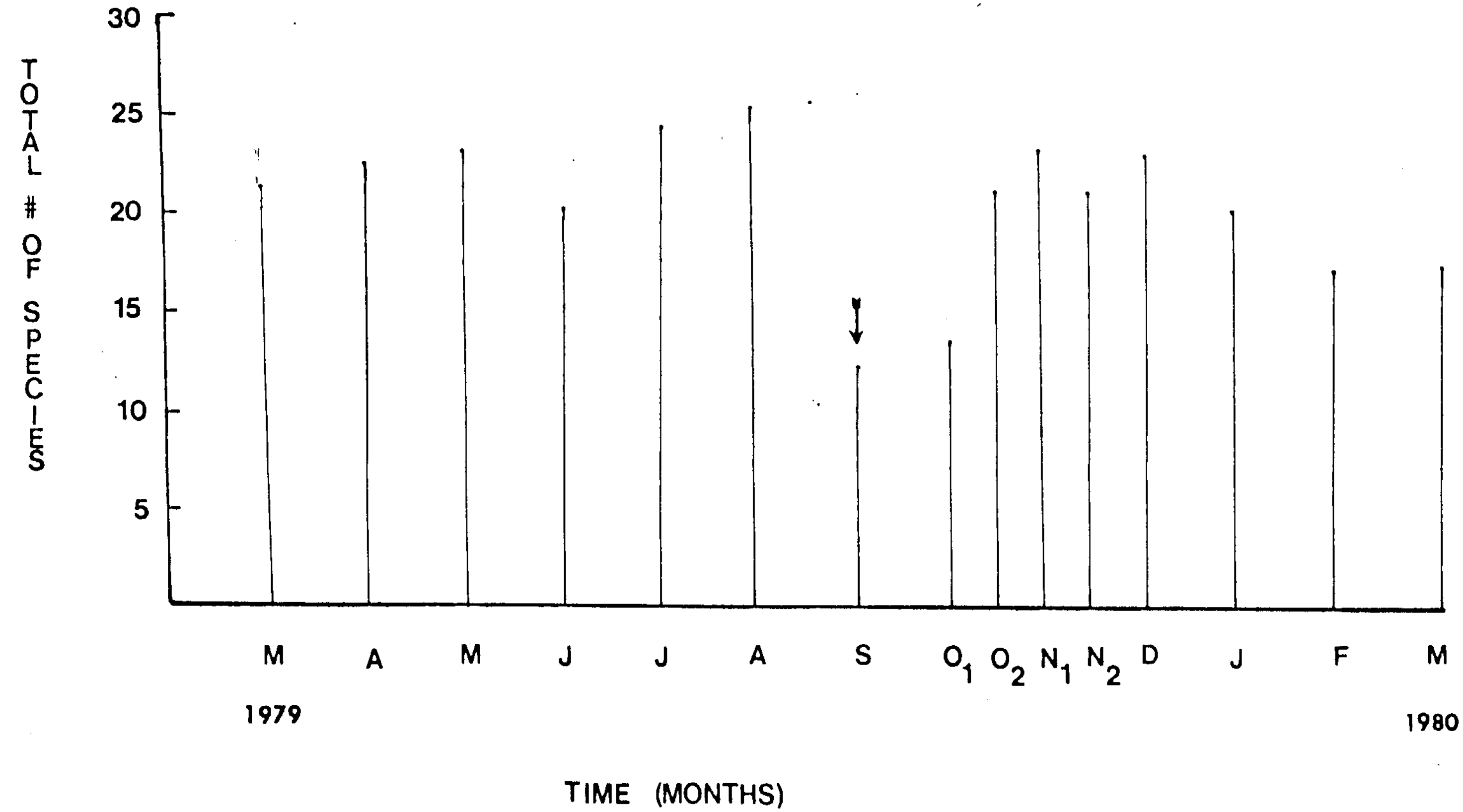


Fig. 9. Total number of algal species present in the study area during each sampling interval between March, 1979 and March, 1980. Arrow indicates the first sampling date after Hurricane David.

Transect 1 had the highest number of species during the study period with 27 species present. Transect 2 had 26 species during the same period or nearly the same as transect 1. These transects were followed by transect 4 with 23 species, transect 5 with 21 species and transect 3 with 20 species. Ten algal species were common to all transects, although not simultaneously. These species were: *Amphiroa fragilissima, Amphiroa rigida, Caulerpa racemosa, Centroceras clavulatum, Cladophoropsis membranacea, Enteromorpha flexuosa, Gelidium corneum, Laurencia obtusa, Laurencia papillosa* and *Trichosolen duchassaingii*. Of the Rhodophycophyta, four species or 22% of the species of such group appeared exclusively after Hurricane David. These were: *Ceramium nitens, Digenea simplex, Herposiphonia tenella* and *Liagora mucosa*. *Ectocarpus breviarticulatus* was the only species of the Phaeophycophyta that appeared exclusively after the hurricane, accounting for 25% of the species of such division. It should be noted that the divisions of the Chlorophycophyta, Rhodophycophyta and Phaeophycophyta had a similar percentage of species increase (21%, 22% and 25% respectively) during the first seven months following Hurricane David.

Tables A1 to A15 of Appendix A present a summary of the benthic macroalgae, the total number of squares where such species occurred and their percentage of occurrence within each of the five transects at Turrumote Reef from March, 1979, to March, 1980, during each sampling interval. Figure 9 shows the total species present at the study sites during each sampling. On August, 1979, the last sampling date before Hurricane David, the highest number of species (25) was found at Turrumote Reef (Table A6, Appendix A). The lowest number of species (12) found corresponded to the first sample (September 12, 1979) after Hurricane David (Table A7, Appendix A). Not only did the total of species decrease by 52% in less than a month, but the luxuriant growth that was formerly existent in the algae of most reef areas was severely reduced.

A random collection of benthic algal species made three days after Hurricane David throughout the reef, including areas beyond the five transects, yielded a total of 10 species: *Amphiroa fragilissima, Amphiroa rigida, Caulerpa racemosa, Dictyosphaeria cavernosa, Dictyota divaricata, Gelidium corneum, Halimeda opuntia, Laurencia obtusa, Laurencia papillosa* and *Valonia ventricosa*. *Halimeda opuntia* was the species most conspicuous in the collection, but also showed the highest percentage of appearance before Hurricane David. This species possesses a widespread rhizoidal system and a compact calcified morphology probably advantageous in situations of rapid water movements (Almodóvar, personal communication). Other species found in various reef areas were *Dictyosphaeria cavernosa, Gelidium corneum* and *Valonia ventricosa*. These may have survived due to their potential to colonize cryptic habitats, which provided more adequate shelter from the strong wave action and abrasion caused by moving coral rubble and other sediments.

Twenty one species was the total found for March, 1979, (Table A1, Appendix A), and seventeen species were found in March, 1980 (Table A15, Appendix A). The decrease in number of species since the beginning of the study was approximately of 20%. However, since transect 4 could not be sampled during March, 1980, due to the high wave action present, it is possible, but not likely, that additional species might have been present. Only one species, *Ectocarpus breviarticulatus,* was present exclusively in transect 4 in February, 1980 (Table A14, Appendix A). Assuming that the species composition in this transect did not change in one month, a total of 17 algal species was present in Turrumote in March, 1980.

Twelve of the algal species were found in March, 1979, and also in March, 1979. These were: *Amphiroa fragilissima, A. rigida, Caulerpa racemosa, Centroceras clavulatu, Cladophoropsis membranacea, Crouania attenuata, Dictyota divaricata, Gelidium corneum, Laurencia obtusa, Laurencia papillosa, Halimeda opuntia* and *Wrangelia argus.* Eight species and one genus were present in March, 1979, but absent in March, 1980: *Acanthophora spicifera, Bryopsis pennata, Caulerpa cupressoides, C. sertularioides, Codium* sp.*, Coelothrix irregularis, Dictyosphaeria cavernosa* and *Valonia ventricosa.*

3. Statistical Analysis

a. Chi-square Test

The chi-square test was applied to part of the data to determine whether significant statistical differences existed in the proportions of presence/absence for a given algal species when-comparing the sampling period of March-August, 1979, (before Hurricane David) with that of September, 1979, to March, 1980, (after Hurricane David). Fourteen benthic algal species considered to be representatives of the algal population of Turrumote Reef were selected for this analysis. Seasonal species and those present exclusively before or after Hurricane David were omitted from the test due to their rather discontinuous distributions. Comparisons of their presence/absence proportions might be of limited statistical value.

Table 2 shows the x^2 values gathered for the 14 algal species whose proportions of presence/absence are being compared. Assuming a .001 level of significance and 1 degree of freedom for all species, it appears from these results that the proportions of presence/absence in the samples of all the species examined for the period of March to August, 1979, are significantly different from those of September, 1979, to March, 1980.

From the x^2 values obtained and by examining figures 11-16 where the annual distributions of 17 algal species are shown, the presence of Hurricane David had a significant ecological impact in the benthic macroalgae of Turrumote Reef. Hurricane David was a sudden, strong selective force which initiated an algal succession that probably would not have otherwise occurred. However, due to the complexity of the coral reef ecosystem, it would be simplistic to exclusively point to one factor for causing the significant variations observed in the algal populations studied. Seasonal periodicity, competition, predation and life cycle differences are among some of the factors that may have influenced these populations. Nevertheless, it is very apparent that Hurricane David was the most important environmental factor affecting the reef ecosystem during this study.

Assuming that the substantial variations found within some of the x^2 values were primarily caused by Hurricane David, it appears that species responded differently to its presence. This could be due to several reasons, but two are particularly important. First, the species being compared may have experienced differences in their mortalities and secondly, these species might have developed different strategies or patterns of recolonization towards freshly cleared spaces.

As to the x^2 values obtained, the highest (6691.3) corresponds to *Halimeda opuntia,* and the lowest (46.5) to *Crouania attenuata*. Similar values were gathered for these species: *Centroceras clavulatum* (444.64) and *Dictyota divaricata* (472.84), *Gelidium corneum* (509.46) and *Laurencia papillosa* (513.68) (Table 2).

When attempting to interpret extreme variations in x^2 values as with *Halimeda opuntia* and *Crouania attenuata,* it is useful to examine the distribution of these species and their habitats. *Halimeda opuntia* achieved a widespread distribution in Turrumote Reef due to its potential to colonize diverse habitats. This species inhabits substrates ranging from muds and clays to coarse sand and gravel as shown by its presence in the sediment samples analyzed. While *Halimeda* was present in all reef areas except in transect 4, *Crouania* was found only in the forereef, mostly in transect 5.

In order to achieve a similar distribution pattern to that existent before Hurricane David, *Halimeda* had to recolonize a larger reef area and more varied habitats than *Crouania.* This recolonization was significantly hindered by the competition of *Trichosolen duchassaingii*, particularly in the backreef transects. However, *Crouania* recolonized the reef area least affected by Hurricane David, and where the fastest algal recolonization occurred. These differences in recolonization strategy are undoubtedly important in accounting for differences in x^2 values between these species.

Table 2

Results of chi-square analysis based on the proportions of presence/absence of 14 benthic algal species when compared for the period of March to August, 1979, with that of September, 1979 to March, 1980 with a significance of .001 and 1 degree of freedom

Species	x^2
Amphiroa fragilissima	3571.49
Amphiroa rigida	834.72
Caulerpa cupressoides	581.39
Caulerpa racemosa	101.59
Centroceras clavulatum	444.64
Cladophoropsis membranacea	1183.64
Crouania attenuata	46.48
Dictyota divaricata	472.84
Gelidium corneum	509.46
Halimeda opuntia	6691.30
Laurencia obtusa	1347.08
Laurencia papillosa	513.68
Neomeris annulata	384.85
Penicillus capitatus	2025.90

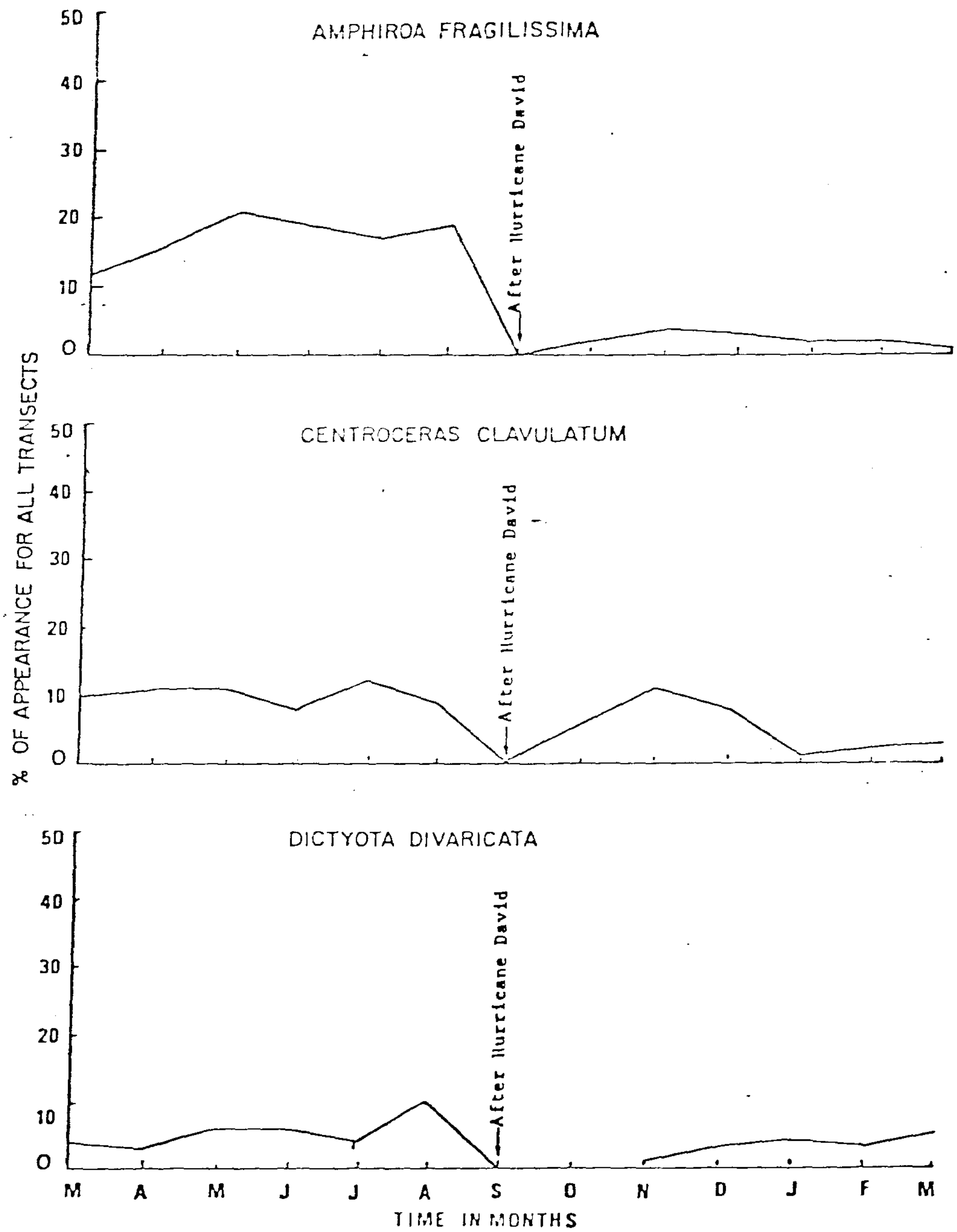
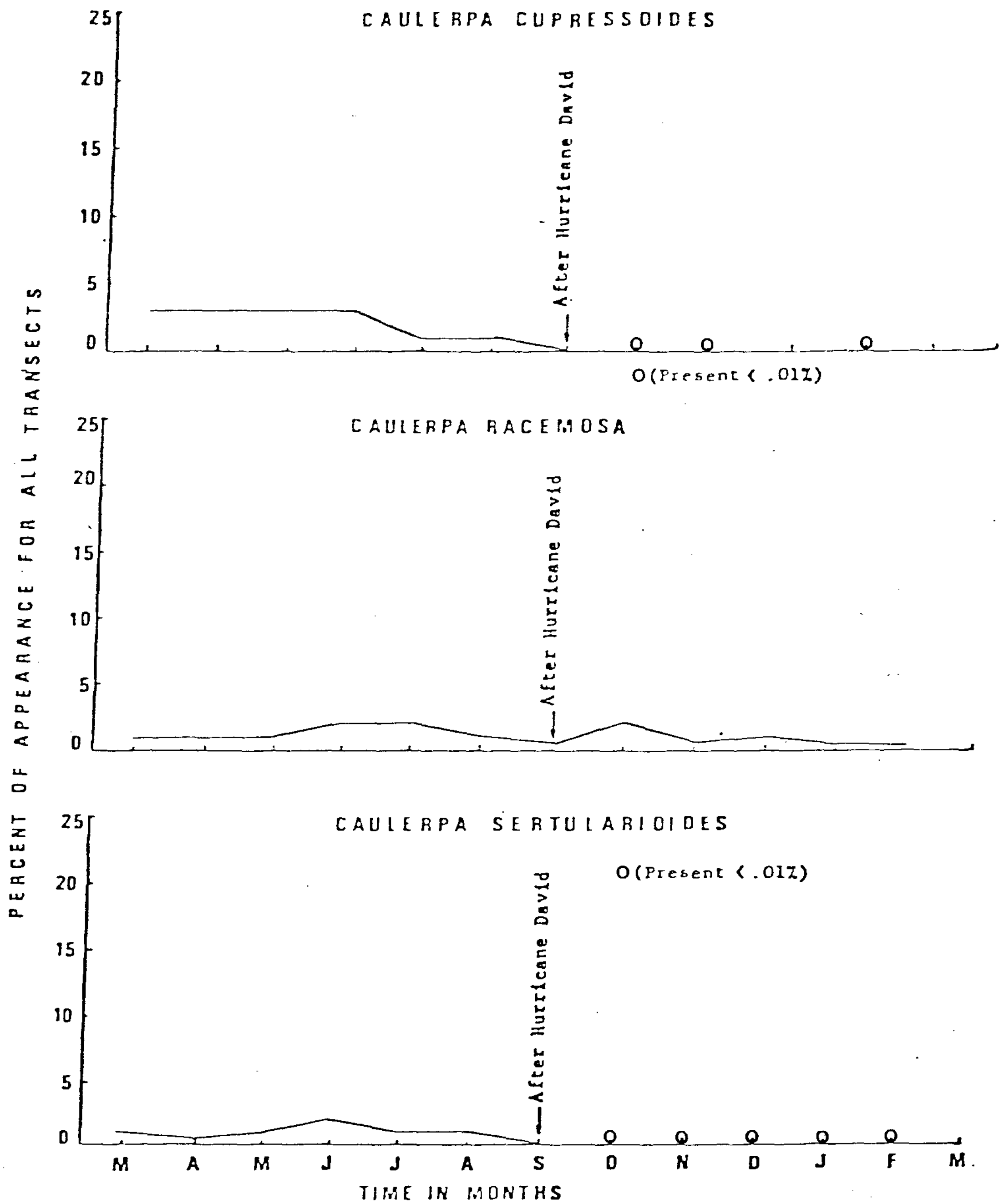


