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Ecology of the Imported Red Seaweed *Eucheuma striatum* Schmitz on Coconut Island, Oahu, Hawaii[1]

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ABSTRACT: The introduced alga *Eucheuma striatum* Schmitz was studied regarding its spread, control, and ecology in Kaneohe Bay, Oahu, Hawaii. Its distribution in Kaneohe Bay during May 1976 was nearly the same as when it was originally planted 2 yr earlier. It lacked the ability to disperse over shallow depressions both in the reef and in deep water, and it did not colonize neighboring reefs without the help of man. Depth was the single most important physical factor limiting its dispersal. A total fresh weight standing crop of from 21 to 24 metric tons of *E. striatum* was recorded on a 500-m-long section of reef edge from December 1976 to June 1977. When protected from grazing its growth rate was about 5.0 percent/day. Data support the conclusion that the population on the reef edge was maintained only by a steady influx of thallus fragments that escaped from enclosed experimental plantings on the reef flat. When the experimental plantings were removed the population could not maintain itself and soon disappeared. *Eucheuma striatum* did not compete with native algal macrophytes and appeared to be the basis of a community richer in animal species than adjacent reefs. It provided 10–20 tons/mo of food for grazing fish, shelter, and a substratum for numerous invertebrates. *Eucheuma striatum* did not attach to corals, but it did cause their death by shading.

THE INTRODUCTION OF ALIEN SEAWEEDS to Hawaii probably occurs regularly. Some have been introduced accidentally by ship (Doty 1961), others for commercial and experimental purposes (Doty 1978). In all, at least 17 species of alien marine algae have come to Hawaii since World War II (Russell 1981). One particular kind of *Eucheuma striatum* Schmitz was imported on 9 September 1974 for scientific experiments in the field (Doty 1977). This large, smooth, erect alga (Figure 1) was discovered by a Filipino seaweed farmer on a reef near Sitang Kai, Sulu Province, Philippines, and is sometimes referred to as *tambalang* (Fortner 1978, Glenn and Doty 1981), apparently after the name of the farmer who found it. In this article it will be called simply *Eucheuma*.

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Once in Hawaii *Eucheuma* was planted in several locations, particularly on nets and in wire holding pens on the northwestern reef bordering Coconut Island in Kaneohe Bay, Oahu (Figure 2). It grew rapidly and was exceedingly prolific, even without cultivation. Indeed, the population of *Eucheuma* grew so rapidly it began to alarm the public and came to the notice of scientists at the Hawaii Institute of Marine Biology (HIMB) located on Coconut Island (McGlinn 1976*a*). On 23 October 1976 a group of 50 volunteers removed about 4 tons of the estimated 50 tons of seaweed on Coconut Island (McGlinn 1976*b*). The concern was that it might continue to grow and spread, disrupt the balance in the food web, and trigger unpredictable changes in the fragile environment of the Hawaiian reefs (Griffin 1977).

Nevertheless, while some people were trying to prevent the spread of *Eucheuma*, others were transplanting the alga to new locations on Oahu and filing for permits to raise it in ponds and on reefs (Tune 1976, Hunter 1978).

The introduction of *Eucheuma* to Hawaii is

FIGURE 1. *Eucheuma striatum* Schmitz from Coconut Island reef-edge population.

a unique occurrence but similar in some respects to the introduction of *Sargassum muticum* (Yendo) Fensholt to the Pacific coast of the United States and Canada (Scagel 1956) and to Great Britain (Farnham, Fletcher, and Irvine 1973); and to the introduction of *Codium fragile* subsp. *tomentosoides* (Van Goor) Silva to the Atlantic coast of the United States (Bouck and Morgan 1957) and Europe (Farnham 1980, Silva 1957). Each was introduced in conjunction with a marine aquaculture project, and each spread into the surrounding environment. The introduction of *Eucheuma* differs, however, because it was introduced for its own cultivation (Doty 1978), while *Sargassum* and *Codium* were incidental introductions associated with the transplanting of oysters from Japan and other locations. In each case man appears to be the most important influence in the dispersal of these alien algae. Man may also be the most important dispersing agent for *Eucheuma* in Hawaii.

When the present research was started little was known about the ecology of the form of *Eucheuma striatum* which had been introduced. It did have an important biological limitation, however. Apparently, *Eucheuma* could reproduce only by vegetative fragmentation. The following hypothesis therefore was proposed: Any physical or biological factor that limits the dispersal of viable vegetative fragments will also prevent the invasion of new territory by *Eucheuma*. Two additional aspects of *Eucheuma* were also studied: its effect on the reef animals and its competitive effects on algae already established on the reef.

MATERIALS AND METHODS

Surveys on Coconut Island and adjacent reefs in Kaneohe Bay were initiated in May 1976 (Figure 2). While being towed beside a motor boat in water 2–3 m deep, I surveyed the extent of the population, and then with SCUBA I determined the distribution of the thalli in deeper water. These surveys were

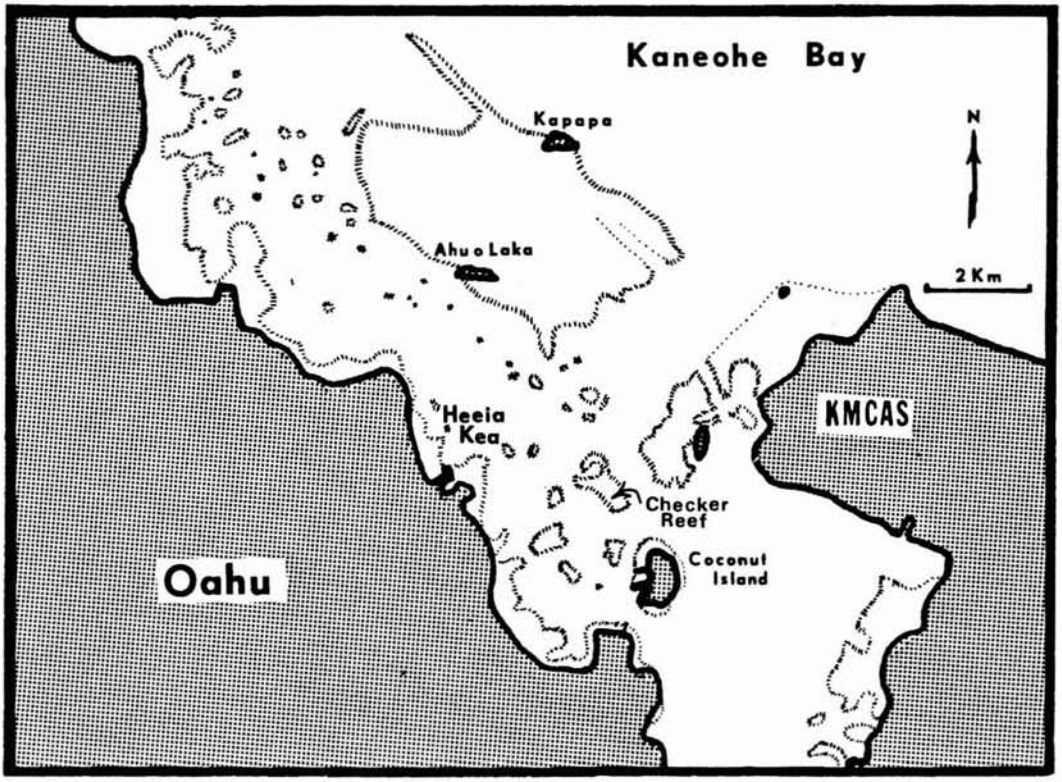

FIGURE 2. Coconut Island, situated in Kaneohe Bay on the Island of Oahu, Hawaii.

repeated intermittently from March 1976 to July 1978.

Quantitative samples were taken using a 46-cm-diameter ring inside of which all the *Eucheuma* was harvested and weighed while still fresh. One sample was taken at each depth—1, 2, and 4 m—at five locations, at approximately 3 mo intervals from December 1976 to March 1978.

An estimate of how much *Eucheuma* was leaving the experimental area located on the reef flat was obtained by removing and weighing the fragments that were caught in a 250-m-long Griff Net, Type NG, 2-cm-mesh size (Griffolyn Co., Inc., Houston, Texas). This net was installed on 1 October 1976, 18 mo after *Eucheuma* was planted on the reef. It was placed in a semicircle downstream from the two largest experimental plantings. These plantings were part of a research project directed by M. S. Doty and were separate experiments indirectly related to the present study.

The sizes of fragments left behind after workers handled *Eucheuma* in the experimental areas were determined by duplicating their efforts, not on the reef but in a flat-bottomed boat. The boat was loaded with thalli and the thalli transferred into rice bags. The pieces that had broken off, and which the workers would normally allow to be washed away, were gathered from the bottom of the boat and each piece weighed individually on an Ohaus triple-beamed balance.