Fig. 10. Percent of appearance of *Amphiroa fragilissima*, *Centroceras clavulatum* and *Dictyota divaricata* in the study area at Turrumote Reef between March, 1979, and March, 1980. Arrow indicates first sampling date after Hurricane David.

Fig



CAULERPA CUPRESSOIDES
CAULERPA RACEMOSA
CAULERPA SERTULARIOIDES
PERCENT OF APPEARANCE FOR ALL TRANSECTS
After Hurricane David
O(Present < .01%)
0
5
10
15
20
25
M A M J J A S O N D J F M.
TIME IN MONTHS

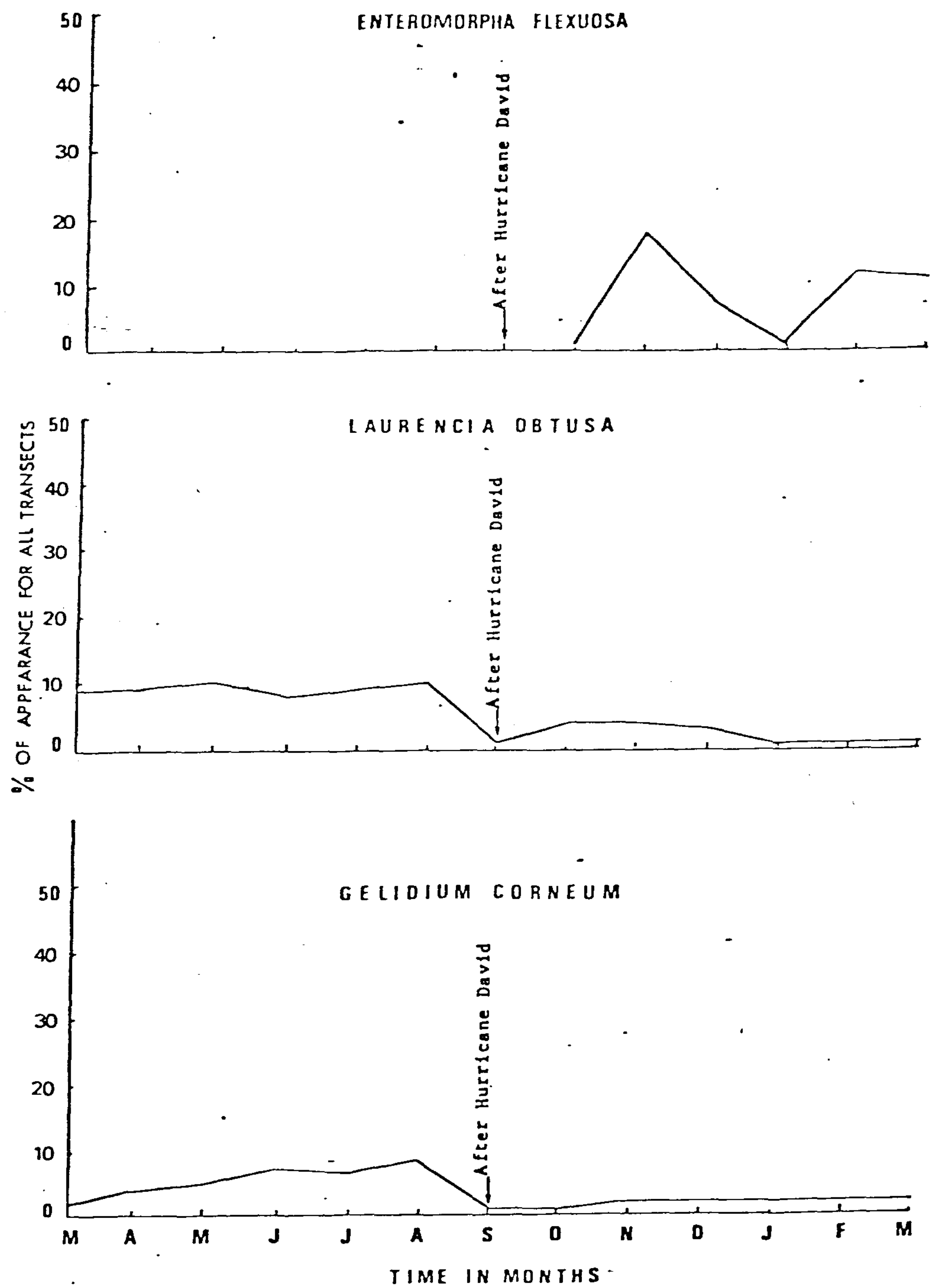


Fig. 12. Percent of appearance of *Enteromorpha flexuosa*, *Laurencia obtusa* and *Gelidium corneum* in the study area at Turrumote Reef between March, 1979, and March, 1980. Arrow indicates the first sampling after Hurricane David.

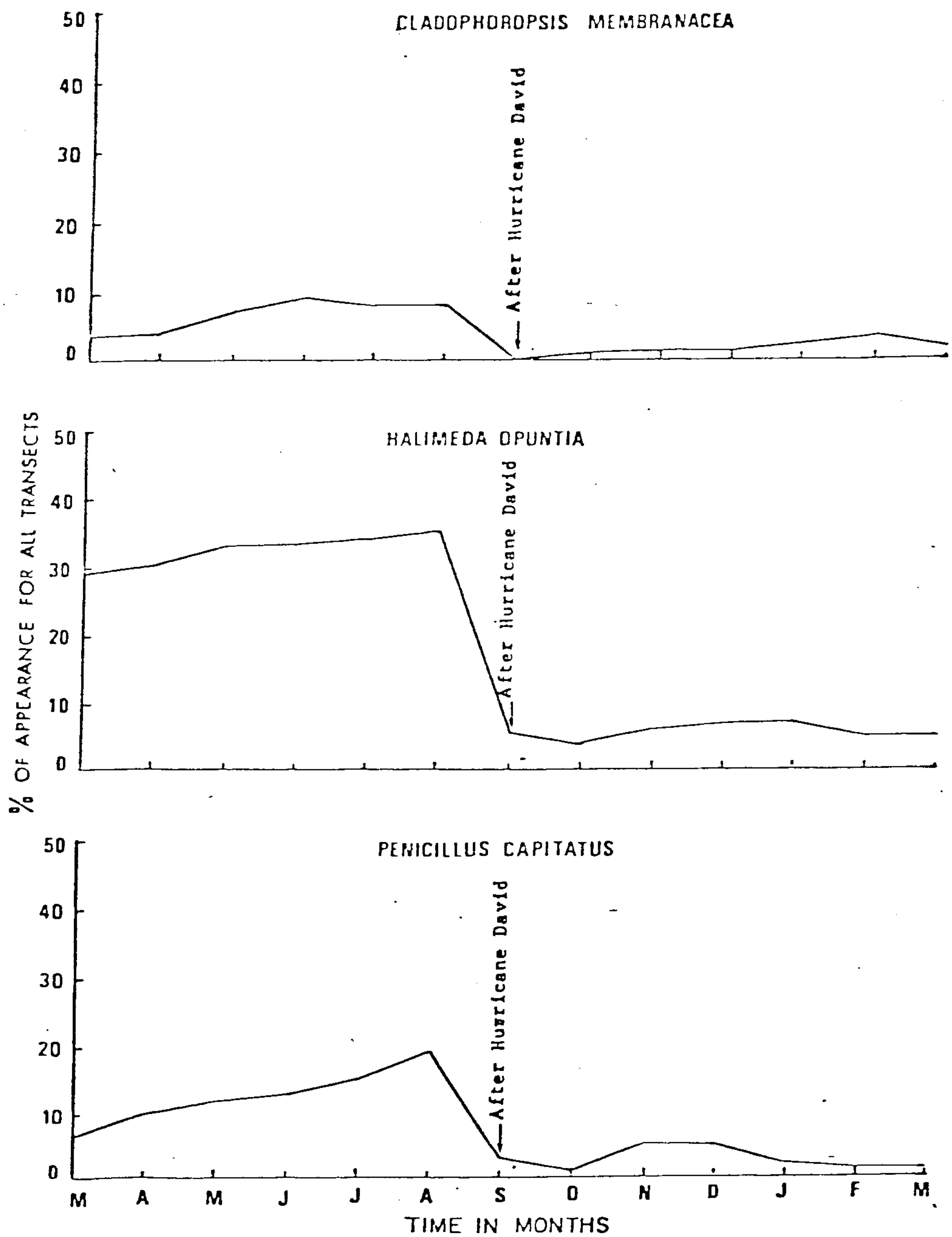


Fig. 13. Percent of appearance of *Cladophoropsis membranacea*, *Halimeda opuntia* and *Penicillus capitatus* in the study area at Turrumote Reef between March, 1979, and March, 1980. Arrow indicates the first sampling after Hurricane David.

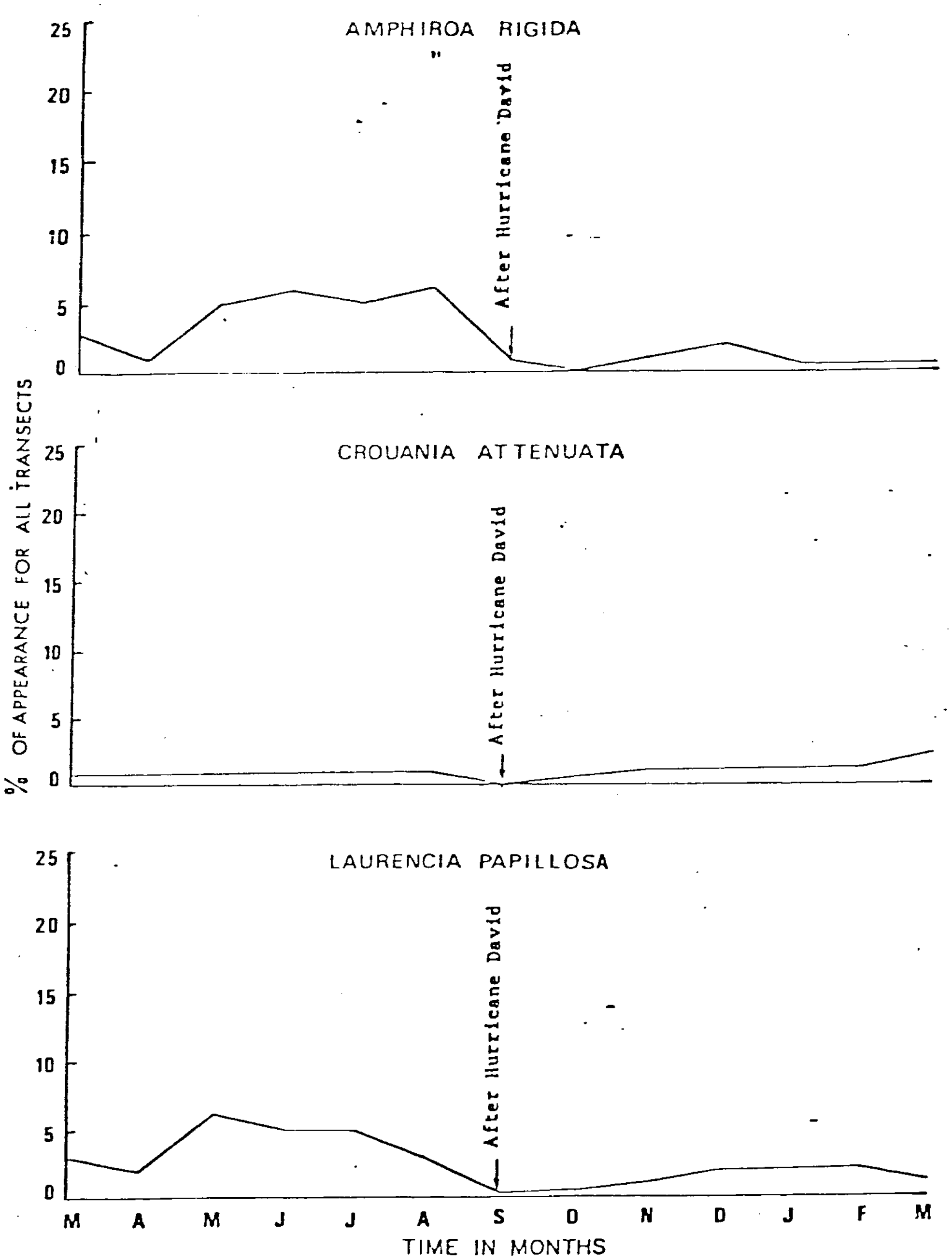


Fig. 14. Percent of appearance of *Amphiroa rigida*, *Crouania attenuata* and *Laurencia papillosa* in the study area at Turrumote Reef between March, 1979, and March, 1980. Arrow indicates the first sampling date after Hurricane David.

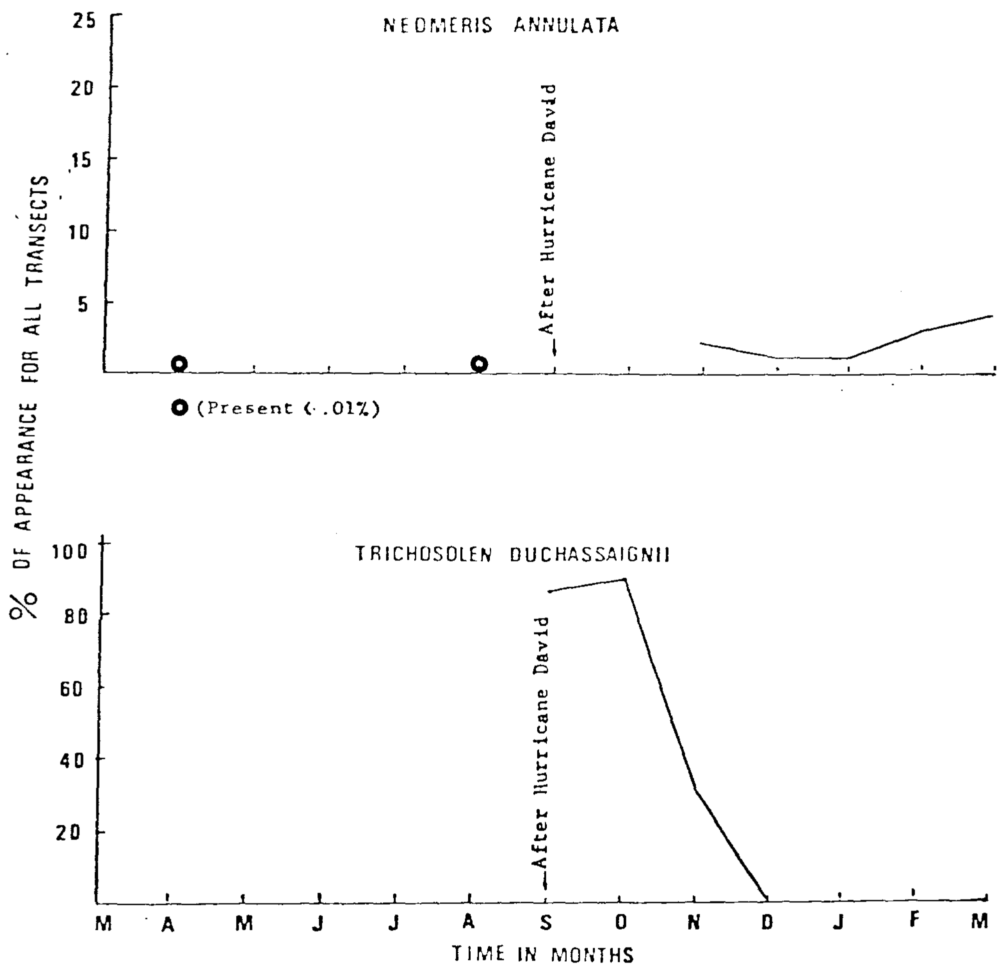


Fig. 16. Percent of appearance of *Neomeris annulata* *Trichosolen duchassaingii* in the study area at Turrumote Reef between March, 1979, and March, 1980. Arrow indicates the first sampling date after Hurricane David

Additional information can be obtained regarding the variations in appearance of certain algal species by examining the percent of presence in the sample and the ratios of several algal species for the periods before and after Hurricane David (Table 3). Considering first *Halimeda opuntia* and *Crouania attenuata,* these species composed 32.45% and 1.22% respectively, of the total sample for the period before Hurricane David. The ratio of presence of the former to the latter was 26.6 for that period. After Hurricane David, *Halimeda* composed 5.26% of the total sample and *Crouania* .007%, their ratio being 8.09 (Table 3). Therefore, the ratio of *Halimeda*/*Crouania* was approximately 70% higher before Hurricane David than afterwards; *Halimeda* experienced a decrease of roughly 83% during the latter period, while *Crouania* decreased its presence in the sample of the same period by only 50%. This suggests, as mentioned previously, that the recolonization by *Halimeda* was more adversely affected than that of *Crouania,* which can account for differences in x^2 values.

Other algal species that showed marked differences in their ratios as to the percent of presence in the samplings before and after Hurricane David, were: *Caulerpa cupressoides* and *C. sertularioides* with a ratio of 1.49 before the hurricane and .14 after; *C. cupressoides,* and *C. racemosa* with 1.67 before and .02 after, and *C. sertularioides* and *C. racemosa* with 1.12 before and .17 after (Table 3). Within the same genus, the species of *Caulerpa* showed the most marked differences as to the ratio of presence in the samples before and after Hurricane David.

Of the intertidal species, *Centroceras clavulatum* and *Cladophoropsis membranacea* showed the greatest differences in such ratios. Before David, *Centroceras* composed 10.23% and *Cladophoropsis membnanacea* 6.9% of the total sampled, for a ratio of the former to the latter of 1.47. After David, *Centroceras* accounted for 5.32% and *Cladophoropsis* for 1.23% of the sample, their ratio was 4.33 (Table 3). If we compare the presence of both species in the samples before and after Hurricane David, it will be noted that *Centroceras* decreased after David by approximately 50% in relation to its presence before, while *Cladophoropsis* decreased by 82% during the same period. This increase of 3:1 in the ratio of *Centroceras* to *Cladophoropsis* shows the diselacement of the latter species caused by the appearance of *Enteromorpha flexuosa. Enteromorpha* appeared only after David and occupied nearly the same position as *Cladophoropsis* along the intertidal region.

Table 3

Percent of presence and ratios between several algal species for the sample before Hurricane David (B.H.D.); March to August, 1979, and after hurricane David (A.H.D.); September, 1979 to March; 1980

Species	% of sample (B.H.D.)	%of sample (A.H.D.)	Ratio (B.H.D.)	Ratio (A.H.D.)
Halimeda opuntia	32.45	5.26	26.6	8.09
Crouania attenuata	1.22	.007		
Caulerpa cupressoides	1.97	.0001	1.49	0.14
Caulerpa sertularioides	1.32	.0007		
Caulerpa cupressoides	1.97	.0001	1.67	0.02
Caluerpa racemosa	1.18	.004		
Caulerpa sertularioides	1.32	.0007	1.12	0.17
Caulerpa racemosa	1.18	.004		
Centroceras clavulatum	10.23	5.32	1.47	4.33
Cladophoropsis membranacea	6.97	1.23		
Amphiroa fragilissima	17.04	2.22	4.05	4.18
Amphiroa rigida	4.21	.005		
Laurencia obtusa	9.27	2.07	2.34	2.11
Laurencia papillosa	3.96	.01		
Dictyota divaricata	5.35	1.87	1.04	1.12
Gelidium corneum	5.17	1.67		

The species within the genera *Amphiroa* and *Laurencia* showed nearly the same ratios of presence before and after Hurricane David, although a marked decrease occurred in the four species after the disturbance. Before David, *Amphiroa fragilissima* had a ratio of 4.05 in relation to *A. rigida,* while their ratio afterwards was 4.18. Within *Laurencia,* the ratio of *L. obtusa* to *L. papillosa* was 2.34 before David and 2.11 afterwards.

Two algal species of the sublittoral zone showed very similar ratios of presence in the samples before and after the hurricane. *Dictyota divaricata* represented 5.35% of the sample before David, and *Gelidium corneum* 5.17% of such sample, and their ratio was 1.04. After David, *Dictyota,* accounted for 1.87% of the sample and *Gelidium* for 1.67% with a 1.12 ratio of the former to the latter.

b. Kendall Coefficient of Concordance

The Kendall Coefficient of Concordance, or W, was computed for each sampling interval to obtain an estimate of the degree of concordance or association among the five transects in terms of the frequency of occurrence of benthic algal species. W ranges from +1 (perfect concordance) to 0 (no concordance). Table 4 shows the values obtained for W for each interval.

During the months of March to August, 1979, W did not exhibit the large variations present between September, 1979, to March, 1980. During the first interval, which corresponded to the months before Hurricane David, the lowest W value obtained was for March, 1979, .2708 (.20 probability) and the highest for April, 1979, .5569 (.01 probability).

For the sampling period after Hurricane David (September, 1979 to March, 1980), fluctuations in W were more apparent. The highest W value for such period corresponded to September, 1979, .7302 (.01 probability) and the lowest value was found for October 31, 1979, .1942 (.50 probability).

Although the level of significance is not equal for every one of those dates, several conclusions can be drawn from these W values. For the study period prior to David, the concordance between the five transects was never higher than .5569. A possible explanation for the rather low values in concordance during those months is that the transects appeared to represent reef areas with different algal populations, probably because of a fairly high degree of variation in habitats. During the first six months of this study, W had a mean value of .44 which suggests that Turrumote Reef was not a highly homogeneous habitat

Table 4

Results obtained for S, W; the Kendall Coefficient of Concordance and the probability of occurrence of such values under chi-square

Sample date	N(*)	S(**)	W	X^2	Prob.
March 16, 17/1979	14	1392.5	.270E	17.60	.20
April 17, 20/1979	12	1414.5	.5569	30.63	.01
May 15-17/1979	14	2340.0	.4384	28.50	.01
June 15-18/1979	14	2339.0	.4255	27.66	.01
July 18-20/1979	15	3173.0	.4808	33.66	.01
Aug. 14, 15/1979	16	3625.5	.4553	34.15	.01
Sept. 12, 19/1979	6	272.0	.7302	18.26	.01
Oct. 3/1979	8	426.0	.5816	20.36	.01
Oct. 16/1979	10	378.0	.2779	12.51	.20
Oct. 31, Nov. 1/1979	16	1123.5	.1942	14.57	.50
Nov. 20/1979	14	1461.0	.3594	23.36	.05
Dec. 5/1979	15	1692.0	.2953	20.67	.20
January 8/1980	11	528.0	.3698	14.79	.20
February 4, 6/1980	12	586.0	.2084	11.46	.50
March 6/1980	12	474.0	.2712	11.93	.50

(*)= number of species

(**)= sum of the squares of the observed deviation from the mean of the species rank in terms of the algal species present in different areas of the reef. Of the 41 algal species found during this investigation, only 10 species occurred in all the transects, although not in the same month. Fewer than 10 algal species were found to occur in all transects if examined monthly (Tables Al to A15, Appendix A).

From September, 1979, to March, 1980, more pronounced variations in W were found. The highest W value during the entire study corresponded to September, 1979, .7303 (.01 probability), or 1.6 times the value of August, 1979. However, this value was probably due to the depletion of species caused by Hurricane David resulting in the higher concordance between the surviving species.

A factor that should be taken into account when interpreting the fluctuations in W values from October to November, 1979, is the dominance of most reef spaces by the population explosion and patchy distribution of *Trichosolen duchassaingii.* A decreasing trend in W during the month of October, 1979, when this species dominated most of the benthos, is apparent in Table 4. The following W values were obtained for that month: October 3, .5816 (.01 prob.); October 16, .2779 (.20 prob.); October 31, .1942 (.50 prob.). These values are apparently in contradiction to what would be expected in a situation where a single algal species is dominant and occupying most of the available benthic space. In such a situation, it would be expected that the concordance or agreement between the transects would increase and be reflected in higher W values. This is not apparent in the values found.

Although *Trichosolen* was initially successful in colonizing most of the available substrate after Hurricane David, this species was not able to dominate all areas in equal measure. This can be appreciated if the backreef transects are compared with those of the forereef during October, 1979.

By October 16, *Trichosolen* had achieved its maximum dominance in Turrumote. The approximate percentage of appearance of this species at that time was: transect 1, 99%; transect 2, 94%; transect 3, 100%, transect 4, 100%; transect 5, 0%. Not only this species, absent entirely from transect 5, but as Table A8 of Appendix A shows, 11 other algal species were present in transect 5 during October 16. The presence of those species in that transect, when *Trichosolen* was dominating the rest of the reef, must have been responsible for the rather low concordance values found in that sample. Also in the sample of October 3, 15 algal species were found in transect 5 although *Trichosolen* was present in nearly 71% of that transect.

In November 20, 1979, after *Trichosolen* had disappeared almost entirely from Turrumote, W increased from .1942 (.50 prob.) on the previous sample to .3594 (.05 prob.) This suggests that some of the substrate previously occupied during the primary stages of algal succession by *Trichosolen* was utilized by other algal species. Species like *Centroceras clavulatum, Cladophora fascicularis* and *Enteromorpha flexuosa* made substantial increases in recolonizing the reef during that period.

4. Successional theory

Succession refers to the changes observed in an ecological community following a perturbation that opens up a relatively large space (Connell and Slatyer, 1977). Most of the research regarding succession has been conducted in terrestrial communities although recent attention has been given to marine communities (Scheer, 1945; Bayne, 1965; Connell, 1972; Harger and Tustin, 1973; Connell and Slatyer, 1977; Sousa, 1979; Littler and Littler, 1980).

The term succession has been controversial when applied to marine colonization because of the apparent lack of consensus in regard to its definition. Scheer (1945) points at the difficulty in separating succession from seasonal progression in some environments, but concluded that certain stages of colonization in panels placed at Newport Harbor, California, did constitute succession because of their occurrence in sequence disregarding the season of exposure. Other studies appear to have reached similar conclusions (Fahey and Doty, 1949; Cirino, 1958; Doty, 1967). However, Lee (1966) reached opposite conclusions regarding succession. Be pointed out that an orderly sequence of events in a community, even if seasonally independent, does not necessarily imply that a particular successional stage has to be dependent on the conditions created by a previous stage in order for it to occur.

Connell and Slatyer (1977) have delineated three different models of ecological succession in a review of successional theory. These models embody major opposing views regarding succession in natural communities.

The first of the three models proposed by Connell and Slatyer (1977) is the facilitation model which assumes that only certain early successional species are able to colonize a site under the existing conditions that follow a disturbance. In this model, later species are dependent upon the earlier species modifying the environment in order to establish themselves.

A second tolerance model predicts that the modifications in the environment caused by the presence of early successional species neither increase nor decrease the establishment of later colonists. A sequence in a community is produced by the existence of species that have evolved different strategies for exploiting the available resources. Later species are more efficient competitors for limited resources than early species, according to this model.

A third inhibition model suggests that all species resist invasions of competitors. Once early colonists dominate most of the resources, they resist the invasion of subsequent colonists. Only when the early colonists die or are damaged can later colonists establish themselves in a community.

Littler and Littler (1980) studied the relationship between morphology, ecological attributes and productivity of certain species of benthic macroalgae. Successional manipulations were performed by disturbing mature, stable intertidal communities. Selection in such environment favored opportunistic species having high net productivity while species persisting in less stressful habitats showed lower photosynthetic rates. Later successional macroalgae showed greater toughness as well as greater resistance to wave shearing forces than the opportunistic species. Data based on succession, productivity and toughness suggest that some species shift from an opportunistic strategy during their juvenile stages to a differentiated complex form able to persist in mature successional stages.

5. Succession in the benthic macroalgae after Hurricane David

Hurricane David was a significant ecological disturbance which caused very high mortalities in the benthic algal populations of Turrumote Reef by either its direct action or by indirect effects, such as increased siltation. Immediately after David, extensive denuded areas composed primarily of sand and coral rubble were noticeable throughout the lagoonal area of Turrumote Reef. On the following week, most portions of the reef acquired a brownish-yellowish appearance. It is likely that the combined effects of bacteria, diatoms and early life stages of algae contributed to this coloration.

The succession in terms of benthic macroalgae began with the appearance of the green alga *Trichosolen duchassaingii*. On the first sample after the hurricane, September 12, 1979 (Table A7, Appendix A), this species was already present in most reef areas. Juvenile plants had a bright green and sometimes brownish coloration depending mostly on depth. Differences in size of plants of this species were also apparent, depending primarily on the degree of exposure to wave action. In the lagoon, the largest plants were observed in transect 3 where the greatest shelter from wave action was available; smaller plants were present in transects 1 and 2. *Trichosolen* dominated the benthos disregarding the type of substrate or habitat, except in the case of living organisms such as corals. This alga was commonly found growing on dead coral rubble, sandy areas, freshly overturned coral colonies, and as an epiphyte on *Halimeda opuntia*.

A bloom was observed during the months of September and October, 1979. The relatively few benthic algal species that survived the impact of the hurricane were ultimately outcompeted and eliminated by *Trichosolen.* The luxuriant filamentous growth of this alga caused a barrier to light penetration for other species adhered closer to the bottom such as *Halimeda opuntia.*

By mid-October this population bloom reached a peak, covering an average of 85% of the area within the transects and in most sites, as in transects 1, 2, 3 and 4, the coverage ranged from 95 to 100%. In a period of approximately two weeks, beginning in November, 1979, the presence of *Trichosolen* sharply declined and, by November 20, it had disappeared in most of the reef. It should be noted that this species vanished from transect 5 earlier than from the other areas. The reason for this is unknown. During mid-October, when the bloom had reached a peak, *Trichosolen* disappeared completely from transect 5. The death and decomposition of this species produced a strong odor throughout the reef. Also, oil spots were frequently observed due to the breakage of intracellular products from diatoms present on *Trichosolen* (Almodóvar, personal communication).