The sinking rates of *Eucheuma* fragments were determined by timing the descent of various branched and unbranched pieces in calm seawater. The sinking rates were compared statistically by converting the weights to $\log_{10}$ and calculating the linear regression of branched and unbranched fragments separately.

The regeneration of branch tips into larger branched thalli was evaluated by placing 100 2-by-5-mm tips into a 20-cm diameter translucent cylinder, which had both ends covered by 1-mm-mesh fiberglass screens. The cylinder was placed in the field and the lengths of the pieces measured once a week for 8 wk. Statistical Package No. 194, Wang Industries, Inc., was used to determine daily growth rates.

Current patterns across the reef flat were determined by following nine drifting 1-gal plastic bottles nearly full of seawater. Currents in deeper water were determined by tracing the path of a methylene blue dye cloud along a meter stick held at various depths. Light intensity was measured with a Seconic Auto-Lumi L-86 light meter in an underwater housing. The light meter was calibrated with a General Electric Model 8DW58Y4 exposure meter. Temperature fluctuations were measured by Taylor maximum–minimum thermometers. Water motion was measured with calcium sulfate blocks (Doty 1971). Dissolved oxygen was determined by the Winkler method (Strickland and Parsons 1972). Standard *t* tests were used to analyze the data.

The growth and survival of *Eucheuma* thalli along the reef edge and at various depths were investigated in several ways. A polypropylene lead-weighted line (50 m long, 1 cm diameter) was anchored on Coconut Island and extended across the channel bottom to the reef located directly to the west. The line was attached to concrete blocks at 3-m intervals, and two thalli of *Eucheuma* were attached to each block until the greatest depth (ca 17 m) was reached, about two-thirds the distance across the channel. The thalli were weighed before being attached to the line and were weighed again 37 and 44 days later.

In another experiment, the same line was moved 2 m north (to avoid the shade of a rock), and four more thalli were tied to the line and weighed once a week for 4 wk. Growth rates for the two experiments were compared.

The significance of both depth and grazing on the survival of *Eucheuma* was tested by placing thalli inside and outside of four polyvinylchloride covered wire-mesh cages (mesh size 2.5 cm) placed at 0.5, 2.0, 6.0, and 12.0 m depths and secured to the reef. Four preweighed thalli were fastened to a length of insulated wire and placed diagonally through the center of each of the cages 30 cm above the cage floor. Four more thalli were placed on a wire outside of the cage 30 cm above the floor. The thalli were weighed every 5 days for 30 days. Analysis of covariance was used to test the significance of the data, and the differences in growth rates were compared by a *t* test.

Four unbranched thallus fragments were taken from the reef edge and placed in a protective pen at the north end of Coconut Island. They were allowed to grow there for 1 mo, photographed, placed on the reef edge for 3.5 hr, and retrieved and photographed again.

A 10-m length of the reef was cleared of all *Eucheuma* fragments to a depth of 12 m. A fence of Griffolyn netting was erected around the cleared area to prevent more fragments from entering and to prevent the fragments that were placed in the clearing from leaving. A 4-mm-diameter polypropylene line was attached to concrete blocks at the corners of the clearing and down the slope. Repeated inspection with SCUBA assured against fragments' intrusion into or loss from the experimental area.

Thalli were gathered from a protected area and placed in the shallow northern corner of the clearing. Thirty kilograms of thalli were allowed to drift into the clearing and remain there for 3 days. Their final positions were mapped before the pieces were gathered and weighed. The same procedure was repeated using 180 kg of thalli, but they were allowed to remain in the clearing for 74 days.

The effects of fish grazing were further studied by capturing the fish that were swimming in the *Eucheuma* and examining the contents of their guts. Algae in the gut were identified, counted, and measured.

Interactions between *Eucheuma* and local algae and invertebrates were noted during the surveys. Some of the interactions were photographed with Ektachrome 135, ASA 160, and Panatomic X, ASA 32, film and a Yashica Electro 35 camera. Quantitative data for determining species diversity were obtained

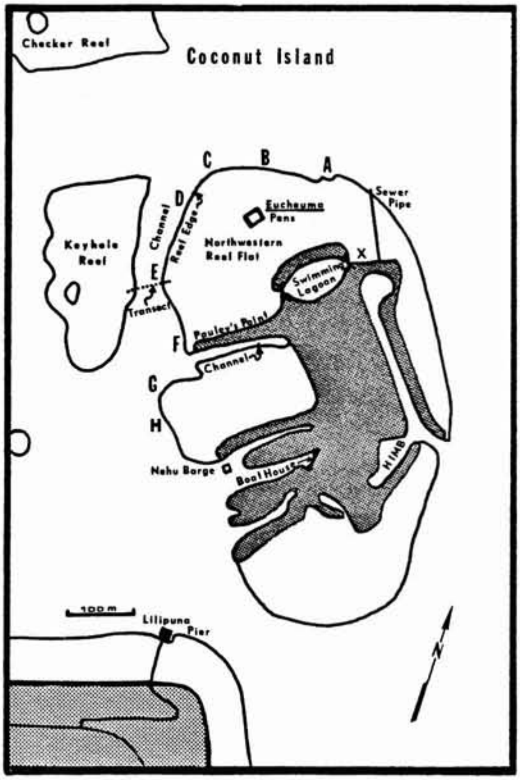

FIGURE 3. Locations of the sampling positions, experimental areas, and transects on Coconut Island. A protected area (*X*) was used for regeneration experiments.

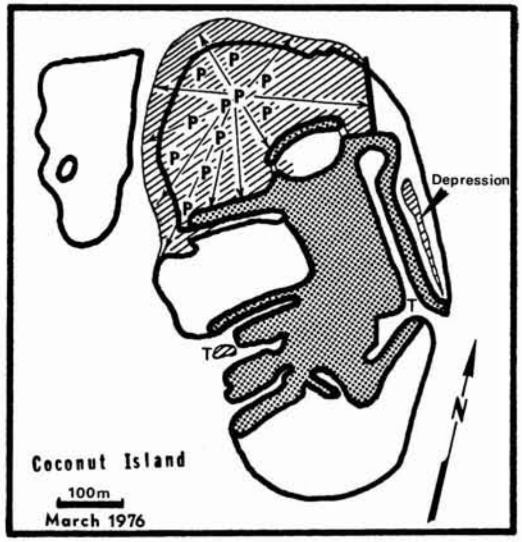

FIGURE 4. The maximum distribution of *Eucheuma* on Coconut Island. The letters *P* indicate where *Eucheuma* was originally planted, and the hatching indicates the maximum distribution. A *T* indicates a transplant location.

by sampling with the ring method. A 46-cm-diameter metal ring was placed over the *Eucheuma* or substratum, and the algae and animals within it gathered by hand. Five ring samples were taken on each of two sections of the reef (Figure 3): at *D* among *Eucheuma* and at *H* where there were no *Euchema* thalli. All of the macroscopic algae and invertebrates, except corals, were gathered and counted.

RESULTS AND DISCUSSION

Distribution of Eucheuma on Coconut Island, 1976 to 1978

In March 1976 *Eucheuma* was located across the entire reef flat and along the reef edge at the northern end of the island (Figure 3) and was distributed 120° southwest around part of the island (Figure 4). Several tons of *Eucheuma* thalli were also located in depressions. *Eucheuma* fragments also were found inside a manmade seawater swimming lagoon near the lagoon's southwestern entrance (Figure 4).

Thallus pieces were found distributed along the reef edge and down slope to a depth of 5–17 m (Figure 5*A*). Loose fragments were located two-thirds of the way across a channel, but only to where the channel reached its maximum depth. Unattached fragments of *Eucheuma* were also found in shallow water (Figure 5*A*), but only in a limited area along the reef edge. The thalli found farthest away from the plantings were also the deepest.