Reports of similar successional developments have been published for Puerto Rico and Guam. Glynn, Almodóvar and Gonzalez (1963) report the appearance of *Bryopsis hypnoides* in the reefs of La Parguera, Puerto Rico, following the path of Hurricane Edith in 1961. Ogg and Koslow (1976) inform the appearance of a bright green mat of early colonizing algae in the reefs of Guam identified as *Bryopsis* sp. and *Enteromorpha* sp. within days of Typhoon Pamela in 1976. Owing to a taxonomic controversy regarding the genera *Bryopsis*, *Pseudobryopsis* and *Trichosolen* (Taylor, 1962; Blomquist and Díaz-Piferrer, 1961; Chihara, Díaz-Piferrer and Papenfuss, 1980), it is quite possible that these successional reports refer to the same genus.

Although no published reports are known that have investigated the single or multiple factors responsible for the opportunistic strategy of *Trichosolen*, some possible explanations are: 1) the elimination and temporary absence of competitors such as other algal species, herbivores or other organisms that function as ecological controls for *Trichosolen;* 2) during hurricanes, algal spores can be transported from areas where their presence is common to where they are rare and sporadic; 3) hurricanes cause the stirring of benthic communities and sediments, thus causing a sudden suspension in the water of considerable amounts of nutrients; 4) the existence of a life cycle that allows this species to colonize recently-cleared surfaces more effectively than other species.

A source of nutrient enrichment in Turrumote Reef is the seasonal presence of seagulls upon the arrival of their reproductive season. Massive migrations of these birds were observed along the eastern shore of the reef, particularly at the boulder rampart where nests were abundantly established between the coral rubble. Nests and eggs were first noticed in. July, 1979, and by late August when David struck, broods and eggs were still abundant, which presumably caused high mortalities in this species. However, within two weeks after Hurricane David, birds were observed nesting again.

The combined presence of these birds and their eggs might have been a factor in causing nutrient enrichment and subsequent eutrophication in certain areas of this reef, particularly in the eastern lagoonal area. During August, a massive proliferation of *Penicillus capitatus* was observed along the shores of the boulder rampart. However, this species was totally absent from the nearby transect 3 in the center of the lagoon and was not common in any other area. The nearness of nests, the absence of other algal species and the failure to observe a similar proliferation by this species in other areas, suggest the existence of eutrophic conditions in this area.

Soto (1978), in a study of the life history of *Spyridia filamentosa* in Enrique Reef, La Parguera, suggested the occurrence of a similar situation caused by the appearance of a population of pelicans *(Pelecanus occidentalis)* during September, 1977. *Spyridia* failed to show an increase in seasonal occurrence only in the station where these birds were located. Nevertheless, other algal species like *Ulva* and *Enteromorpha* apparently adapted to high nutrient levels appeared in that area. Soto reported a similar phenomenon for nearby Cayo de Caballo Blanco Island where a heron *(Bubulcus ibis ibis)* population is permanently located. A decrease of certain species of algae and other marine organisms has been observed, while periodic blooms of other species adapted to such high nutrient levels were observed. *Enteromorpha flexuosa* was the second algal species that contributed substantially to the algal recolonization of Turrumote Reef after Hurricane David. It appeared first in the littoral zone of transect 2 during the first week of October, 1979. At that time it was seen interweaved with *Trichosolen* and appeared as a fine, hair-like, fairly uniform coating on the substrate. On the subsequent months its presence increased throughout the study area. *Enteromorpha* was particularly abundant in the first horizontal 11 m of transect 1 and in transect 3, where it appeared scattered and patchy possibly because of the uniform bathymetry of that area.

Doty (1967) made similar observations regarding the appearance of *Enteromorpha* in the pioneer intertidal algal populations that developed after the volcanic eruptions of 1955 in Hawaii. *Enteromorpha* was a pioneer species on all the fresh lava surfaces examined by Doty, regardless of the time of the year or the vertical position in the intertidal region. However, in this study, this species appeared only after the initial invasion by *Trichosolen* had begun to recede while in Hawaii it appeared before any other algal species. Differences in substrate, water temperature and other factors can account for the observed variations in the time of appearance in Hawaii and the coral reef studied in Puerto Rico.

Ectocarpus breviarticulatus was a second algal species reported by Doty in Hawaii in recently exposed surfaces, and was present in Turrumote after the passing of Hurricane David. The presence of this species from December, 1979, to February, 1980, was restricted only to transect 4 where it appeared only at the upper intertidal region. The lower tufts of *Ectocarpus* were sometimes found intermixed with *Cladophora* in that transect. Doty reports a similar observation for these two algal species in Hawaii. However, the appearance of *Ectocarpus* and *Cladophora* in Turrumote only during the winter months of December to February, suggests that such happening might be a seasonal response by these species to lower water temperatures rather than to a successional event.

In addition to those already cited, two algal species were present in abundance on Turrumote Reef after Hurricane David. The first was *Liagora ceranoides,* which appeared after a massive bloom during the first week of October, 1979, but only in deeper water around the reef and not in the study area. *Liagora* was the dominant species in these deeper waters down to approximately 10 meters. The second was *Microcoleus lyngbyaceus,* which became very abundant in certain transects after the disappearance of *Trichosolen* in November, 1979. In the samples of November 20, this species was very common in the first 13 horizontal meters of transect 2 and from 41 to 65 m of transect 3. On December 5, 1979, it was seen forming thin algal mats across large portions of transect 3. On later months its appearance declined and became sporadic, but was nevertheless present in the forereef as well as the backreef of Turrumote.

From the information on Tables Al and A15, Appendix A, it can be concluded that the algal flora present in March, 1980, is very limited in regard to the percentage of appearance and distribution among the transects when compared with March, 1979. This can be interpreted as an intermediate stage in the algal succession but not a climax state, if the data from March through August, 1979, are used as a point of reference of algal populations undisturbed for over 15 years by a storm.

6. Periodicity of benthic macroalgal species

There have been few published investigations regarding the periodicity or seasonality of tropical algal species. An important reason for this is the assumption that the tropical algal flora is essentially perennial because the sharpest variations in environmental conditions occur in cold and temperature zones (Feldmann, 1951). This hypothesis regarding the absence of seasonality in tropical algal species should be examined in the light of recent studies to determine the extent of its validity. Recent phycological studies (Ogden and Lobel, 1978; Soto, 1978) point to the necessity of further studies regarding the occurrence of seasonality in tropical species.

Variations in the population density of marine algae in relation to seasonal changes have been studied by Svedelius (1906) for Sri Lanka; by Hoyt (1920) and Williams (1948, 1949) for the coasts of North Carolina; by Bell (1927) and McFarlane and Bell (1933) for the coasts of Nova Scotia; by Bernatowicz (1952) for Bermuda; by Humm (1952), Phillips (1961), Croley and Dawes (1970), and Mathieson and Dawes (1975) for Florida; by Lawson (1957) for the coast of Ghana, Africa; by Nisra (1959) for the west coast of India; by Conover (1958, 1964), Edwards (1969), Earle (1969), and Edwards and Kapraun (1973) for Texas and the eastern Gulf of Mexico; by Zaneveld and Barnes (1965) for Chesapeake Bay; by Colinvaux (1970) for the Bay of Fundy, Canada; by Reynolds and Mathieson (1975) for a New Hampshire tidal rapid, and by Sears and Wilce (1975) for southern Cape Cod.

Most of these studies cite seasonal changes in temperature and illumination as the primary factors in causing changes in density in algal populations, while some conclude that other factors might be responsible for this. Svedelius (1906) and Misra (1959), correlate the changes in algal populations with the arrival of the monsoon season of heavy rains in Sri Lanka and India respectively. Lewis (1910), and Bell (1927) concluded that the liberation of gametes in *Dictyota* was closely related to the tidal cycle of the region. Lawson (1957) also suggests the tidal factor as responsible for causing seasonal changes in zonation and abundance of intertidal species of marine alga in the coast of Ghana, Africa.

Soto (1978), in a study of the life cycle of *Spyridia filamentosa*, examined several factors that affected the seasonal reproduction and abundance of this species in Cayo Enrique, La Parguera, Puerto Rico. He concluded that the observed increase in reproduction and population abundance of *Spyridia* during March through May was caused primarily by an increase in solar radiation. The combined effects of lower tides, direct solar exposure, higher temperatures and winds had an adverse effect on this species causing a sharp population decrease after midday.

During the thirteen months that Turrumote Reef was studied, observations were made regarding fluctuations in abundance and the sudden appearance or disappearance of certain algal species. The following species showed fluctuations in their distributions:

Note: (B) indicates species present before Hurricane David

(A) indicates species present after Hurricane David

a. *Bryopsis pennata.* (B) - a few plants present in March, April and July, 1979, with a maximum abundance in August, 1979, and absent the rest of the year. Presence restricted to transect 4 except for August, when it appeared in transects 1 and 4.

b. *Ceramium nitens* (A) - a few plants present in transect 5 during the months of December and March, 1980.

c. *Chaetomorpha linum* (A) - one plant appeared in transect 4 in December, 1980.

d. *Cladophora fascicularis* and *Cladophora* sp. (B) and (A) - a few plants appeared in August, November and December, 1979, in transects 1, 3 and 4.

e. *Ectocarpus breviarticulatus* (A) - present in transect 5 only during the winter months (December, 1979 to February, 1980).

f. *Enteromorpha flexuosa* (A) - appeared only after Hurricane David in October, 1979, and remained abundant until March, 1980. Most abundant in the littoral with a decrease in plants towards the sublittoral.

g. *Gelidiella acerosa* (B) - a few plants present only during the summer months of May, June and August, 1979, mostly in transects 4 and 5.

h. *Herposiphonia tenella* (A) - appeared in November, 1979, exclusively in the littoral zone of transect 4.

j. *Liagora mucosa* (A) - appeared in the deeper waters surrounding the reef in October, 1979, producing a population bloom that lasted several months.

k. *Neomeris annulata* (B) and (A) - a few plants present in April, May and August, 1979, disappeared afterward's and was later present from November, 1979, until March, 1980 when its presence reached an annual peak.

l. *Struvea anastomosans* (B) - restricted to transect 4, a few plants present only during July and August, 1979.

m. *Trichosolen duchassaingii* (A) - bloomed after Hurricane David forming thick filamentous algal mats with a coverage of as much as 100% in many reefs throughout La Parguera. This bloom began in September, reached a peak by mid-

October and disappeared almost entirely by mid-November, 1979.

n. *Wrangelia argus* (B) and (A) - present in moderate abundance in transect 5 from March to May, 1979, disappeared afterwards and was observed again in March, 1980.

7. Twenty-four hour monthly experiments and the effects of temperature, oxygen and salinity on the algal populations

Figures 16, 17, 18 and Tables B1 to B9 of Appendix B summarize the yearly results for stations A, B and C of the monthly twenty-four hour continuous measurements for temperature, dissolved oxygen and salinity obtained at Turrumote Reef from April, 1979, to March, 1980.

a. Temperature

Station A had a temperature range between 23.5 and 31°C (Table B1, Appendix B). The lowest value was registered in April, 1979, and the highest on November, 1979. The monthly mean temperature values usually varied from 25 to 28°C, the highest mean value obtained was 29.6°C in November, 1979, and the lowest mean value was 25.3°C in April, 1979. The lowest consecutive mean temperatures occurred during the months of January (25.4°C), February (25.8°C) and March (25.5°C), 1980.

Station B had temperature ranges from 23°C (April, 1979) to 34°C (May, 1979) (Table B2, Appendix B). This station showed the most pronounced temperature fluctuations of the three stations (Fig.17). Monthly mean temperatures usually varied between 25°C and 28°C; the highest monthly mean was registered in November, 1979, (29.2°C) and the lowest corresponded to January, 1980, (24.9°C). The lowest consecutive monthly temperatures occurred during January (24.9°C), February (25.4°C) and

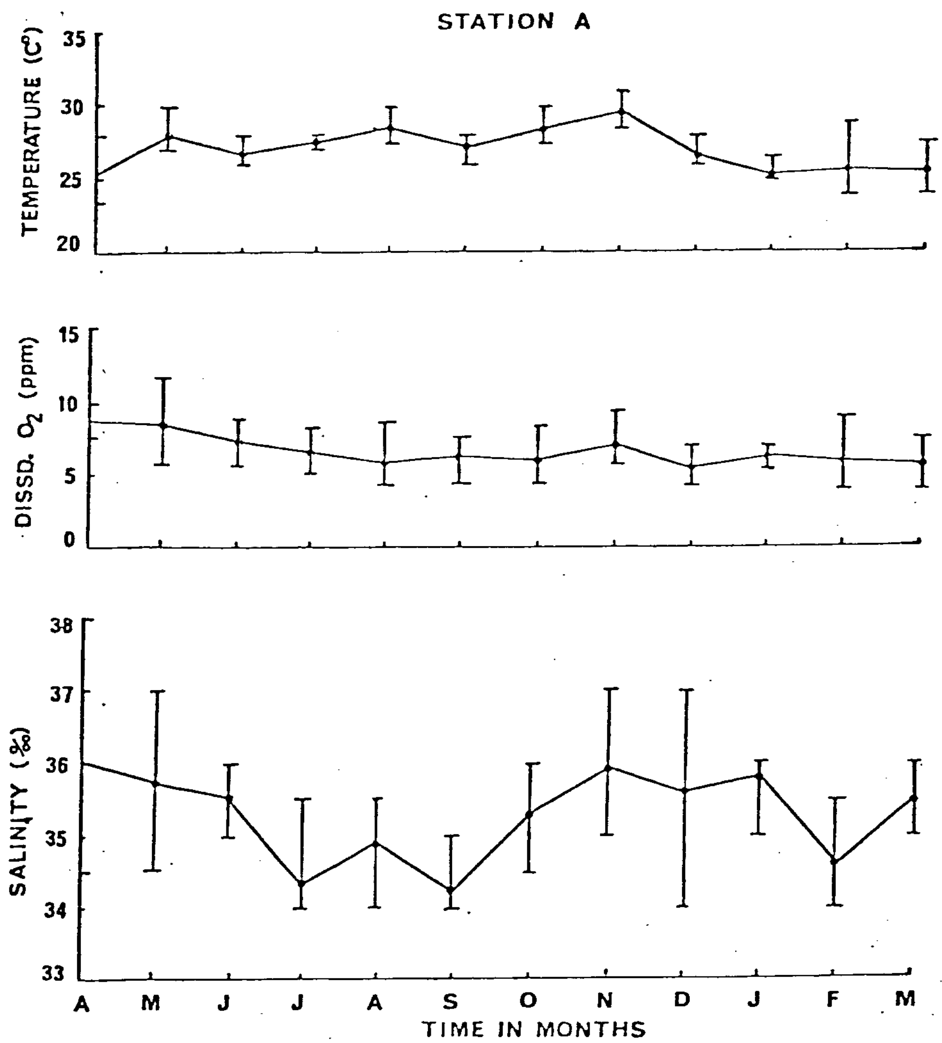


Fig. 16. Results of the twenty-four hour continuous monthly measurements of temperature, dissolved oxygen and salinity at Station A, Turrumote Reef between April, 1979, and March 1980. ∘ represents mean value, and ⊤ and ⊥, the highest and lowest values respectively.

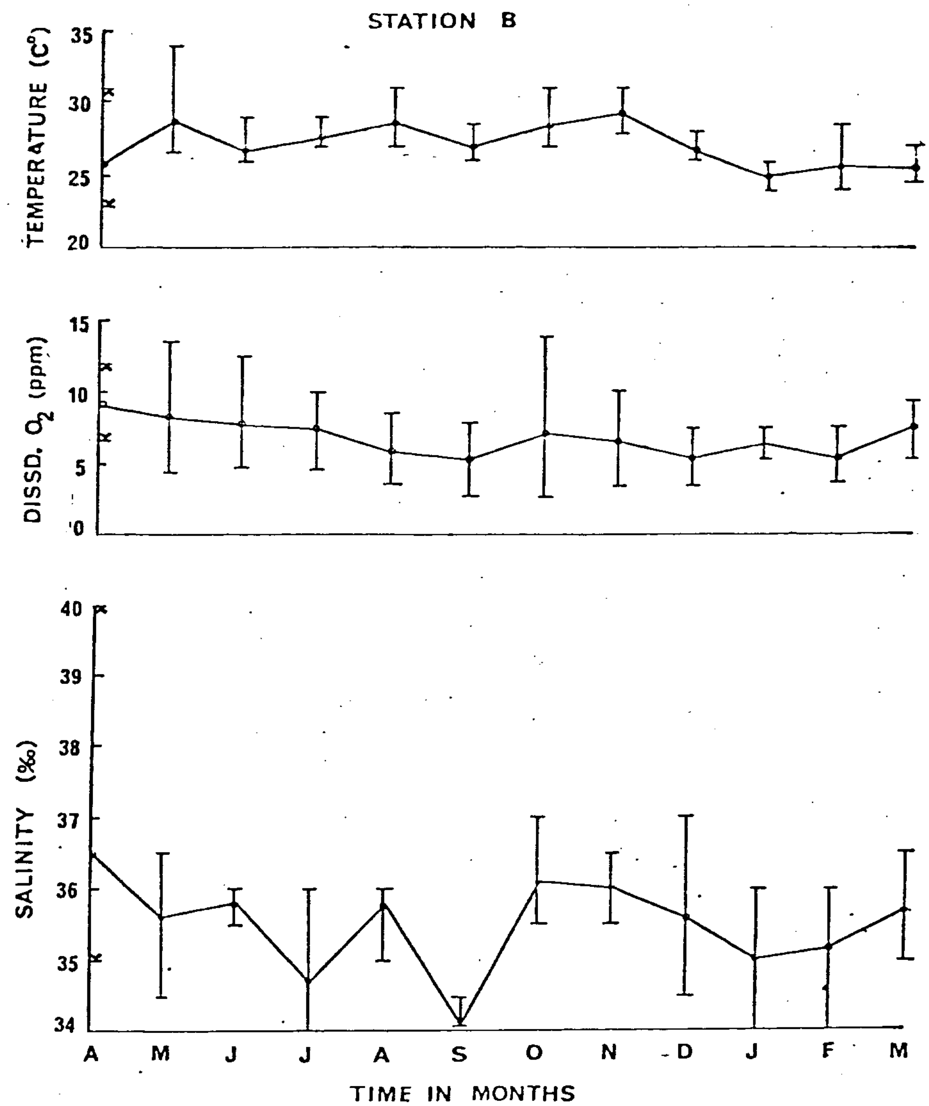


Fig. 17. Results of the twenty-four hour continuous monthly measurements of temperature, dissolved oxygen and salinity at Station B, Turrumote Reef between April, 1979, and March, 1980. ∘ represents mean value, ⊤ and ⊥, the highest and lowest values respectively

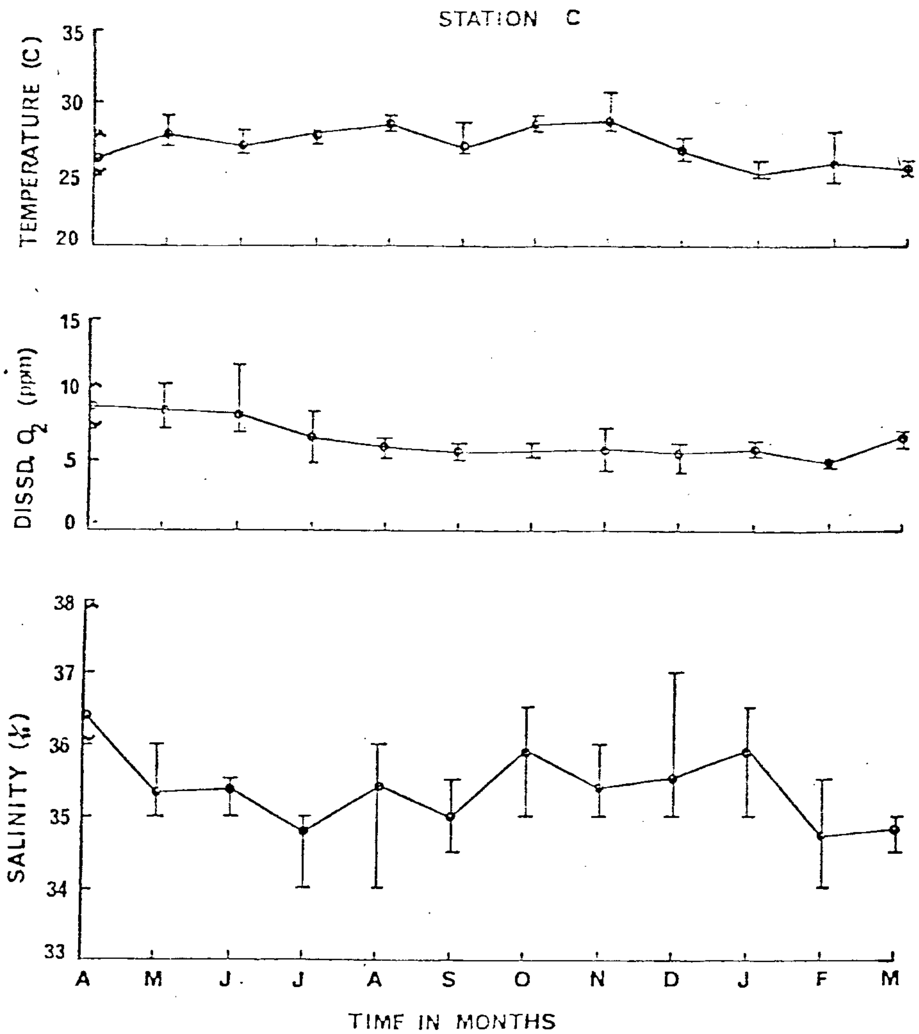


Fig. 18. Results of the twenty-four hour continuous monthly measurements of temperature, dissolved oxygen and salinity at Station C, Turrumote Reef between April, 1979, and March, 1980. ∘ represents mean value, T and ⊥, the highest and lowest values respectively.

March (25.4°C), 1980.

Station C had temperature ranges from 24.5°C (February, 1980) to 30.5°C (November, 1979) (Table B3, Appendix B). Of the three stations, station C showed the narrowest temperature range (Fig.18), The highest monthly mean (28.8°C) in November, 1979, coincided with the highest mean of stations A and B, and the lowest mean (25.1°C) in January, 1980, coincided with the lowest mean of station B during the same month.

Setchell (1915) proposed a scheme for the distribution of marine algae in the world based on various isotherms. According to him, the zone of tropical algae is located between the isotherms of 25°C and 30°C. The yearly monthly temperature means for stations A, B, and C shown in figures 16, 17 and 18 fall within the tropical zone scheme proposed by Setchell.

Taking into account the variations in temperature and the approximate duration of these changes, it is concluded that temperature was not a limiting factor for the algal populations studied, except when its influence was enhanced by other environmental factors. During the months of May to July, 1979, when extremely low tides occurred, temperature in combination with direct exposure to solar radiation, strong winds and dessication, induced significant mortalities to the algae of the upper intertidal zone. This was observed on several occasions in the intertidal zone of all five transects. Plants of *Centroceras clavulatum, Cladophoropsis membranacea* and *Halimeda opuntia* were particularly affected. Soto (1978) suggests that the combination of the factors mentioned previously caused a sharp decrease in the populations of *Spyridia filamentosa* at Cayo Enrique after the middle of May, 1977.

b. Oxygen

Station A had oxygen values that fluctuated between 3.8 ppm (February 1980) and 11.1 ppm (May, 1979) (Table B4, Appendix B). The highest monthly mean values for oxygen in this station occurred in April, 1979, (8.6 ppm) and the lowest in December, 1980 (5.4 ppm) (Fig. 16).

Station B had dissolved oxygen values from 2.7 ppm (October, 1979) to 13.8 ppm within the same month (Table B5, Appendix B). That range accounts for the most pronounced oxygen fluctuations of the three stations. The highest monthly mean oxygen value was 9.0 ppm for April, 1979, and the lowest was 5.1 ppm for September, 1979 (Fig. 17).

Station C had dissolved oxygen values that fluctuated between 11.9 ppm (June, 1979) and 4.1 ppm (December, 1979) (Table B6, Appendix B). The highest monthly O_2 mean occurred in April, 1979 (8.8 ppm) and the lowest during February, 1980 (4.9 ppm (Fig. 18). The narrowest oxygen fluctuations occurred at this station.

Table C1 of Appendix C shows the monthly maxima and minima saturation values in ppm for stations A, B and C. From these values it can be concluded that dissolved oxygen was not limiting to the algal populations studied. Stations A and B in the lagoon usually had higher maximum oxygen saturation values than station C in the forereef as well as lower minimum saturation values. In the forereef, oxygen saturation values in general showed lower maxima and higher minima, which suggests that the dissolved oxygen present in that area is mostly a function of the influence of aeration processes caused by wave action, as opposed to the lagoon where photosynthesis appears to be more important. The most pronounced fluctuations between the maximum and minimum dissolved oxygen saturation values were registered at station B during October, 1979. These maximum and minimum saturation values for dissolved oxygen were 226.2% and 42.5% respectively (Table C1, Appendix C), and coincided with the dominance of *Trichosolen.*

c. Salinity

Station A had salinity fluctuations between 34% and 38% (Table B7, Appendix B). The highest monthly mean corresponded to April, 1979 (36%) and the lowest to July, 1979 (34.3%) (Fig. 16). Salinity monthly means showed a relatively narrow range for this station (Fig. 16).

For station B salinity ranged from 34% to 40% (Table B8, Appendix B). This constituted the greatest fluctuation for that parameter for the three stations. Monthly salinity means were from 34.1% for September, 1979, to 36.5% for April, 1979 (Fig. 17). In this station, salinity monthly means had narrow ranges similar to those of station A.

Station C had salinities that ranged from 34% (several months) to 38% in April, 1979 (Table B9, Appendix C). The lowest monthly salinity mean occurred during February, 1980 (34.7%) and the highest during April, 1979 (36.5%) (Fig. 18). Salinity ranges for this station were similar to those of stations A and B, although narrower in most instances.

Variations in salinity along stations A and C were small. The lowest values registered were related closely with precipitation while taking the reading in situ. The maximum salinity values registered at station B were caused by a higher evaporation as a result of the shallow waters and restricted circulation existent in that area. The upper salinity values occasionally registered at station B combined with higher temperatures could have a negative effect for algal species not adapted to such regimes. Station C showed the greatest uniformity in temperature, oxygen and salinity as a result of direct exposure to oceanic waters in the forereef area. Experiments with a portion of the algal species present at Turrurrote Reef by Almodóvar and Biebl (1962), Biebl (1962), Montalvo (1970) and Muñoz

(1973), suggested that the species studied were able to survive changes of 0.2% to 4% in seawater concentration for up to 24 hours of exposure.

Stations A and B, located in the leeward or lagoonal area, had higher affinities in temperature, oxygen and salinity in relation to station C. Station B had the most pronounced variations in dissolved oxygen, temperature and salinity as a result of the shallow waters and restricted circulation present in its location. Station C was the most stable of all three stations in regard to the parameters measured. The aeration caused by breaking waves in the windward area is the most important factor in maintaining the rather uniform dissolved oxygen values gathered at station C.

8. Sediment analysis

Table 5 shows the percentages of gravel, sand and silt present in samples 1 to 10. The percentage of gravel varied from .07% in sample 4 to a maximum of 8.39% in sample 8. The percent of sand ranges from 54.47% to 99.97% in samples 9 and 4 respectively. For silt we have a minimum of .04% in sample 3 and a maximum of 39.38% in sample 9. Only samples 6 and 9 had more than 5% fine material; both samples correspond to the eastern side of the lagoonal area.

Table 5

Percent of gravel, sand and silt obtained for the sediment samples 1-10 collected at Turrumote Reef in March, 1979.

Sample	% Gravel	% Sand	% Silt
1	1.90	94.31	3.36
2	2.92	95.51	1.05
3	0.34	99.62	0.04
4	0.07	99.97	0.26
5	1.12	94.93	4.00
6	2.80	80.34	16.48
7	1.31	98.25	0.21
8	8.39	90.44	1.15
9	5.82	54.47	39.38
10	1.84	95.46	2.33

Sand was found to be the most important component of all sedimentary material analyzed, followed by gravel and silt. This can be appreciated in figure 19, which shows a ternary diagram for the gravel-sand-mud mixed ratios. Table 6 shows the values obtained for the statistical parameters of mean and sorting in samples 1 to 10. Mean values ranged from .18 θ for sample 3 to a maximum of 1.82 θ in sample 9, which gives a range from coarse to medium sand sediments. Coarse sand was predominant in samples 2, 3, 4, 5, 7 and 10 while medium sand was predominant in samples 1, 6, 8 and 9.

The values obtained for sorting ranged from .54 in sample 3 to 1.78 in sample 9. These values suggest that the sediments analyzed range from poorly to moderately sorted. Poorly sorted sediments were found in samples 5, 6, 7, 8 and 9, while moderately sorted ones were predominant in samples 1, 2, 3, 4 and 10.

Several conclusions can be drawn from the sediment analysis. First, it appears that Turrumote Reef is a relatively homogeneous environment in terms of sediments except in the eastern part of the lagoon (samples 6 and 9, Fig. 3) where the greatest abundance of silt is found. This reef does not have a terrigenous sediment input such as a river that could account for greater variations in the sediments.

The greatest variation in sediments was encountered in samples 6 and 9 which had a fine material content of 16% and 39% respectively. These samples correspond to the reef area with the lowest energy level in terms of wave action (Fig. 20). This makes a suitable environment for the deposition and accumulation of fine sediments. The high abundance of *Zoanthus sociatus* in the eastern lagoonal area is an important factor in consolidating the fine material and thus preventing it from being carried away easily by waves, currents, tidal fluctuations or other forces. Another important biological factor in this area is the presence of *Callianasa* and also of certain holothuroids. According to Matthews (1974) these organisms affect considerably the sedimentary environment around their burrows by converting coarse sediments into fines. It appears, from visual inspection, that these organisms have successfully colonized the eastern part of the lagoon as indicated by the abundance of their burrows. Even though these organisms are present in other reef areas, their abundance was observed to decrease as one moved away from the eastern part of the lagoon.