The distribution of fragments in the channel was in the shape of a trapezoid (Figure 5*A*). This pattern would be expected if the fragments were being dispersed simply at random from the top of the underwater slope at the reef edge to the channel bottom. It appeared that the alga spread into deep water and stopped. Thalli were not present beyond the deepest portion of the channel, and no

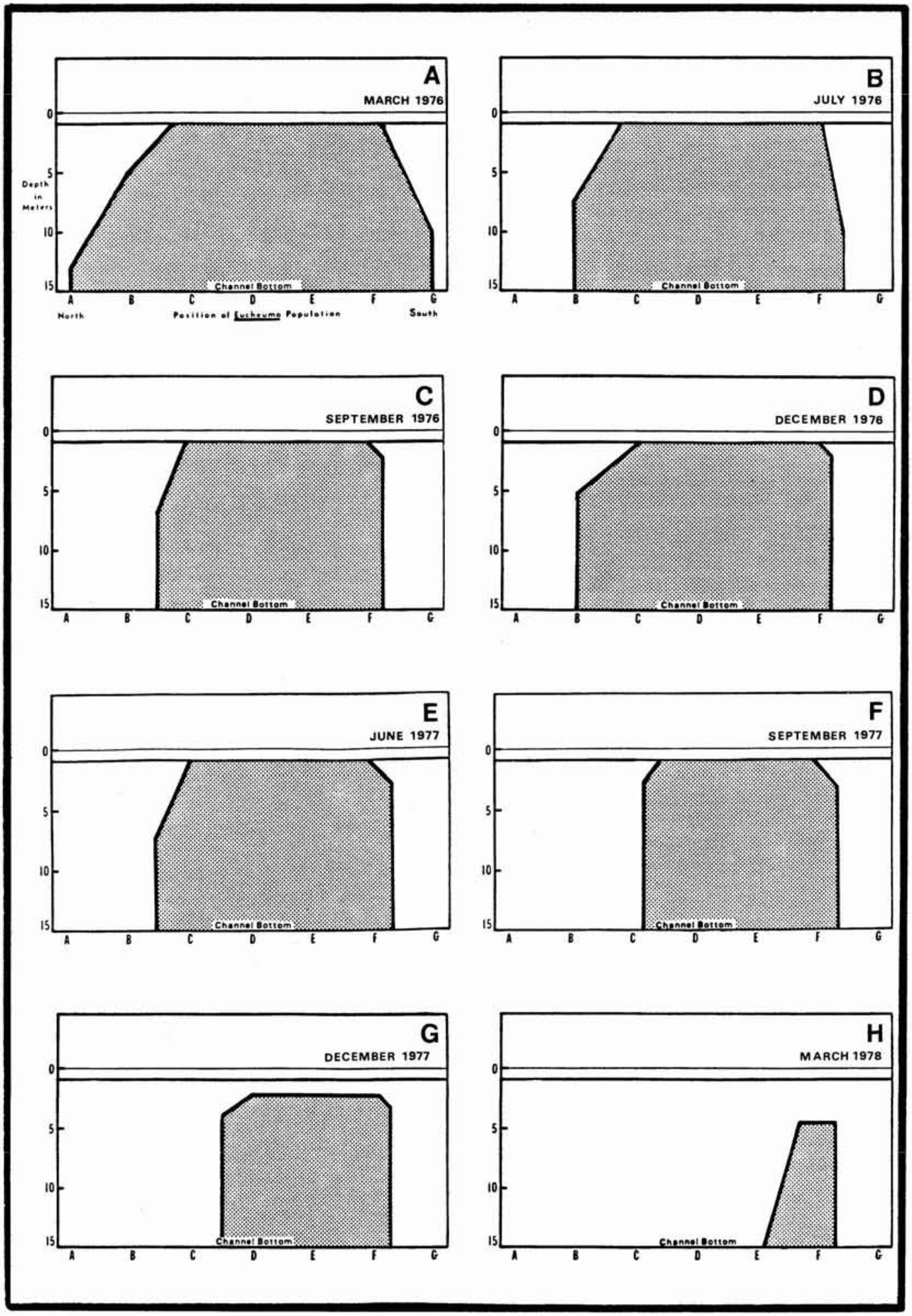

FIGURE 5. Presence of *Eucheuma* fragments on the reef edge and channel slope. The letters *A–H* correspond to the same positions indicated in Figure 3. The surface of the graph represents the face of the reef slope from the edge of the reef flat to the maximum depth of the channel (ca 17 m), between Coconut Island and Keyhole Reef. Exact dates are (*A*) 20 March 1976, (*B*) 13 July 1976, (*C*) 14 September 1976, (*D*) 10 December 1976, (*E*) 3 June 1977, (*F*) 10 September 1977, (*G*) 14 December 1976, (*H*) 20 March 1978.

TABLE 1

AMOUNTS OF *Eucheuma* ON THE REEF EDGE OF COCONUT ISLAND (KG)

	DECEMBER 1976 DEPTH (m)			JUNE 1977 DEPTH (m)			SEPTEMBER 1977 DEPTH (m)			DECEMBER 1977 DEPTH (m)		
POSITION	1	2	4	1	2	4	1	2	4	1	2	4
A	0	26	0	0	0	0	0	0	0	0	0	0
B	0	31	26	0	20	3	0	0	21	0	10	0
C	0	34	0	0	46	6	0	17	10	0	0	0
D	4	34	0	0	63	34	0	69	16	0	21	4
E	28	20	9	0	40	33	0	20	1	0	31	9
Total	32	145	35	0	169	76	0	106	48	0	62	13
Sample averages	6	29	7	0			0	21	10	0	12	3
Grand total	212			245			154			75		
Average	14 ± 7.3			16 ± 10.8			10 ± 9			5 ± 5		
× 1,500 m²	21,000 ± 10,950			24,000 ± 16,200			15,000 ± 13,500			7,500 ± 7,500		

thalli or germlings of *Eucheuma* were found on Keyhole Reef (see Figure 4).

In July 1976 a decline in the area of occurrence of thallus fragments was noted (Figure 5*B*). In September 1976 a further decline in distribution had occurred (Figure 5*C*). In October 1976 a Griff Net was installed on the reef to try to stop the flow of fragments from the experimental pens to the reef edge. By December 1976, however, a survey showed the distribution of fragments had increased rather than declined as expected (Figure 5*D*). The results of ring samples indicated there were 22 metric tons, wet weight, of *Eucheuma* on the reef edge and slope (Table 1, Figure 6). In June 1977 the distribution was the same as it had been nearly 1 yr earlier (Figure 5*E*), and the estimated amount of *Eucheuma* had increased to about 24 tons (Table 1).

The experimental pens, which appeared to be the source of the fragments in spite of the Griff Net, and the large *Eucheuma* thalli that were on the reef flat west of position A, were removed later in June 1977. Three months later, in September, the area of occurrence had narrowed (Figure 5*F*), and the biomass had declined to 17 tons (Table 1). By December 1977, 6 mo after the pens had been removed, the entire distribution had narrowed still further and the thalli, which had been in shallow water, had settled 1 m deeper than early in June 1977 (Figure 5*G*). In March 1978 the population of fragments had declined to a fraction of its size 2 yr earlier (Figure 5H), the fragments were not observed in water shallower than 2 m, and the estimated biomass for *Eucheuma* along the reef edge and slope was only 10 kg.

The most extensive distribution of *Eucheuma* appeared in March 1976, 16 mo after the original thalli were placed on the reef (Figures 4, 5). The source of the thalli was the experimental plantings from which fragments drifted with the currents (Figure 7), across the reef to the edge, and into the currents in deeper water (Figure 8).

A map of *Euchuema* distribution showed that the outer boundaries ended abruptly wherever there were shallow depressions or deep water, such as the 2-m-deep shallow channel near Pauley's Point and the 17-m-deep channel between Coconut Island and Keyhole Reef (Figure 4). *Eucheuma* did not cross either channel but accumulated in the hollows and depressions on the reef, especially in the dredged portions near shore.

These data do not imply that *Eucheuma* had completely disappeared from Coconut Island. It was still present on the reef flat after the reef-edge population disappeared, but in much smaller amounts and in sandy areas not occupied by many other forms of marine life.

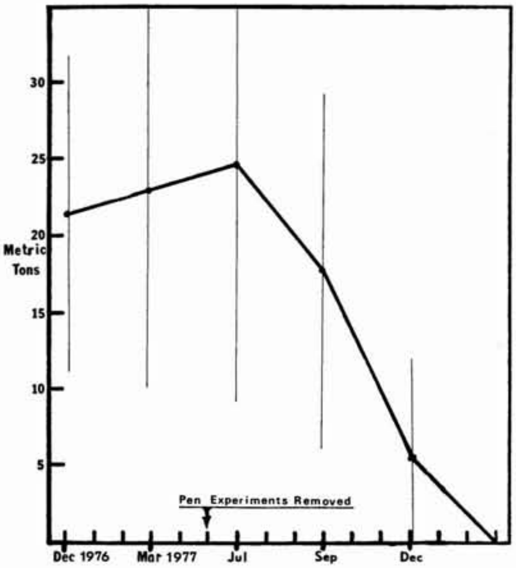

FIGURE 6. The total estimated fresh weight amount of *Eucheuma* present on the northwestern reef edge of Coconut Island as a function of time. Vertical lines represent 95 percent confidence intervals.

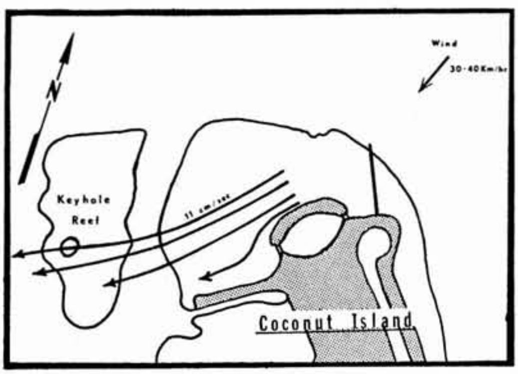

FIGURE 7. The paths taken by drifting bottles across the northwestern reef flat of Coconut Island during a normal trade-wind day.

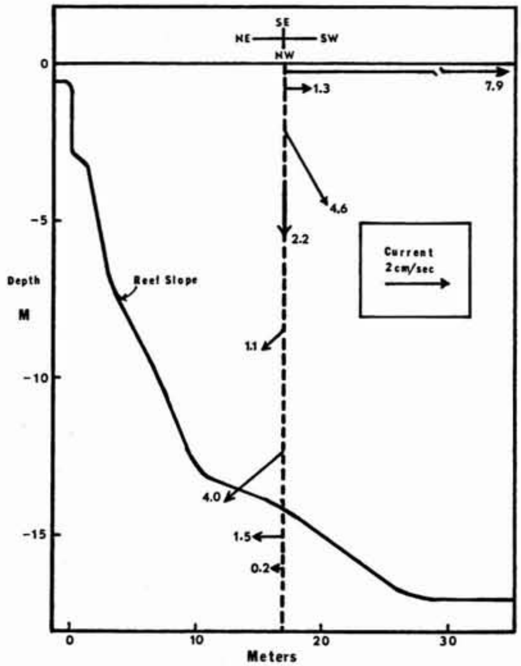

FIGURE 8. Strength and direction of current as a function of depth at position *E* on Coconut Island.

In March 1978, after *Eucheuma* had disappeared from the reef edge, there still were several accumulations of actively growing thalli in depressions on the reef flat. The largest amount that remained was in a depression on the more eastern reef flat (Figure 4). This dredged depression contained an estimated 0.1 tons of *Eucheuma* on 14 December 1976, 3.0 tons on 3 July 1977, 13.0 tons on 12 December 1977, and 13.0 tons again in March 1978. An estimated 0.5 tons also occupied a depression near an unused sewer pipe in March 1978 (Figure 3). Near the northeastern entrance to the swimming lagoon were located 2 tons, and 0.03 ton was located 10 m west of the southwestern entrance to the swimming lagoon.

Dispersal of Eucheuma by Man

When *Eucheuma* was planted on the northwest reef flat of Coconut Island, it grew so rapidly that it attracted the attention of several people not associated with the planned experiments. Some of these people soon became interested in growing the alga for themselves, and transplanted thalli to other areas in Kaneohe Bay (Figure 4). *Eucheuma* grew in each of these places although most of the thallus pieces were eventually removed by hand during the various control efforts.

Eucheuma thalli were planted by fishermen near Heeia Kea in Kaneohe Bay (Figure 2), and a worker on Coconut Island sent some *Eucheuma* to friends in Hilo, Hawaii. About 12 kg was sent to residents at Ewa Beach, Oahu, but the fate of these thalli is not known. Several transplants were made from Kaneohe Bay to an enclosed seawater pond at Kahuku Farms, Oahu.

Eucheuma was sent from Kaneohe Bay to Fiji, Christmas Island, Fanning Island, and other locations in the Pacific. The desirability of *Eucheuma* as a commercial crop inspired marine agronomists to transplant it to five or more countries in the Pacific Ocean within 3 yr of its introduction to Hawaii (Doty 1979, Russell 1983).

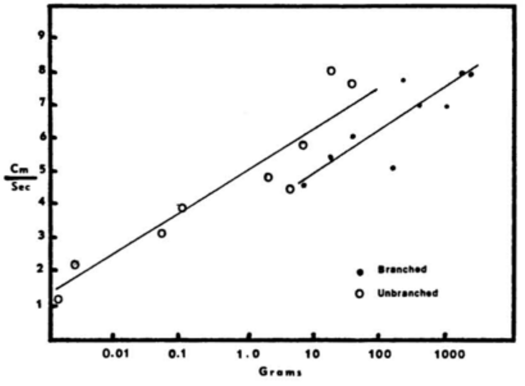

FIGURE 9. Regression of the sinking rates for branched and unbranched *Eucheuma* thalli as a function of size.

Physical Limits to the Spread of Eucheuma

Because this particular kind of *Eucheuma* was not found to produce viable spores in Hawaii, other means of reproduction were investigated. At the tip of each branch this alga has a cluster of apical cells potentially high in regenerative capabilities; they may be able to regenerate new thalli after breaking off from larger thalli. Small size would allow dissemination to greater distances on weaker currents than is true for the bulk of *Eucheuma* found on the reef. Results support the conclusion, however, that this means of dispersal is unlikely.

The slowest sinking rate (1 cm/sec) was with 2-mg apical tips (Figure 9). These fragments did sink slower and would be carried farther by currents than the larger pieces. However, it was found that if these tips were carried by currents and washed over the reef edge they would be moving across the bottom of the reef flat at a depth of 50 cm and already would be in slow-moving currents that would direct them away from neighboring reefs (Figure 8). If they were dropped into a 10-cm/sec surface current, they would be carried only 5 m from the reef edge before sinking 50 cm into slower currents and eventually to the bottom of the channel. It is possible that an extreme current or turbulence could buoy small fragments and carry them farther, but how far and in what direction would be impossible to predict.

The importance of very small fragments would be even more significant to reproduction if they were produced in abundance by the alga. However, small thallus branch tips or pieces, such as those described, were in areas of a harvest. Most of the thalli growing on the reef edge had no small acute tips characteristic of the thalli growing in the experimental pens or in the depressions near land. The reef-edge thalli were gnarled and lacked branches of small diameter, except at their bases.

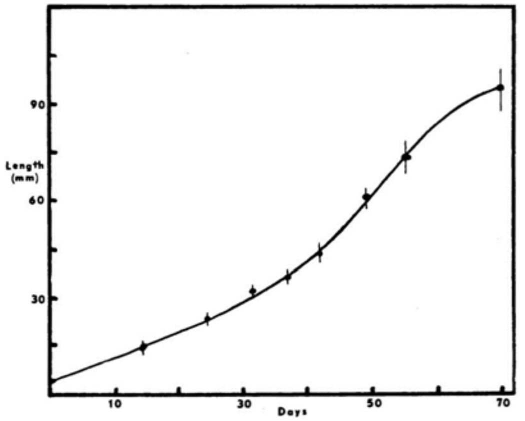

FIGURE 10. Growth curve for the increase in length of 2-by-5-mm *Eucheuma* branch tips.

One hundred apical tips (2×5 mm) were cultured to see if they would grow into full-sized thalli. Only 50 percent survived the first 2 wk (Table 2), and after 10 wk 28 percent were still living and had increased substantially in size. Growth in length of the tips

TABLE 2

GROWTH IN LENGTH OF *Eucheuma* APICAL TIPS

DATE DAYS	31 MAY 0	13 JUNE 13	23 JUNE 23	30 JUNE 30	5 JULY 35	11 JULY 41	18 JULY 48	25 JULY 55	8 AUG 64
Number of tips	100	50	44	42	41	38	32	31	30
Average length (mm)	5 ± 0.0	15 ± 0.7*	23 ± 1.6	31 ± 1.6	36 ± 2.1	44 ± 2.8	61 ± 4.3	75 ± 8.1	95 ± 9.6
Standard deviation	0	2.3	5.4	5.4	6.7	8.7	12.3	23.0	26.7

* Confidence interval of 95 percent.

followed an S-shaped curve with the rate of length increase slowing as girth expanded (Figure 10). The experiment demonstrated that it was possible to obtain full-sized thalli from apical tips in spite of high mortality.

Regeneration in culture, however, apparently has little bearing on survival on the reef. The potential may be present, as was demonstrated with *Codium fragile* (Fralick and Mathieson 1972, Malinowski and Ramus 1973), or as in the Fletcher and Fletcher (1975*a*, 1975*b*) experiments with *Sargassum muticum* fragments, but other factors prevent the realization by *Eucheuma* of this asexual reproduction potential. *Eucheuma* fragments do not form holdfasts, and the most buoyant pieces with regenerative capability are not found on the reef except after a harvest. Thus, there is no evidence that such small pieces are important in the dispersal of this alga. It appears that *Eucheuma* does not have any effective mechanism for dispersal over deep water or out of depressions, hollows, or channels and is unable to colonize neighboring reefs without human help.