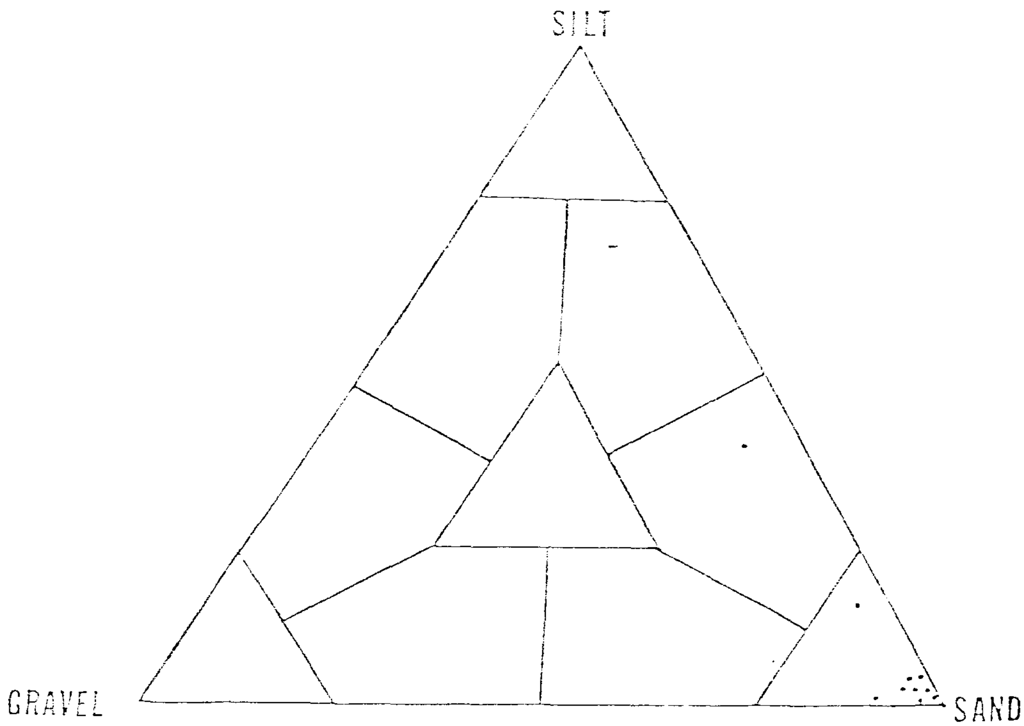


Fig. 19. Diagram of the percent of gravel, sand and silt of 10 bottom sediments collected at Turrumote Reef in March, 1979

Table 6

Statistical parameters of mean and sorting obtained for the sediment samples 1-10 collected at Turrumote Reef in March, 1979

Sample #	Mean (θ)	Sorting	Classification
1	1.27	0.98	Moderately sorted
2	0.30	0.93	Moderately sorted
3	0.18	0.54	Moderately sorted
4	0.30	0.73	Moderately sorted
5	0.40	1.17	Poorly sorted
6	1.68	1.37	Poorly sorted
7	0.73	1.0	Poorly sorted
8	1.47	1.68	Poorly sorted
9	1.82	1.78	Poorly sorted
10	0.41	0.88	Moderately sorted

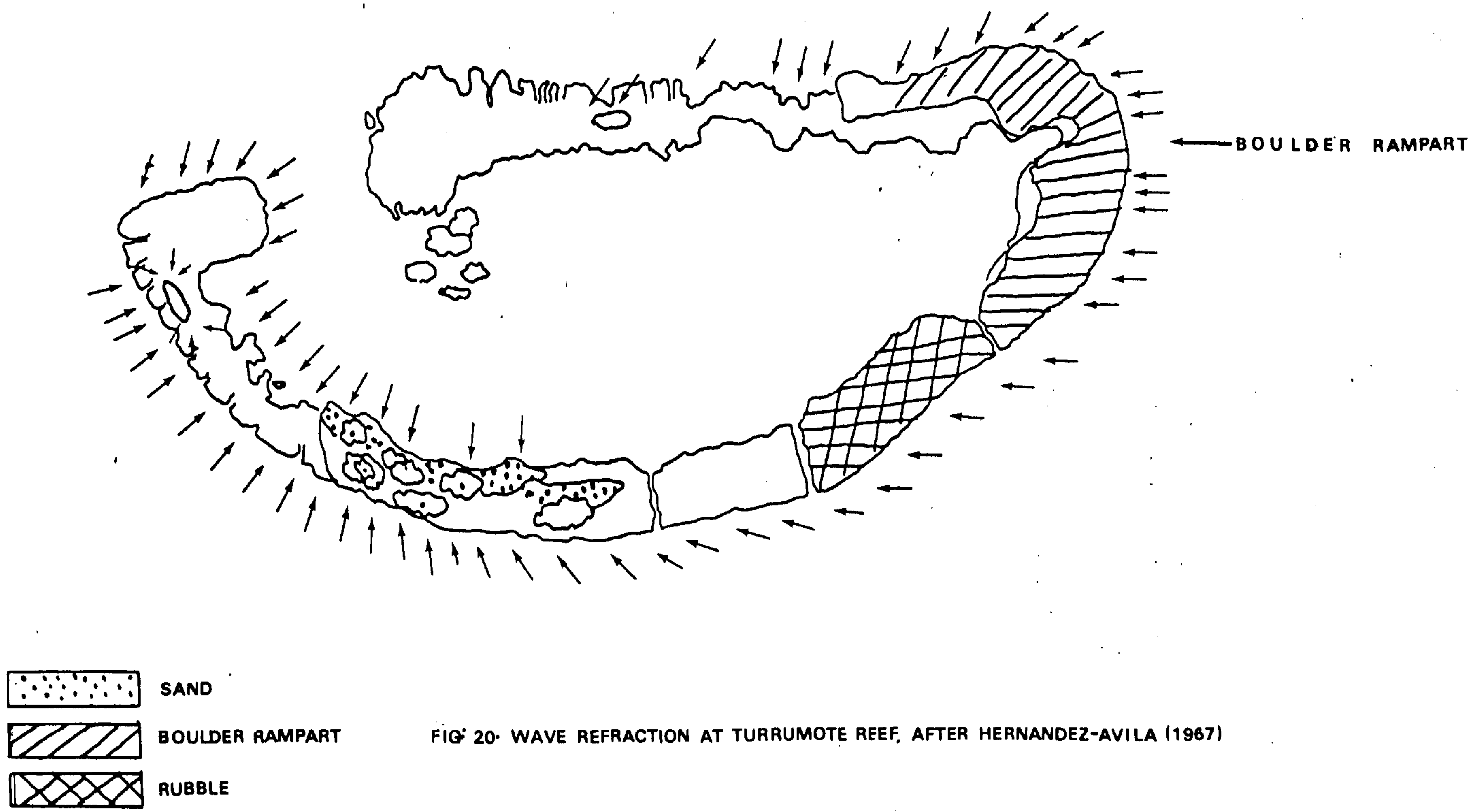


FIG. 20. WAVE REFRACTION AT TURRUMOTE REEF, AFTER HERNANDEZ-AVILA (1967)

A mean and sorting trend is apparent for the values shown in Table 18. Two sorting groups are evident from the samples: moderately and poorly sorted sediments. This could point to differences in energy levels in the two environments delineated by these values, since sorting is strongly influenced by the degree of energy in the environment (Folk, 1968). By drawing a dividing line along a north-south axis in this reef, an approximation is obtained of the two environments delineated by the two sorting groups mentioned. The first environment encompasses roughly the western side of-the lagoon and includes samples 1, 2, 3, 4 and 10 with moderately sorted sediments. The second environment is found in the eastern side of the lagoon and includes samples 5, 6, 7, 8 and 9 with poorly sorted sediments.

Figure 20 indicates a general view of the wave refraction for Turrumote Reef. It is noticeable that the first environment corresponds roughly to where the waves strike the reef with more intensity while the second corresponds to more sheltered sites. Thus, wave action acts as an important factor in the sediment distribution for this reef. Sediment distribution in combination with water movement is known to influence the algal communities present in a given environment (Schwenke, 1964, 1971; Hartog, 1971). Thus, wave action affects the algal populations of this reef in at least two ways: first, by the direct impact in areas such as the forereef and, indirectly, by influencing the sediment constituents for a given area.

As for the biogenic constituents, it can be concluded that they serve as a reflection of the environment from where they are obtained. In highly protected areas on the reef organisms were found which are adapted to a low energy environment. These organisms are either scarce or absent in other reef areas with higher energetic regimes. This is shown by higher abundance of organisms like sponges, tunicates and foraminiferans in low-energy areas such as the eastern lagoon when compared to the forereef where wave action is much stronger (Table C2, Appendix C).

Halimeda opuntia is a very important component of the sediments of this reef. This is shown by its mean presence of 28.7% in the samples studied and values as high as 56.4% in one instance. The presence of this alga is particularly important in the littoral zone because, after extremely low tides, mass mortalities were observed in *Halimeda,* thus causing a sudden increase in the sediment.

9. Tides

The tides in La Parguera, Puerto Rico, are basically diurnal with a semidiurnal component and have a small amplitude that exhibits a maximum range of 30-34 an (U.S. Dept. of Commerce).

Table 7

Minimum monthly tides at Magueyes Island from March, 1979, to March, 1980. (From U.S. Dept. of Commerce, tide prediction tables 1979-1980)

Month	Hour	Minimum Monthly Tide Height (feet)
March 16, 1979	13:24	0.10
17	12:06	0.30
April 16, 1979	14:32	0.00
17	5:24	0.60
19	14:04	0.00
May 15, 1979,	14:16	-0.10
16	15:12	0.00
17	16:20	0.05
June 14, 1979	15:39	0.00
15	16:35	0.05
17	7:38	0.15
18	8:27	0.05
July 18, 1979	8:05	-0.10
19	9:35	-0.15
20	10:17	-0.15
August 13, 1979	16:29	0.50
14	5:31	0.05
15	6:35	0.00
September 12, 1979	5:26	0.10
19	11:34	0.25
October 3, 1979	10:04	0.20
October 16, 1979	9:11	0.35
October 31, 1979	9:32	0.30
November 1, 1979	10:31	0.35
November 20, 1979	0:26	-0.05
December 5, 1979	0:34	-0.20
20	0:12	-0.30
January 8, 1980	3:29	0.00

TABLE 7 (contd.)

Month	Hour	Minimum Monthly Tide Height (feet)
February 4, 1980	2:19	-0.10
6	13:31	0.05
March 7, 1980	15:35	0.05

During the course of this study, the minimum tidal level occurred during the daytime in the months of May to July, 1979, and at night during November, 1979, to January, 1980, according to the U.S. Dept. of Commerce, Tide Prediction Tables for 1979-1980 (Table 31).

During the months when the minimum tides occurred during the day time, part of the benthic algae of the littoral were exposed to the combined effects of dessication, winds and higher temperature and light intensities, causing a stressful environment for the survival of some species. This situation was particularly apparent during June and July, 1979, when extremely low tides were followed by a sharp decline in the algae of the upper littoral zone.

Lawson (1957) studied the variation of the intertidal zonation of algae on the coast of Ghana, Africa, in relation to tidal factors. He found that variations in seasonal zonation and in abundance of intertidal algal species were positively correlated with seasonal tidal changes. Soto (1978), in a study of the life cycle of *Spyridia filamentosa* in Cayo Enrique, La Parguera, reached similar conclusions as the author in regard to the negative effects of the extreme daytime low tides during the summer on the algal population. However, González (1980), in a study of the vertical distribution of the algae of the supralittoral rocky coast of Guánica and Cayo Enrique, did not consider the tidal factor as limiting for the algal populations.

CONCLUSIONS

It is concluded from the results obtained that:

1. Hurricane David had a significant ecological impact on the benthic algal populations of Turrumote Reef. It was the most important environmental factor affecting the reef ecosystem during this study. Extremely high algal mortalities were caused by its direct action and by the deposition of sediment upon algae that initially survived its impact.

2. Using chi-square analysis, significant differences were found in fourteen perennial algal species examined in regard to their proportions of presence/absence for the study period before and after Hurricane David.

3. The Kendall Coefficient of Concordance test indicates that the concordance between transects in terms of algae was rather low in the months before Hurricane David. This suggests that different algal populations were present throughout the reef as a result of habitat variations. Most of the more pronounced variations in concordance between transects found after Hurricane David were related to the patchy distribution of *Trichosolen duchassaingii* and to changes in the algal succession.

4. The algal succession began within days of the catastrophic mortalities caused by Hurricane David. The macroalgal succession was initiated with a bloom of the opportunistic species *Trichosolen duchassaingii,* which showed a patchy but dominant distribution throughout most of the reef during the first two months after the disturbance.

5. Based on the total number of algal species, the algal populations present at the end of this study represented an intermediate successional state but not a climax community in regard to the period before Hurricane David.

6. Exposure to wave action and sediment composition are determinant factors as to what algal species are found in different areas of this reef.

7. Turrumote Reef is a relatively homogenous environment in regard to its sediments due to the absence of a terrigenous sediment source. A greater degree of shelter from wave action is provided in the eastern lagoon where the highest amounts of silts are found. *Halimeda opuntia* is a very important component of the biogenic sediments of this reef.

8. Salinity, oxygen and temperature do not seem to be limiting factors to the benthic algae except in the shallow eastern end of the lagoon. In that area, shallow waters and a restricted circulation cause higher temperatures and salinities. The lowest total number of algal species were found in this reef area.

9. Tides are a limiting factor to the supralittoral algae, particularly during the summer months when the lowest tides occur during the daytime and the combined effects of direct sunlight, wind, dessication and high temperatures are detrimental. High algal mortalities in the littoral were observed after a few days when those conditions prevailed.

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APPENDIX A

Table A1

Summary of the benthic algal species present in the study area at Turrumote Reef during March 16 and 17, 1979. Left side value represents the total number of squares where the species was present; ( ) represents the % occurence for the transect.

	1	2	3	4	5
Acanthophora spicifera	---	---	2(.002)	---	---
Amphiroa fragilissima	84(.09)	1(.001)	50(.04)	179(.59)	115(.38)
Amphiroa rigida	94(.10)	1(.001)	---	---	---
Bryopsis pennata	---	---	---	7(.02)	---
Caulerpa cupressoides	90(.09)	3(.003)	---	---	---
Caulerpa racemosa	3(.003)	14(.02)	9(.01)	6(.02)	6(.02)
Caulerpa sertularioides	4(.004)	19(.02)	25(.02)	---	---
Centroceras clavulatum	55(.06)	66(.08)	---	195(.64)	49(.16)
Cladophoropsis membranacea	29(.03)	---	25(.02)	76(.25)	73(.24)
Codium sp.	---	---	---	1(.003)	---
Coelothrix irregularis	---	---	---	---	4(.01)
Crouania attenuata	---	---	---	---	51(.17)
Dictyosphaeria cavernosa	---	---	1(.009)	5(.02)	---
Dictyota divaricata	143(.15)	---	---	---	---
Gelidium corneum	6(.006)	65(.07)	---	---	1(.003)
Halimeda opuntia	514(.54)	334(.38)	148(.12)	---	72(.24)
Laurencia obtusa	5(.005)	---	159(.13)	116(.38)	48(.16)
Laurencia papillosa	49(.05)	---	8(.007)	---	46(.15)
Penicillus capitatus	258(.27)	8(.01)	---	---	---

APPENDIX A

Table A1 (contd.)

	1	2	3	4	5
Valonia ventricosa	---	---	5(.004)	---	2(.01)
Wrangelia argus	---	---	---	1(.003)	---

APPENDIX 1

Table A2

Summary of the benthic algal species present in the study area at Turrumote Reef during April 17 and 20, 1979. Left side value represents the total number of squares where the species was present; ( ) represents the % of occurence for the transect.

	1	2	3	4	5
Acanthophora spicifera	---	---	4(.003)	---	---
Amphiroa fragilissima	81(.08)	111(.13)	91(.08)	181(.60)	110(.36)
Amphiroa rigida	35(.04)	5(.005)	---	---	---
Bryopsis pennata	---	---	---	3(.01)	---
Caulerpa cupressoides	64(.07)	27(.03)	---	---	---
Caulerpa racemosa	21(.02)	5(.006)	---	3(.01)	5(.02)
Caulerpa sertularioides	17(.02)	5(.006)	12(.01)	---	---
Centroceras clavulatum	40(.04)	103(.12)	---	204(.67)	47(.15)
Cladophoropsis membranacea	29(.03)	12(.01)	11(.008)	69(.23)	40(.13)
Coelothrix irregularis	9(.001)	1(.001)	---	---	---
Dictyosphaeria cavernosa	---	---	4(.003)	---	3(.01)
Dictyota divaricata	95(.10)	5(.006)	---	---	---
Ernodesmis verticillata	---	1(.001)	---	---	---
Gelidium corneum	10(.01)	99(.11)	---	36(.12)	---
Halimeda opuntia	421(.44)	350(.40)	175(.15)	---	137(.45)
Laurencia obtusa	6(.006)	---	168(.14)	101(.33)	69(.23)
Laurencia papillosa	47(.05)	8(.009)	12(.01)	---	4(.01)
Neomeris annulata	---	5(.006)	---	---	---
Penicillus capitatus	312(.33)	33(.04)	---	---	---

APPENDIX A

Table A2 (contd.)

	1	2	3	4	5
Polysiphonia ferulacea	1(.001)	---	---	---	---
Valonia macrophysa	2(.002)	---	---	---	---
Valonia ventricosa	---	---	2(.002)	2(.007)	---

APPENDIX A

Table A3

Summary of the benthic algal species present in the study area at Turrumote Reef during May 15, 16 and 17, 1979. Left side value represents the total number of squares where the species was present; ( ) represents the % of occurence for the transect.

	1	2	3	4	5
Acanthophora spicifera	---	2(.002)	6(.005)	---	---
Amphiroa fragilissima	172(.18)	197(.22)	79(.01)	166(.55)	137(.45)
Amphiroa rigida	164(.17)	12(.01)	1(.0008)	---	7(.02)
Caulerpa cupressoides	74(.08)	30(.03)	---	---	---
Caulerpa racemosa	6(.006)	8(.009)	---	5(.02)	8(.03)
Caulerpa sertularioides	26(.03	13(.01)	8(.007)	---	---
Centroceras clavulatum	56(.06)	78(.09)	2(.0016)	195(.64)	70(.23)
Cladophoropsis membranacea	59(.06)	72(.08)	6(.005)	88(.29)	44(.14)
Coelothrix irregularis	8(.008)	3(.003)	---	---	1(.003)
Crouania attenuata	---	---	---	---	52(.17)
Dictyosphaeria cavernosa	---	---	2(.002)	14(.05)	---
Dictyota bartayresii	---	3(.003)	---	---	---
Dictyota divaricata	212(.22)	18(.02)	1(.0008)	---	---
Galaxaura sp.	---	---	1(.0008)	---	---
Gelidiella acerosa	---	---	---	---	1(.003)
Gelidium corneum	19(.02)	99(.11)	---	34(.11)	19(.06)
Halimeda opuntia	543(.57)	361(.41)	226(.19)	---	66(.21)
Hypnea spinella	6(.006)	---	1(.0008)	---	---
Laurencia obtusa	57(.06)	3(.003)	100(.08)	110(.36)	101(.33)

APPENDIX A

Table A3 (contd.)