The greatest accumulation of *Eucheuma* (23 tons) occurred on the reef edge, but this was not a permanent or established population. It was only a temporary accumulation of fragments that was moving slowly into deeper water unsuitable for its growth. This conclusion is supported by the following evidence.

Approximately 1400 kg/mo was being lost from the thalli in the experimental pens and plantings (Table 3). These thalli moved across the reef flat at 10 m/hr during a normal trade-wind day. They washed over the reef edge and were added to the mass of *Eucheuma* accumulating there. The growth rate of *Eucheuma* thalli in shallow water is 4–5 percent/day (Doty 1977). These data would indicate that 23 tons along the reef edge should increase to about 60 tons in 1 mo. No substantial increase was seen, however (Table 1). The thalli appeared to be healthy, yet 37 tons/mo were not being realized or were disappearing from the reef edge.

TABLE 3

AMOUNT OF *Eucheuma* CAUGHT IN A GRIFF NET LOCATED DOWNSTREAM FROM THE EXPERIMENTAL PENS

Date (42 days)	AMOUNTS GATHERED (kg)	RATE (kg/day)
1 Oct 76	14	
5 Oct 76	18	5
8 Oct 76	182	61
10 Oct 76	109	55
19 Oct 76	23	3
22 Oct 76	27	9
29 Oct 76	109	16
30 Oct 76	182	182
5 Nov 76	209	35
7 Nov 76	134	67
12 Nov 76	151	30
Total	1158	463
Average	105 ± 43.6*	46 ± 32.9†
Standard deviation	73.7	53.1

* Confidence interval of 95 percent.
† 1380 kg/mo.

An experiment was designed to follow the path of fragments that drifted over the reef edge. Thalli (180 kg) were allowed to drift into a cleared portion on the reef edge where they were left undisturbed for 74 days (Figure 11). When they were recovered the total weight (131 kg) was 27 percent less than the original amount released. Of the remaining thalli, 82

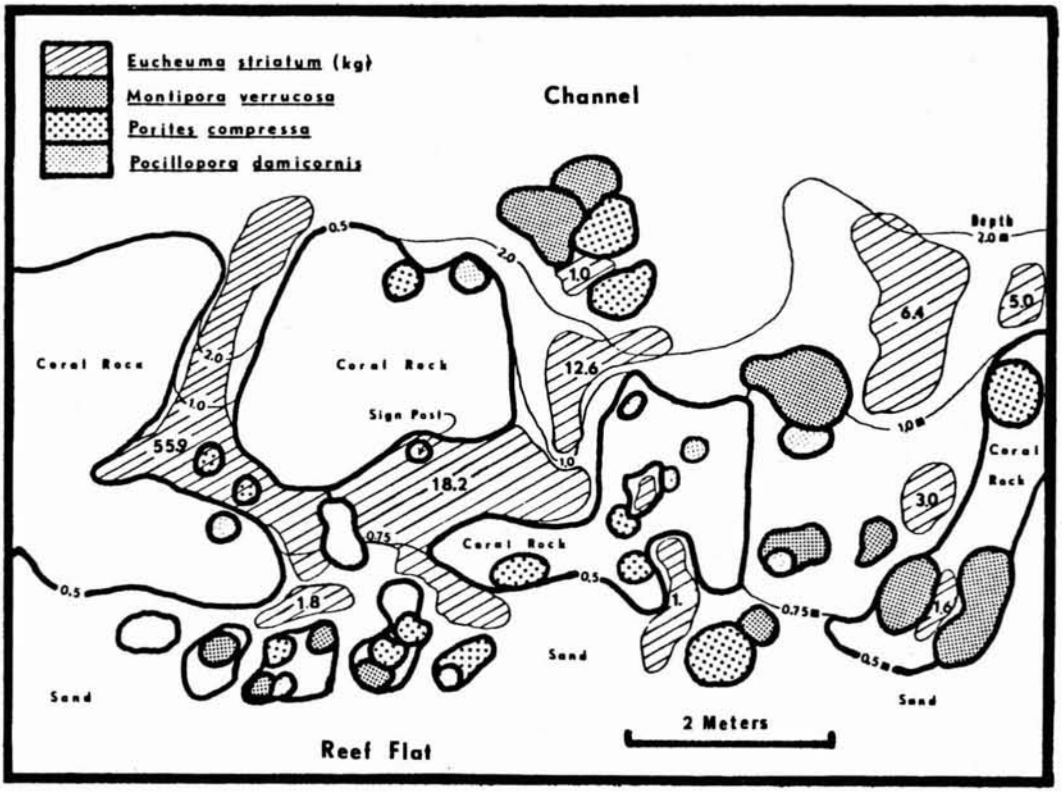

FIGURE 11. Top view of the area at position *E* showing the quantities of *Eucheuma* thalli that remained in the cleared area 74 days after they were released and their relation to rock and coral.

percent were retained between coral heads and rock (Figure 11) and 18 percent had slid down the slope into water deeper than 2 m (Figure 12). None of the surviving pieces had small branches on them, and no small branch fragments were found in the vicinity. The loss of algal material was so great that no net increase in this mass of released *Eucheuma* fragments could be demonstrated.

The *Eucheuma* thalli that drifted into the deep, stagnant channel water did not survive. Thalli were monitored along a transect line to a depth of 16 m (Figure 13): thalli on the channel floor either lost two-thirds their original weight in 37 days or were reduced to decaying masses; thalli 6 to 9 m deep lost weight during the final 17 days; and those at 1 m depth were the only pieces that gained weight during the 54 day experiment (Table 4).

A second similar experiment was more definitive. The transect line was moved 2 m north to avoid the problems of shading by a rock in shallow water. Four thalli on the reef flat averaged 4.3 percent growth per day (Table 5). There was a significant drop in weight for most of the thalli that were between 1.0 and 3.5 m, and thalli below 6 m lost weight (Table 5, Figure 14).

Even though a few healthy looking thalli were found to a depth of 17 m during the surveys, experimental evidence suggests that thalli below 6 m eventually die. The few healthy looking thalli seen on the channel bottom during the surveys may have been recent immigrants that had not yet begun to decay. There was, however, an anomalous decrease in weight between 1 and 3 m depths (Figure 14) which could not be explained on the basis of physical properties that change with depth. The losses were far greater than expected con-

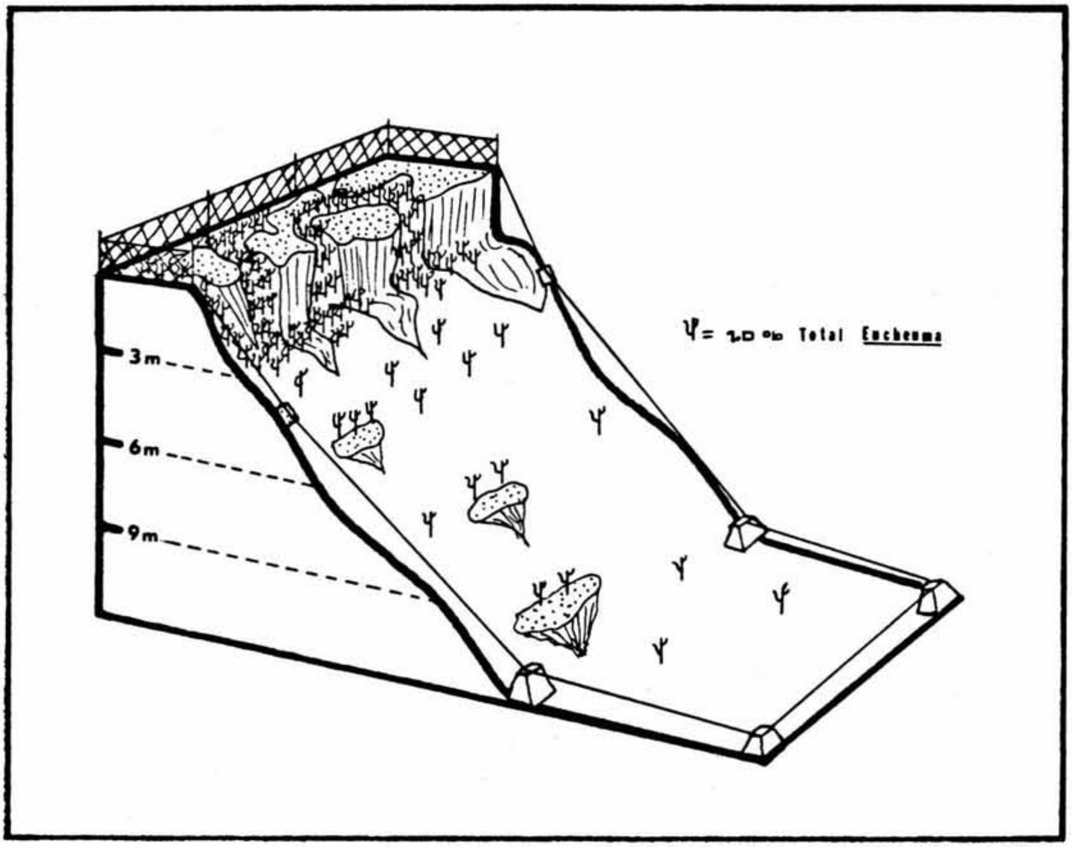

FIGURE 12. Sectional view showing the horizontal and vertical positions of *Eucheuma* thallus locations on the reef edge and channel slope. Each diagrammatic thallus represents 1 percent of the total weight recovered.

sidering the thalli just below them gained slightly in weight. It appeared that fish might be feeding on the thalli. Another experiment was designed that eliminated the fish by placing *Eucheuma* inside protective wire-mesh cages. Then, growth rates of *Eucheuma* at different depths were compared.

The results of these tests showed a significant decrease in the growth rates of thalli between 0.5 and 2.0 m depths (Figure 15). This decrease corresponded to a significant decrease in light intensity and water motion (Table 6). The effect of fish grazing is discussed in the following section.

The maximum depth at which *Eucheuma* grew differed slightly from experiment to experiment. This problem may have been a result of changing conditions in Kaneohe Bay rather than experimental error. These data, nevertheless, support the conclusion that the uneven edge of the reef flat, with its coral heads and ledges of rock dissected by deep grooves, was not holding the fragments securely in place, but was acting as a sieve. It was simply delaying the progress of the fragments as they drifted into deeper water where they could not live.

The final evidence for this conclusion came after the June 1977 survey, when the reef flat experiments were removed (Figure 6). This abruptly ended the flow of fragments across the reef. By September 1977 the thalli had receded from the northern end of the reef slope (Figure 5*F*) and the total amount of *Eucheuma* had declined (Figure 6). By December 1977 no fragments were in water less than 2 m deep

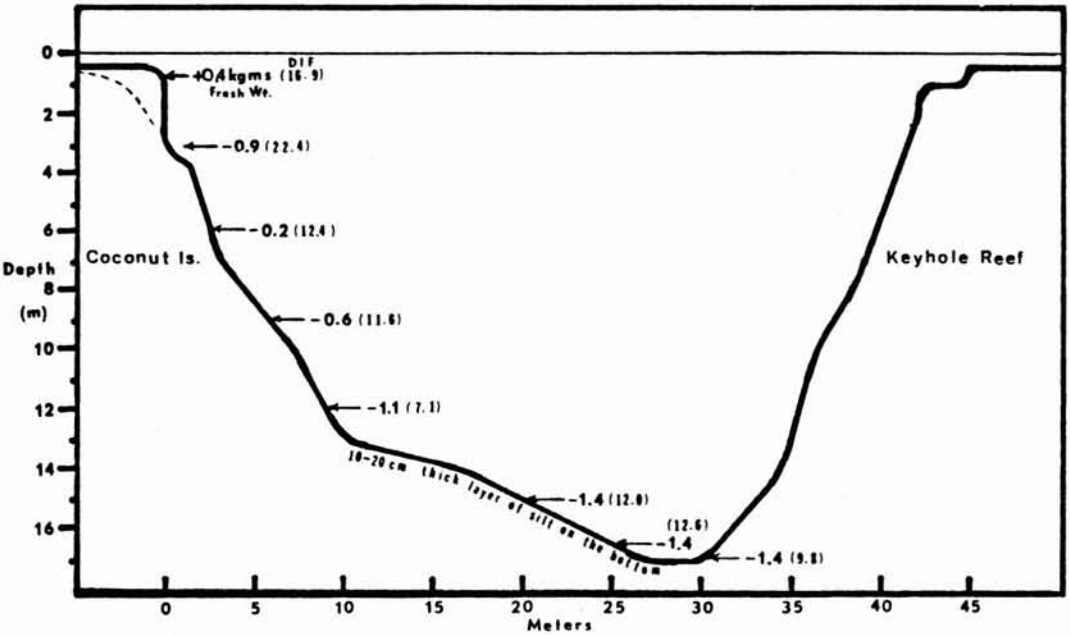

FIGURE 13. The fresh weight gained or lost by *Eucheuma* thallus fragments after remaining tied to concrete blocks for 44 days at various depths across the channel at position *E*. Diffusion Index Factor (DIF) values are in parentheses; the lower the value the slower the water motion.

TABLE 4

GROWTH AND SURVIVAL OF *Eucheuma* AS A FUNCTION OF DEPTH, 13 JULY–4 SEPTEMBER 1976

DEPTH (m)	DATE: 12 July	18 August	4 September	CHANGE IN WEIGHT (kg)	FINAL AVERAGE WEIGHT (kg)	AVERAGE IN WEIGHT (kg)
1.0	2.3	8.3	4.6	+2.3		
	2.3	3.8	2.7	+0.4	2.7	+0.4
3.0	1.4	4.5	—	−1.4		
	1.4	2.0	1.0	−0.4	0.5	−0.9
6.0	1.4	1.3	1.8	+0.5		
	1.4	0.7	0.5	−0.9	1.2	−0.2
9.0	1.4	0.9	0.5	−0.9		
	1.4	0.9	1.0	−0.4	0.8	−0.6
12.0	1.4	0.5	0.5	−0.9		
	1.4	0.0	0.0	−1.4	0.3	−1.1
15.0	1.4	0.0	0.0	−1.4		
	1.4	0.1	0.0	−1.4	0.0	−1.4
16.0	1.4	0.5	0.0	−1.4		
	1.4	0.2	0.0	−1.4	0.0	−1.4
	1.4	0.0	0.0	−1.4		
	1.4	0.0	0.0	−1.4	0.0	−1.4

TABLE 5

CHANGES IN FRESH WEIGHT OF *Eucheuma* THALLI GROWING ON THE REEF FLAT AT VARIOUS DEPTHS TO 9.5 METERS, 29 OCTOBER–26 NOVEMBER 1976

DEPTH (m)	29 OCTOBER (g)	5 NOVEMBER (g)	CHANGE IN WEIGHT (%/day)	12 NOVEMBER (g)	CHANGE IN WEIGHT (%/day)	19 NOVEMBER (g)	CHANGE IN WEIGHT (%/day)	26 NOVEMBER (g)	CHANGE IN WEIGHT (%/day)
0.5	117.0	154.0	(+4.0)	230.0	(+5.9)	312.0	(+4.5)	398.0	(+3.5)
0.5	62.0	80.0	(+3.7)	118.0	(+5.7)	157.0	(+4.2)	198.0	(+3.4)
0.5	71.0	99.0	(+4.9)	140.0	(+5.1)	185.0	(+4.1)	238.0	(+3.7)
0.5	42.0	54.0	(+3.7)	76.0	(+5.0)	99.0	(+3.9)	123.0	(+3.2)
1.0	65.0	68.0	(+0.7)	185.0*	(—)	108.0	(−7.4)	125.0	(+2.1)
1.5	75.0	86.0	(+2.0)	105.0	(+2.9)	122.0	(+2.2)	140.0	(+2.0)
2.0	98.0	104.0	(+0.9)	66.0	(−6.3)	67.0	(+0.2)	76.0	(+1.8)
2.5	102.0	107.0	(+0.7)	121.0	(+1.8)	84.0	(−5.1)	88.0	(+1.0)
3.0	95.0	96.0	(+0.2)	113.0	(+2.4)	129.0	(+1.9)	139.0	(+1.1)
3.5	94.0	103.0	(+1.3)	107.0	(+0.6)	111.0	(+0.5)	114.0	(+0.4)
4.0	76.0	88.0	(+2.1)	97.0	(+1.4)	102.0	(+0.7)	100.0	(−0.3)
4.5	87.0	91.0	(+0.6)	96.0	(+0.8)	88.0	(−1.2)	88.0	(0.0)
5.0	99.0	104.0	(+0.7)	107.0	(+0.4)	111.0	(+0.5)	113.0	(+0.3)
6.0	100.0	104.0	(+0.6)	112.0	(+1.1)	140.0	(+3.2)	148.0	(+0.8)
6.5	109.0	99.0	(−1.4)	95.0	(−0.6)	97.0	(+0.3)	97.0	(0.0)
7.0	104.0	96.0	(−1.1)	97.0	(−0.2)	97.0	(0.0)	92.0	(−0.8)
7.5	87.0	94.0	(+1.1)	94.0	(0.0)	90.0	(−0.6)	89.0	(−0.2)
8.0	127.0	120.0	(−0.8)	63.0	(−8.8)	62.0	(−0.2)	64.0	(+0.5)
8.5	77.0	75.0	(−0.4)	72.0	(−0.6)	58.0	(−3.0)	58.0	(0.0)
9.5	104.0	100.0	(−0.6)	99.0	(−0.1)	99.0	(0.0)	98.0	(−0.2)

* The original thallus was lost and replaced at this point.