	1	2	3	4	5
Laurencia papillosa	94(.10)	43(.05)	16(.01)	---	52(.17)
Penicillus capitatus	391(.41	(49(.06)	---	---	---
Valonia ventricosa	---	---	10(.008)	2(.007)	---
Wrangelia argus	---	---	---	---	2(.007)

APPENDIX A

Table A4

Summary of the benthic algal species present in the study area at Turrumote Reef during June 15, 17 and 18, 1979. Left side value represents the total number of squares where the species was present; ( ) represents the % of occurence for the transect.

	1	2	3	4	5
Acanthophora spicifera	8(.008)	2(.002)	2(.002)	---	---
Amphiroa fragilissima	197(.21)	200(.23)	59(.05)	166(.55)	58(.19)
Amphiroa rigida	188(.18)	19(.02)	20(.02)	1(.003)	2(.007)
Caulerpa cupressoides	60(.06)	32(.04)	---	---	---
Caulerpa racemosa	21(.02)	17(.02)	---	11(.04)	9(.03)
Caulerpa sertularioides	37(.04)	28(.03)	10(.008)	---	---
Centroceras clavulatum	14(.02)	78(.09)	4(.003)	152(.50)	58(.19)
Cladophoropsis membranacea	88(.09)	91(.10)	14(.01)	35(.12)	88(.29)
Crouania attenuata	---	---	---	1(.003)	41(.14)
Coelothrix irregularis	3(.003)	3(.003)	---	---	3(.009)
Dictyota divaricata	199*.21)	15(.02)	---	---	---
Dictyosphaeria cavernosa	1(.001)	---	4(.003)	5(.02)	---
Gelidiella acerosa	---	---	---	2(.007)	---
Gelidium corneum	20(.02)	149(.17)	---	24(.08)	48(.16)
Halimeda opuntia	522(.54)	407(.46)	208(.17)	---	80(.26)
Hypnea spinella	10(.01)	---	5(.004)	---	---
Laurencia obtusa	45(.05)	5(.006)	47(.04)	83(.27)	127(.42)
Laurencia papillosa	94(.10)	65(.07)	27(.02)	1(.003)	---

APPENDIX A

Table A4 (contd.)

	1	2	3	4	5
Penicillus capitatus	433(.45)	51(.06	---	---	---
Valonia ventricosa	5(.005)	---	2(.002)	1(.003)	---

APPENDIX A

Table A5

Summary of the benthic algal species present in the study area at Turrumote Reef during July 18, 19 and 20, 1979. Left side value represents the total number of squares where the species was present; ( ) represents the % of occurrence for the transect.

	1	2	3	4	5
Acanthophora spicifera	8(.008)	4(.005)	16(.01)	---	---
Amphiroa fragilissima	146(.15)	208(.24)	37(.03)	156(.51)	70(.23)
Amphiroa rigida	153(.16)	16(.02)	---	---	5(.02)
Bryopsis pennata	---	---	---	4(.01)	---
Caulerpa cupressoides	17(.02)	8(.009)	---	---	---
Caulerpa racemosa	19(.02)	13(.02)	4(.003)	5(.02)	15(.05)
Caulerpa sertularioides	29(.03)	17(.02)	3(.003)	---	---
Centroceras clavulatum	108(.11)	79(.09)	---	226(.74)	40(.13)
Cladophora fascicularis	---	---	---	2(.007)	---
Cladophoropsis membranacea	101(.11)	75(.09)	29(.02)	80(.26)	16(.05)
Coelothrix irregularis	1(.001)	4(.005)	---	---	1(.003)
Crouania attenuata	---	---	---	1(.003)	44(.15)
Dictyosphaeria cavernosa	1(.001)	---	---	8(.03)	---
Dictyota divaricata	134(.14)	25(.03)	---	---	---
Gelidium corneum	10(.01)	148(.17)	---	39(.13)	4(.01)
Halimeda opuntia	607(.63)	378(.43)	188(.16)	---	80(.26)
Hypnea spinella	3(.003)	---	---	---	---
Laurencia obtusa	41(.04)	11(.01)	65(.05)	101(.33)	98(.32)

APPENDIX A

Table A5 (contd.)

	1	2	3	4	5
Laurencia papillosa	90(.09)	73(.08)	12(.01)	---	1(.003)
Lomentaria baileyana	---	1(.001)	---	---	---
Penicillus capitatus	486(.51)	76(.09)	---	---	---
Polysiphonia ferulacea	---	10(.01)	---	---	---
Struvea anastomosans	---	---	---	1(.003)	---
Valonia ventriculosa	3(.003)	---	1(.0008)	---	---

APPENDIX A

Table A6

Summary of the benthic algal species present in the study area at Turrumote Reef during August 14 and 15, 1979. Left side value represents the total number of squares where the species was present; ( ) represents the % of occurence for that transect.

	1	2	3	4	5
Acanthophora spicifera	6(.006)	2(.002)	20(.02)	---	---
Amphiroa fragilissima	159(.17)	211(.24)	35(.03)	165(.54)	108(.36)
Amphiroa rigida	175(.18)	25(.03)	1(.0008)	---	8(.03)
Bryopsis pennata	77(.08)	---	---	5(.02)	---
Caulerpa cupressscides	15(.02)	8(.009)	2(.002)	---	---
Caulerpa racemosa	7(.007)	7(.008)	---	3(.01)	28(.09)
Caulerpa sertularioides	16(.02)	12(.01)	7(.006)	---	---
Centroceras clavulatum	15(.02)	44(.05)	1(.0008)	214(.70)	46(.15)
Cladophora fascicularis	---	---	---	1(.003)	---
Cladophoropsis membranacea	80(.08)	70(.08)	14(.01)	104(.34)	8(.03)
Coelothrix irregularis	1(.001)	3(.003)	---	---	4(.01)
Crouania attenuata	---	---	---	---	35(.12)
Dictyosphaeria cavernosa	1(.001)	---	---	---	1(.003)
Gelidiella acerosa	---	---	---	---	3(.01)
Gelidium corneum	22(.02)	174(.20)	6(.005)	26(.09)	74(.24)
Halimeda opuntia	574(.60)	388(.24)	238(.20)	---	86(.28)
Halimeda tuna	4(.004)	---	---	---	---
Hypnea spinella	3(.003)	1(.001)	6(.005)	---	---

APPENDIX A

Table A6 (contd.)

	1	2	3	4	5
Laurencia obtusa	19(.02)	2(.002)	73(.06)	139(.46)	130(.43)
Laurencia papillosa	38(.04)	67(.08)	18(.02)	---	1(.003)
Neomeris annulata	---	2(.002)	---	---	---
Padina vickerseae	---	2(.002)	---	---	---
Penicillus capitatus	521(.54)	157(.18)	---	---	---
Struvea anastomosans	---	---	---	6(.02)	---
Valonia ventricosa	1(.001)	---	---	---	1(.003)

APPENDIX A

Table A7

Summary of the benthic algal species present in the study area at Turrumote Reef during September 12 and 19, 1979. Left side value represents the total number of squares where the species was present; ( ) represents the % of occurrence for the transect.

	1	2	3	4	5
Amphiroa fragilissima	2(.002)	---	---	---	2(.007)
Amphiroa rigida	21(.02)	9(.01)	---	---	---
Caulerpa racemosa	---	---	---	---	10(.03)
Caulerpa sertularioides	1(.001)	---	---	---	---
Centroceras clavulatum	5(.005)	---	1(.001)	---	8(.03)
Crouania attenuata	---	---	---	---	1(.003)
Gelidium corneum	11(.01)	7(.008)	1(.001)	---	21(.07)
Halimeda opuntia	115(.12)	36(.04)	1(.001)	---	46(.15)
Laurencia obtusa	---	---	---	---	16(.05)
Laurencia papillosa	2(.002)	---	---	---	2(.007)
Penicillus capitatus	96(.10)	4(.005)	1(.001)	---	---
Trichosolen duchassaingii	930(.39)	506(.58)	1037(.99)	181(.94)	219(.72)

APPENDIX A

Table A8

Summary of the benthic algal species present in the study area at Turrumote Reef during October 3, 1979. Left side value represents the total number of squares where the species was present; ( ) represents the % of occurrence for the transect.

	1	2	3	4	5
Amphiroa fragilissima	5(.005)	---	---	---	4(.01)
Caulerpa racemosa	---	---	---	---	8(.03)
Centroceras clavulatum	---	---	---	---	150(.49)
Cladophoropsis membranacea	---	---	---	---	20(.07)
Coelothrix irregularis	---	---	---	---	1(.003)
Crouania attenuata	---	---	---	---	11(.04)
Enteromorpha flexuosa	---	32(.04)	---	---	---
Gelidium corneum	9(.01)	2(.002)	---	---	27(.09)
Halimeda opuntia	13(.01)	12(.01)	---	---	70(.23)
Laurencia obtusa	---	---	---	---	94(.31)
Laurencia papillosa	---	---	---	---	1(.003)
Penicillus capitatus	11(.01)	10(.01)	---	---	---
Trichosolen duchassaingii	935(.99)	792(.90)	896(.86)	192(1.0)	216(.71)

APPENDIX A

Table A9

Summary of the benthic algal species present in the study area at Turrumote Reef during October 16, 1979. Left side value represents the total number of squares where the species was present; ( ) represents the % of occurrence for the transect.

	1	2	3	4	5
Acanthophora spicifera	1(.001)	---	---	---	---
Amphiroa fragilissima	31(.03)	---	---	---	102(.34)
Amphiroa rigida	1(.001)	---	---	---	---
Caulerpa cupressoides	1(.001)	---	---	---	---
Caulerpa racemosa	---	---	---	---	12(.04)
Caulerpa sertularioides	2(.002)	---	---	---	---
Centroceras clavulatum	---	---	---	---	226(.74)
Cladophoropsis membranacea	---	---	---	---	64(.21)
Coelothrix irregularis	3(.003)	---	---	---	6(.02)
Crouania attenuata	---	---	---	---	18(.06)
Dictyosphaeria cavernosa	---	---	---	---	4(.01)
Dictyota divaricata	1(.001)	---	---	---	---
Enteromorpha flexuosa	1(.001)	13(.01)	---	---	---
Gelidium corneum	5(.005)	4(.005)	---	---	20(.07)
Halimeda opuntia	54(.06)	19(.02)	---	---	66(.22)
Laurencia obtusa	---	---	---	---	126(.41)
Laurencia papillosa	---	1(.001)	---	---	18(.06)
Liagora seranoides	---	---	---	5(.03)	---

APPENDIX A

Table A9 (contd.)

	1	2	3	4	5
Penicillus capitatus	53(.06)	15(.02)	---	---	---
Trichosolen duchassaingii	934(.99)	831(.94)	1040(1.0)	192(1.0)	---
Valonia ventricosa	1(.001)	---	---	---	3(.01)

APPENDIX A

Table A10

Summary of the benthic algal species present in the study area at Turrumote Reef during October 31 and November 1, 1979. Left side value represents the total number of squares where the species was present; ( ) represents the % of occurrence for the transect.

	1	2	3	4	5
Acanthophora spicifera	4(.004)	---	---	---	3(.009)
Amphiroa fragilissima	45(.05)	---	---	---	132(.43)
Amphiroa rigida	18(.02)	3(.003)	---	---	---
Caulerpa cupressoides	1(.001)	---	---	---	---
Caulerpa racemosa	---	---	---	---	21(.07)
Caulerpa sertularioides	5(.005)	---	---	---	---
Centroceras clavulatum	137(.15)	---	---	---	104(.34)
Cladophoropsis membranacea	---	---	---	---	49(.16)
Coelothrix irregularis	8(.008)	1(.001)	---	---	4(.01)
Crouania attenuata	---	---	---	---	16(.05)
Dictyosphaeria cavernosa	---	---	---	---	2(.007)
Dictyota divaricata	34(.04)	8(.009)	---	---	---
Enteromorpha flexuosa	122(.13)	43(.05)	---	18(.09)	---
Gelidium corneum	9(.009)	---	---	---	67(.22)
Halimeda opuntia	90(.10)	16(.02)	---	---	82(.27)
Herposiphonia tenella	---	---	---	23(.12)	---
Laurencia obtusa	---	---	---	---	138(.45)
Laurencia papillosa	---	1(.001)	---	---	28(.09)

APPENDIX A

Table A10 (contd.)

	1	2	3	4	5
Neomeris annulata	24(.03)	62(.07)	---	---	---
Penicillus capitatus	137(.15)	11(.01)	2(.002)	---	---
Trichosolen duchassaingii	432(.46)	539(.61)	1040(1.0)	---	---
Valonia macrophysa	---	---	---	---	1(.003)
Valonia ventricosa	---	---	---	---	3(.01)

APPENDIX A

Table A11

Summary of the benthic algal species present in the study area at Turrumote Reef during November 20, 1979. Left side value represents the total number of squares where the species was present; ( ) represents the % of occurrence for the transect.

	1	2	3	4	5
Acanthophora spicifera	4(.004)	---	---	---	1(.003)
Amphiroa fragilissima	5(.005)	---	---	---	63(.21)
Amphiroa rigida	11(.01)	7(.008)	---	---	---
Caulerpa racemosa	---	---	---	---	23(.08)
Caulerpa sertularioides	3(.003)	---	---	---	---
Centroceras clavulatum	263(.28)	2(.002)	---	7(.04)	226(.74)
Cladophora fascicularis	14(.01)	---	---	---	---
Cladophoropsis membranacea	---	---	---	---	17(.06)
Coelothrix irregularis	3(.003)	---	---	---	2(.007)
Crouania attenuata	---	---	---	---	21(.07)
Dictyota divaricata	7(.007)	13(.01)	---	---	---
Digenea simplex	1(.001)	---	---	---	---
Enteromorpha flexuosa	336(.36)	250(.28)	288(.28)	16(.08)	1(.003)
Gelidium corneum	10(.01)	1(.001)	---	---	63(.21)
Halimeda opuntia	78(.08)	21(.02)	---	---	76(.25)
Herposiphonia tenella	---	---	---	10(.05)	---
Laurencia obtusa	---	---	---	1(.005)	120(.39)
Laurencia papillosa	23(.02)	---	---	---	---

APPENDIX A

Table A11 (contd.)

	1	2	3	4	5
Neomeris annulata	1(.001)	36(.04)	---	---	---
Penicillus capitatus	96(.10)	27(.03)	---	---	---
Valonia ventricosa	2(.002)	---	---	---	2(.007)

APPENDIX A

Table A12

Summary of the benthic algal species present in the study area at Turrumote Reef during December 5 and 20, 1979. Left side value represents the total number of squares where the species was present; ( ) represents the % of occurrence for the transect.

	1	2	3	4	5
Acanthophora spicifera	5(.005)	---	---	---	1(.003)
Amphiroa fragilissima	11(.01)	2(.002)	---	---	83(.27)
Amphiroa rigida	53(.06)	6(.01)	---	---	---
Caulerpa racemosa	---	---	---	---	31(.10)
Caulerpa sertularioides	5(.01)	---	---	---	---
Chaetomorpha linum	---	---	---	1(.01)	---
Centroceras clavulatum	167(.18)	2(.002)	---	3(.02)	110(.36)
Ceramium nitens	---	---	---	---	4(.01)
Cladophora fascicularis	---	1(.001)	---	---	---
Cladophora sp.	---	---	---	5(.005)	---
Cladophoropsis membranacea	---	---	---	---	18(.06)
Coelothrix irregularis	2(.002)	---	---	---	1(.003)
Crouania attenuata	---	---	---	---	17(.06)
Dictyota divaricata	43(.05)	41(.05)	---	---	---
Ectocarpus breviarticulatus	---	---	---	19(.10)	---
Enteromorpha flexuosa	176(.19)	14(.02	25(.02)	14(.07)	---
Gelidium corneum	11(.01)	4(.01)	---	1(.005)	64(.21)
Halimeda opuntia	139(.14)	16(.02)	1(.001)	---	77(.25)

APPENDIX A

Table A12 (contd.)