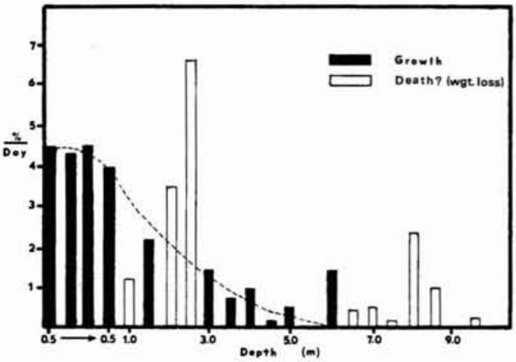

FIGURE 14. Percent growth per day of *Eucheuma* thalli tied at 1-m intervals along a line from 0.5 to 9.0 m depth at position *E*. Each histogram represents a single thallus, and the dashed line represents the expected growth rates.

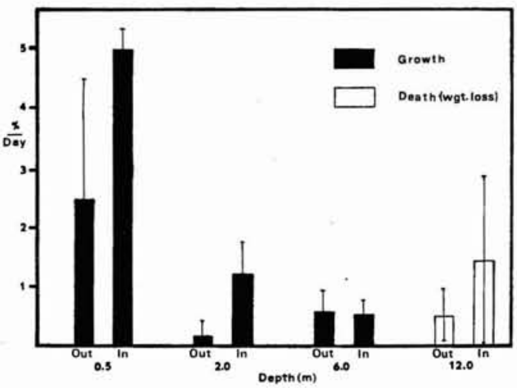

FIGURE 15. The average percent growth per day of four *Eucheuma* thalli tied to the outside and four thalli tied to the inside of protective cages at four depths at position *E*.

(Figure 5*G*), and by March 1978 only a few fragments were on the reef edge (Figure 5*H*). The reef "sieve" was emptied of its contents in 8 mo.

Biological Factors Limiting Eucheuma Growth

The following evidence supports the conclusion that fishes grazing along the reef edge contributed to a significant loss of algal biomass and a lowered growth rate.

Different species of fishes were seen swimming between and beneath the loose clumps of *Eucheuma* thalli. Most were juvenile scarids (parrotfish) and acanthurids (surgeonfish), although several carnivorous fishes were also present. The gut contents of both herbivores and carnivores were examined for *Eucheuma* (Table 7). As expected, none of the carnivorous fish species had any algae in their digestive tracts, but four out of five captured individuals of *manini* (*Acanthurus triostegus sandvicensis* Randall and Gaimard) and the yellow tang (*Zebrasoma flavescens* Randall) contained from 6 to 166 pieces of *Eucheuma* branch tips and cross sections in their guts (Table 7). These pieces ranged from 1 to 2 mm wide and from 1 to 3 mm long. A few pieces (less than 1 percent) of *Acanthophora spicifera* (Vahl) Boerg. and *Gracilaria bursapastoris* (Gmel.) Silva were also present, but *Eucheuma* was the primary food item. Grazing was intense and partially responsible for the lack of growth by the reef-edge population of *Eucheuma*.

When *Eucheuma* cuttings were taken from the reef edge and placed in a protective pen they produced an abundance of branches. These newly branched pieces were again placed on the reef edge; all of the new branches disappeared within 3.5 hr. All of the branches had been severed to their bases, and only the 2.0-cm-thick portions of the thalli were left. The herbivorous fishes appeared to selectively graze on the smaller branches of *Eucheuma*. This explains the gnarled, branchless appearance of thalli on the reef edge. During the final stages of the disappearance of *Eucheuma*, the fishes began eating the thicker portions of the thalli that were still available.

The best estimate of how much was being eaten by fishes was obtained by combining the results of several experiments. A 515-g branched *Eucheuma* thallus was lowered into a holding pen with 40 *palani* (*Acanthurus dussumieri* Randall). The fish ate 51 g from the thallus in 3.5 hr. Another thallus weighing 500 g was placed into a pen with four *kala* (*Naso unicornis*), twelve *A. dussumieri*, one *A. triostegus sandvicensis*, and two Ambon tobys (*Canthigaster amboinensis*), and after 2 hr the thallus had lost 35 g to the fishes. The individuals of *A. dussumieri* were the most aggressive fish in this group and the only ones actually seen eating the thallus. They placed their

TABLE 6

PHYSICAL CHARACTERISTICS MEASURED DURING THE CAGED AND NONCAGED *Eucheuma* EXPERIMENT

DEPTH (m)	OXYGEN (μg-at O_2/L)*	WATER MOTION (DIF)	TEMPERATURE (°C)	LIGHT LUX
0.5				
Inside cage		33.9 ± 6.3		
Outside cage	0.495 ± 0.013	36.9 ± 5.1	27.4 ± 0.59	38,000 ± 8,500
2.0				
Inside cage		12.8 ± 1.9		
Outside cage		11.4 ± 1.0	26.5 ± 0.42	20,000 ± 11,000
6.0				
Inside cage		13.5 ± 2.5		
Outside cage	0.422 ± 0.0	14.6 ± 3.0	26.3 ± 0.45	12,000 ± 5,000
12.0				
Inside cage		9.7 ± 2.7		
Outside cage	0.389 ± 0.0	14.4 ± 3.1	26.0 ± 0.30	2,000 ± 1,400

* Microgram-atoms of oxygen per liter.

TABLE 7

GUT ANALYSES OF FISHES CAPTURED NEAR *Eucheuma*

FISH SPECIES	NUMBER OF *Eucheuma* PIECES IN GUT	AVERAGE FRAGMENT WIDTH × LENGTH (mm)
Acanthurus triostegus		
#1	166	1.0 × 2.0
#2	6	1.5 × 2.0
#3	18	1.0 × 2.0
Zebrasoma flavescens	37	1.5 × 2.0
Chaetodon miliaris		
#1	0	
#2	0	
Chaetodon trifasciatus	0	

mouths over the seaweed branch tips and swam onto them while biting repeatedly. The *palani* stopped feeding after 30 min when all the small branches had been eaten. Under these conditions fishes ate 7.1 percent of the thalli within 3.5 hr.

In one experiment, 32 percent of the thallus weight was eaten from fragments allowed to drift over the reef edge, and 27 percent was lost when the experiment was repeated. When growth rates of caged and uncaged thalli were compared (Figure 15, Table 8) they showed that the fishes reduced the growth rate at 0.5 m depth by 50 percent and at 2.0 m depth by 80 percent, an average reduction of 65 percent. If these figures are extrapolated the fishes could graze from 10 to 20 tons/mo from the reef edge.

Effects of Eucheuma on Reef Animals

Eucheuma thalli provided shelter for reef fishes, especially the bluespotted goby (*Asterropteryx semipunctatus* Ruppell) and the conger eel (*Conger marginatus* Valenciennes). Nearly every time *Eucheuma* thalli were harvested, individuals of *A. semipunctatus* were inadvertently taken with the thalli into the boat. The eel, *C. marginatus*, which was nearly the same color as *Eucheuma*, was often found swimming among the loose thalli, as were moray eels (*Gymnothorax* spp.).

TABLE 8

GROWTH RATES OF *Eucheuma* THALLI GROWN OUTSIDE AND INSIDE PROTECTIVE CAGES AT FOUR DEPTHS, 8 JUNE–18 JULY 1977

DEPTH (m)	DATES							
	28 June (%/day)	3 July (%/day)	8 July (%/day)	13 July (%/day)	18 July (%/day)	TOTAL	AVERAGE	STANDARD DEVIATION
0.5								
Outside the cage	0.9	3.5	4.4	4.5	−0.9	12.4	2.5	3.09
Inside the cage	4.6	5.2	4.6	5.5	4.9	24.8	5.0	0.39
2.0								
Outside the cage	−0.5	0.5	0.2	0.2	0.2	0.6	0.1	0.29
Inside the cage	1.7	2.1	0.4	0.6	1.0	5.8	1.2	0.72
6.0								
Outside the cage	0.2	1.2	0.1	0.8	0.9	3.2	0.6	0.47
Inside the cage	0.5	0.8	0.8	0.3	−0.1	2.3	0.5	0.56
12.0								
Outside the cage	0.3	−0.8	−0.4	−0.3	−0.9	−2.2	−0.4	0.58
Inside the cage	−0.2	0.2	−0.2	−3.7	−0.9	−6.6	−1.3	2.46

Eucheuma thalli also provided a substratum for numerous invertebrates. Among the invertebrates recorded were sessile solitary and colonial ascidians, sponges and peristome ciliates (which covered the bases of the thalli like a white fur), and several mobile holothurians.

The numbers of invertebrates living among the *Eucheuma* thalli were compared to a similar area on an adjacent reef where *Eucheuma* thalli had never been present (Figure 3*H*). In the *Eucheuma* area, 97 individual macroscopic invertebrates, not counting corals, were found on *Eucheuma* thalli, for an average of 5 ± 2 species per sample (Table 9). At the control site, 25 invertebrates were recorded with an average of 1.8 ± 1 species per sample ($P = 0.05$). The reef with *Eucheuma* on it had a significantly higher index of diversity than did the reef without the alien (Table 9).

Effects of Eucheuma on Corals

When fragments of *Eucheuma* were allowed to sink or drift onto the reef edge, thalli weighing 55.9 kg covered two small living *Porites compressa* coral heads (Figure 11). After 74 days the corals were dead. Larger coral heads nearby, not covered by *Eucheuma* thalli, were not damaged. Coral death was probably a result of shading (Table 10).

It was more common to find damaged *Eucheuma* than damaged coral when the two were found in contact. Usually no attachment was formed by either the animal or the alga; instead, *Eucheuma* became abraded by the coral. Several branches of *Eucheuma* thalli were found next to *Porites compressa*, which attached to the alga (Figure 16). Yet, the alga did not form a connection with the coral, but rather a callus formed on the alga where the two were in contact.

An erect sponge, *Toxadocia violacea*, was also found attached to *Eucheuma*, which reacted by forming a wartlike callus on itself where the animal was attached. This interaction was found only once, although *T. violacea* occurred regularly among the *Eucheuma* thalli.

Effects of Eucheuma on Other Algae

Only two nonalien algal macrophytes grew with *Eucheuma* on the reef edge. These algae, *Dictyosphaeria cavernosa* (Forsk.) Boerg. and *Caulerpa racemosa* var. *peltata* Lam., were present in small quantities beneath *Eucheuma*

TABLE 9

INDEX OF SPECIES DIVERSITY AT POSITION E COMPARED TO POSITION H

SPECIES	SAMPLE REPLICATES 1	2	3	4	5	TOTAL
			POSITION E			
Solitary Ascidians						
#1	11	6	1	4	4	26
#2	7	7	0	1	0	15
#3	11	0	0	0	5	16
#4	2	1	0	0	0	3
Colonial Ascidians						
#5	2	2	0	0	0	4
#6 (This species was found on the base of every *Eucheuma* examined.)						
Echinoderms						
#7	3	4	6	2	9	24
#8	1	2	2	0	0	5
#9	0	0	0	0	2	2
#10	0	0	0	0	0	0
Sponges						
#11	0	0	0	1	0	1
#12	0	0	0	0	0	0
#13	0	0	0	1	0	1
Total	37	22	9	9	20	97
Average 5 ± 2						
Total species 11; a = 3*						
			POSITION H			
Solitary Ascidians						
#1	7	5	2	1	4	19
#2	0	0	0	0	0	0
#3	0	0	0	0	0	0
#4	0	0	0	0	0	0
Colonial Ascidians						
#5	0	0	0	0	0	0
#6	0	0	0	0	0	0
Echinoderms						
#7	0	0	0	1	0	1
#8	0	0	0	0	0	0
#9	0	0	0	0	0	0
#10	0	0	0	1	0	1
Sponges						
#11	0	0	0	0	0	0
#12	1	0	0	0	3	4
#13	0	0	0	0	0	0
Total	8	5	2	3	7	25
Average 1.8 ± 1						
Total species 4; a = 1						

NOTE: The formula used to estimate the Index of Diversity was $S = a\text{Log}_e\left[1 + \frac{N}{a}\right]$, where a is the Index of Diversity, S is the total number of species, and N is the total number of individuals (Lewis and Taylor 1967).

* Significant at the 5 percent level.

TABLE 10

THE EFFECT OF *Eucheuma* ON CERTAIN PHYSICAL FACTORS

	POSITION OF MEASUREMENT	
PHYSICAL FACTORS	Beside the thalli	Under the thalli
Light (lux)	40,000 (100%) ±25,000	1,000* (2.5%) ±563
Oxygen (μg-at O_2/L)†	0.482 ± 0.003	0.454 ± 0.019
Water motion (DIF)‡	8.1 ± 0.47	9.4 ± 2.34

* Significant at the 1 percent level.
† Microgram-atoms of oxygen per liter.
‡ Diffusion index factor.

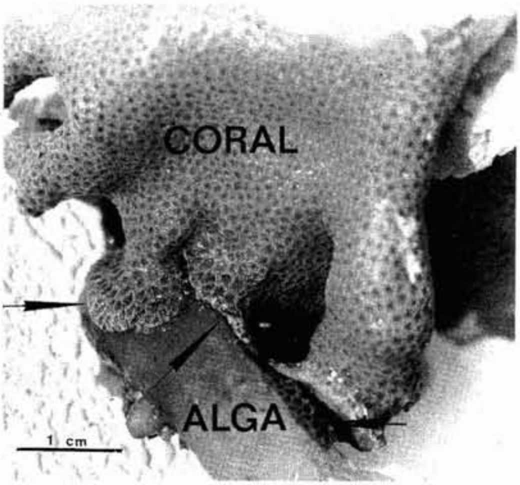

FIGURE 16. *Porites compressa* attached to *Eucheuma* (indicated by arrows).

thalli. No other large algae inhabited the grooves in the reef edge in the area or the grooves on adjacent reefs, although several species, which appeared to be unaffected by *Eucheuma*, grew on the coral substrate between the grooves.

In Kaneohe Bay, *Eucheuma* inhabited the barren sand-covered grooves on the reef edge which were not inhabited by native algae and thus appeared to be noncompetitive. A similar situation occurred in Puget Sound, Washington, where *Sargassum muticum* entered a niche empty of other large native algae (Scagel 1956). In Europe Farnham et al. (1981) reported that *S. muticum* invaded and increased in biomass at Bembridge, Isle of Wight, but did so without harm to the local population. *Codium fragile*, which was introduced to France, did not compete with native algae (Feldmann, 1956) because it occupied substrata not utilized by native species.

SUMMARY

1. *Eucheuma striatum* Schmitz was imported on 9 September 1974 from the Philippines and placed on a Coconut Island reef flat in Kaneohe Bay, Oahu, for scientific experimentation. Fragments from these thalli drifted across the reef flat and established an unstable population (ca 24 metric tons) along the reef edge.

2. People not associated directly with the Coconut Island experiments transplanted *Eucheuma* to other locations in Hawaii (Heeia Kea, Ewa Beach, Kahuku, and Hilo). It was also sent to Fiji, Christmas Island, Fanning Island, and other locations in the Pacific.

3. This particular kind of *Eucheuma* did not produce spores; reproduction was by fragmentation. Small fragments of branch tips were capable of disseminating over short distances and would regenerate into full-sized thalli. Tips were not an effective mechanism for dispersal over deep water; they did not form holdfasts and were not found on the reef except after a harvest.

4. *Eucheuma* did not have the ability to cross channels and accumulated in depressions on the reef. The greatest accumulation

was on the reef edge, but this was only a temporary population that was moving into deeper water unsuitable for its growth.

5. After the experimental holding pens on the reef flat were removed, the reef-edge population disappeared in 8 mo. This population was actually moving slowly into deeper water.

6. Fish were grazing an estimated 10–20 tons of *Eucheuma* per month, which resulted in a significant loss of algal biomass and a lowered apparent growth rate.

7. *Eucheuma* provided a substratum for numerous invertebrates. The reef with *Eucheuma* had a higher index of invertebrate species diversity than a control reef.

8. *Eucheuma* inhabited barren sand-covered grooves on the reef edge which were not inhabited by native algae. *Eucheuma* thus appeared to be noncompetitive.

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