	1	2	3	4	5
Laurencia obtusa	4(.004)	1(.001)	---	1(.005)	87(.29)
Laurencia papillosa	26(.03)	5(.01)	---	---	30(.10)
Neomeris annulata	5(.005)	20(.02)	---	---	---
Penicillus capitatus	124(.13)	35(.04)	4(.004)	---	---
Valonia ventricosa	1(.001)	---	---	---	---

APPENDIX A

Table A13

Summary of the benthic algal species present in the study area at Turrumote Reef during January 8, 1980. Left side value represents the total number of squares where the species was present; ( ) represents the % of occurrence for the transect. X = not sampled on that month.

	1	2	3	4	5
Amphiroa fragilissima	1(.001)	---	---	X	69(.22)
Amphiroa rigida	9(.01)	1(.001)	---	X	1(.003)
Caulerpa cupressoides	1(.001)	---	---	X	---
Caulerpa racemosa	2(.002)	---	---	X	10(.03)
Caulerpa sertularioides	1(.001)	---	---	X	---
Centroceras clavulatum	7(.01)	---	---	X	14(.05)
Cladophoropsis membranacea	---	---	---	X	69(.23)
Coelothrix irregularis	2(.002)	---	---	X	1(.003)
Crouania attenuata	---	---	---	X	23(.08)
Dictyosphaeria cavernosa	---	---	---	X	1(.003)
Dictyota divaricata	32(.03)	92(.10)	---	X	---
Ectocarpus breviarticulatus	---	---	---	X	2(.007)
Enteromorpha flexuosa	28(.03)	16(.02)	---	X	---
Gelidium corneum	10(.01)	---	---	X	43(.14)
Halimeda opuntia	107(.11)	13(.01)	4(.004)	X	84(.28)
Laurencia obtusa	1(.001)	---	---	X	1(.003)
Laurencia papillosa	2(.002)	---	---	X	60(.20)
Neomeris annulata	12(.01)	8(.01)	---	X	---

APPENDIX A

Table A13 (contd.)

	1	2	3	4	5
Penicillus capitatus	59(.06)	13(.01)	1(.001)	X	----
Valonia ventricosa	3(.003)	---	---	X	1(.003)

APPENDIX A

Table A14

Summary of the benthic algal species present in the study area at Turrumote Reef during February 4, 1980. Left side value represents the total number of squares where the species was present; ( ) represents the % of occurrence for the transect.

	1	2	3	4	5
Amphiroa fragilissima	4(.004)	---	---	---	61(.20)
Amphiroa rigida	7(.007)	1(.001)	---	---	---
Caulerpa racemosa	2(.002)	---	---	---	2(.007)
Caulerpa sertularioides	3(.003)	---	---	---	---
Centroceras clavulatum	6(.006)	---	---	2(.01)	69(.23)
Cladophoropsis membranacea	---	---	---	3(.02)	82(.27)
Crouania attenuata	---	---	---	---	37(.12)
Dictyota divaricata	4(.004)	111(.13)	---	---	---
Ectocarpus breviarticulatus	---	---	---	16(.08)	---
Enteromorpha flexuosa	24(.03)	51(.06)	288(.28)	13(.07)	---
Enteromorpha sp.	---	---	3(.002)	---	---
Gelidium corneum	5(.005)	1(.001)	---	---	65(.21)
Halimeda opuntia	80(.08)	10(.01)	---	---	86(.28)
Laurencia obtusa	---	---	---	---	9(.03)
Laurencia papillosa	3(.003)	---	---	---	50(.16)
Neomeris annulata	23(.02)	74(.08)	---	---	---
Penicillus capitatus	23(.02)	16(.01)	1(.001)	---	---

APPENDIX A

Table A15

Summary of the benthic algal species present in the study area at Turrumote Reef during March 7, 1980. Left side value represents the total number of squares where the species was present; ( ) represents the % of occurrence for the transect. X = not sampled on that month.

	1	2	3	4	5
Amphiroa fragilissima	---	1(.001)	---	X	39(.13)
Amphiroa rigida	10(.01)	1(.001)	---	X	---
Caulerpa racemosa	___	---	---	X	2(.007)
Centroceras clavulatum	32(.03)	7(.08)	---	X	41(.13)
Ceramium nitens	---	---	---	X	1(.003)
Cladophoropsis membranacea	---	---	---	X	44(.14)
Crouania attenuata	---	---	---	X	50(.16)
Dictyota divaricata	7(.01)	165(.19)	---	X	---
Enteromorpha flexuosa	79(.08)	48(.05)	177(.17)	X	---
Gelidium corneum	6(.006)	---	---	X	30(.10)
Halimeda opuntia	71(.08)	10(.01)	---	X	87(.29)
Laurencia obtusa	---	---	---	X	20(.07)
Laurencia papillosa	---	---	---	X	39(.13)
Liagora sp.	---	2(.002)	---	X	---
Neomeris annulata	113(.12)	174(.20)	---	X	---
Penicillus capitatus	18(.02)	9(.01)	---	X	---
Wrangelia argus	---	---	---	X	1(.003)

APPENDIX B

Table B1

Field records of temperature in °C as registered at Station A in Turrumote Reef from April, 1979, to March, 1980.

Hour	April	May	June	July	August	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March
00:00	24	27	26	27	27.5	28	28	28.5	26	25.5	25	24
03:00	24	27.5	26	--	28	26.5	28	--	26	25	24	--
06:00	24	27.5	26	27	27.5	26	27.5	28.5	26	25	24	24.5
09:00	25	27.8	26.5	27.5	28.5	27	28	29.5	26.5	25	25	25
12:00	27	20	27.5	28	20	28	20	20	28	26	27	27
15:00	28	29	28	28	29	28	29.5	31	27.5	26.5	29	27.5
18:00	25	28.5	27	27	29	27	28.5	30	27	25	27	25.5
21:00	24.8	17	17	--	28	27	28	29	26	25.5	25	25

APPENDIX B

Table B2

Field records of temperature in °C as registered at Station B in Turrumote Reef from April, 1979, to March, 1980.

Hour	April	May	June	July	August	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March
00:00	24.5	26.5	26	27	27	26	27	28	26	24	24	24.5
03:00	23.5	27	26	--	27	26	27	--	26	24.5	24	--
06:00	23.5	27	25.5	27	27.5	26	27	28	26	24.5	24	24.5
09:00	25	28	26	27.5	29	27	28	28.5	26.5	25	25	25
12:00	29	31.5	28	29	31	28.5	30	30	28	26	27	27
15:00	30.5	33	29	28.5	30	28.5	31	31	28	26	28.5	27
18:00	25.5	30.5	28	27	29	27.5	29	30	27	24.5	26	25.5
21:00	24.5	27.8	26	--	28	26.5	28	29	26.5	24.5	25	24.5

APPENDIX B

Table B3

Field records of temperature in °C as registered at Station C in Turrumote Reef from April, 1979, to March, 1980.

Hour	April	May	June	July	August	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March
00:00	25	27.5	27	27	28	26.5	28	28	26.5	24.5	25	25
03:00	25	27.8	26.5	--	28	27	28	--	26.5	15	25	--
06:00	25	27.5	26.5	27.5	28	26.5	28	28	26	25	24.5	25
09:00	25.8	28	26.5	28	28.5	27	29	29	27	25	25.5	25
12:00	27.5	29	28	28	29	27.5	29	30.5	27.5	25.5	27.5	26
15:00	27.8	28.3	27	28	29	27	29	30	27	26	28	26
18:00	26.5	27	27	28	28.5	27	28	29	27	28	25.5	25
21:00	25	27.5	27	--	28	26.5	28	28	27	25	25	25

APPENDIX B

Table B4

Field records of oxygen in ppm as registered at Station A in Turrumote Reef from April, 1979, to March, 1980

Hour	April	May	June	July	August	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March
00:00	9.5	5.8	6.6	5.7	4.8	5.0	4.6	5.8	4.2	6.5	4.5	6.1
03:00	7.8	7.0	6.3	--	4.7	4.4	4.4	--	4.5	5.6	4.3	--
06:00	7.8	7.6	5.6	5.1	4.3	4.7	4.6	5.9	4.7	5.3	3.8	6.8
09:00	7.8	9.6	7.2	7.0	6.8	7.6	6.9	7.2	6.1	6.6	6.1	7.5
12:00	9.4	11.4	8.7	8.1	8.6	7.6	8.2	8.9	6.7	6.8	7.5	8.2
15:00	8.4	10.1	8.8	6.6	6.8	7.2	7.5	9.3	7.0	6.9	8.8	9.3
18:00	8.8	8.8	7.6	6.4	6.1	6.5	5.6	6.9	5.5	6.0	7.0	7.1
21:00	10.0	6.6	6.1	--	4.9	5.4	4.0	6.2	4.7	6.4	4.8	6.5

APPENDIX B

Table B5

Field records of oxygen in ppm as registered at Station B in Turrumote Reef from April, 1979, to March, 1980.

Hour	April	May	June	July	August	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March
00:00	8.3	4.8	5.1	6.1	4.3	3.1	3.0	3.5	3.5	5.5	3.9	5.1
03:00	7.4	5.4	4.9	--	3.9	2.8	2.7	--	4.3	5.3	3.6	5.0
06:00	6.7	6.8	5.2	4.7	3.6	3.0	2.9	3.8	4.7	5.6	4.1	5.9
09:00	9.5	11.3	10.6	8.4	7.2	7.9	9.4	7.8	5.9	6.5	5.5	7.9
12:00	12.0	12.8	12.4	10.0	8.5	7.5	13.8	10.0	7.4	4.5	7.2	9.3
15:00	9.3	11.3	10.0	7.9	7.4	7.3	12.9	9.6	7.1	7.5	7.6	8.8
18:00	10.0	8.8	8.1	7.1	6.1	5.6	8.0	6.2	5.4	6.2	6.4	7.5
21:00	9.6	5.0	5.3	--	4.4	3.3	3.4	3.9	4.2	6.0	4.3	5.3

APPENDIX B

Table B6

Field records of oxygen in ppm as registered at Station C in Turrumote Reef from April, 1979, to March, 1980.

Hour	April	May	June	July	August	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March
00:00	9.6	7.2	7.1	4.9	5.1	5.1	5.4	4.3	4.1	5.4	4.6	6.5
03:00	8.9	7.9	7.0	--	5.2	5.0	5.3	--	4.8	5.2	4.8	--
06:00	8.5	8.5	7.1	5.8	5.4	5.4	5.8	6.0	5.7	5.8	4.8	6.4
09:00	9.4	10.0	7.1	7.9	6.3	6.1	5.6	6.2	6.0	6.2	5.4	6.9
12:00	8.6	9.9	11.8	8.3	6.5	5.5	5.9	7.1	6.1	6.3	5.0	7.0
15:00	7.5	8.8	8.7	6.6	6.2	5.8	6.2	6.9	5.9	6.0	5.4	6.7
18:00	8.2	7.2	7.9	5.7	5.7	5.6	5.4	5.1	5.8	5.9	4.9	5.9
21:00	9.9	8.0	7.9	--	5.6	5.2	5.6	4.9	5.2	5.4	4.6	6.1

APPENDIX B

Table B7

Field records of salinity in o/oo as registered at Station A in Turrumote Reef from April, 1979, to March, 1980.

Hour	April	May	June	July	August	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March
00:00	35	35.5	35.5	34	35.5	34	35	36	36	36	35	35
03:00	36.3	36.3	35	--	35	34	35	--	36	35.5	35	--
06:00	36	37	35.5	34	35.5	35	35	35	37	35.5	34	35.5
09:00	35.3	35.3	36	34	35	34	35.5	35.5	37	35	34.5	36
12:00	37.5	36	35.5	34	34	34	34.5	37	34	36	34.5	36
15:00	37.5	35.8	35.5	34	35	34.5	36	36.5	35	36	35.5	35.5
18:00	34	35	35.5	35.5	35	34	36	36	35	36	34.5	35
21:00	35.5	35	35.5	--	34	35	35.5	35.5	34.5	36.5	34	35.5

APPENDIX B

Table B8

Field records of salinity in o/oo as registered at Station B in Turrumote Reef from April, 1979, to March, 1980.

Hour	April	May	June	July	August	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March
00:00	35	35	36	34	36	34	36	35.5	35.5	36	35	35
03:00	35.8	36	36	--	36	34	36	--	35.5	35	35	--
06:00	36	35	35.5	34	36	34	35.5	36	37	35	35.5	35.5
09:00	36.3	34.8	35.5	34	36	34	36.5	36.5	36.5	34.5	35.5	36.5
12:00	39	36	35.5	34	35	34	37	36	35.5	34	36	36
15:00	39.5	36	36	36	36	34	36	36	35	34.5	36	35
18:00	35	36	36	36	36	34	36	36	34.5	35.5	34	36
21:00	35.3	35.8	35.5	--	35	34	36	36	35	35.5	34.5	36

APPENDIX B

Table B9

Field records of salinity in o/oo as registered at Station C in Turrumote Reef from April, 1979, to March, 1980.

Hour	April	May	June	July	August	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March
00:00	36	36	35.5	34	35.5	35	36	35	35	35.5	34.5	34.5
03:00	36.8	35.8	35.5	—	36	34	34	—	36	35	34.5	—
06:00	36	35	35.5	34.5	36	35	35.5	35	37	36	35	34.5
09:00	36.8	34.3	35.5	35	36	34.5	36.5	35.5	36.5	36.5	34.5	34.5
12:00	38	35	35	35.5	35	35	36	35	34.5	36	35.5	35
15:00	37.3	35.3	35.5	35	34	35	36	36	35	36	35	35
18:00	35	36	35.5	35	35	35	36	35.5	35	36	34.5	35
21:00	36	35.5	35.5	—	35.5	35	36.5	35.5	35	36	34	35

APPENDIX C

Table C1

Maximum and minimum monthly dissolved oxygen saturation values in % as obtained at Stations A, B, C in Turrumote Reef from April, 1979 to March, 1980.

Month	A	B	C
April	147.1 111.4	196.7 97.1	150.0 112.7
May	181.3 89.2	214.3 69.2	160.9 109.2
June	137.5 83.5	187.5 73.1	181.5 106.1
July	126.6 77.3	158.7 74.6	127.7 77.8
August	138.7 66.2	139.3 55.4	101.6 81.0
September	116.9 65.7	119.7 41.2	92.4 75.8
October	132.3 68.8	226.2 41.5	98.4 81.5
November	155.0 92.2	161.3 54.7	116.4 67.2
December	106.1 62.7	113.9 52.2	92.4 62.1
January	104.6 77.9	110.3 76.8	94.0 76.5
February	139.7 54.3	120.6 52.2	79.4 67.7
March	140.9 88.4	140.9 73.9	104.5 85.5

APPENDIX C

Table C2

Biogenic composition in % of sediment samples 1 to 10 collected at Turrumote Reef in March, 1979.

Sample #	1	2	3	4	5	6	7	8	9	10
Foraminiferans	.7	.8	-	-	-	8.52	2.4	2.4	7.43	1.6
Spicules	-	-	-	-	.8	6.98	-	1.6	5.72	.8
Bryozoan	.7	-	-	-	-	-	-	-	-	-
Molluscan	3.2	3.2	1.6	3.96	2.41	2.32	2.4	.8	1.65	.8
Coral and coralline algae	32.8	71.2	87.2	48.41	67.74	47.30	47.2	80.8	51.24	88.0
Halimeda	56.35	22.2	9.6	46.44	26.61	28.68	45.6	13.6	29.75	8.0
Crustacean	-	8	1.6	-	-	.77	.8	-	.82	-
Echinoderm	2.38	1.6	-	1.6	1.6	2.32	1.55	1.6	2.38	-
Calcareous worm tube	2.38	-	-	1.6	-	.77	-	-	-	.8
Scaphopod	1.50	-	-	-	-	-	-	-	.82	-
Ostracod	-	-	-	-	-	-	-	-	-	-
Pteropod	-	-	-	-	.80	1.55	-	-	-	-