
**HERBIVORY, ALGAL DISTRIBUTION, AND THE MAINTENANCE OF
BETWEEN-HABITAT DIVERSITY ON A TROPICAL FRINGING REEF****MARK E. HAY***Smithsonian Tropical Research Institute, Box 2072, Balboa, Panama and Department of Ecology and
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The bases of coral reefs in the Caribbean often abut sandy plains covered by sea grasses (Randall 1965; Ogden et al. 1973*b*) or algae (Earle 1972; Dahl 1973). Interactions occurring at the border of reefs and sea grass beds have been studied on several occasions (Randall 1965; Ogden et al. 1973*b*; Ogden 1976; Parrish and Zimmerman 1977; Ogden and Lobel 1978), but little is known about those which occur between reefs and sandy plains dominated by algae.

Unlike sea grasses, which root into the sand, many of the algal species that occur on sand plains require hard substrates (Dahl 1973) such as shells and coral fragments. Suitable attachment sites are uncommon on the sand plain at Galeta Point, Panama, and many are periodically buried or turned over during heavy seas. Paradoxically algal species that predominate on the sand plain tend to be rare or absent from the shallower reef slope where stable, hard substrate is abundant.

The maintenance of such distinct distributional boundaries is often attributed to differential competitive abilities (Connell 1961; Holmes 1961) or to restrictive specialization to particular physical regimes (Doty 1946; Terborgh 1971). These factors have been hypothesized to be especially important (Dobzhansky 1950; Janzen 1967; Ashton 1969; Diamond 1975) in diverse tropical communities where specialization to narrow niches is thought to promote resource partitioning and allow increased coexistence. While such explanations are often consistent with observed patterns, they are seldom tested using controlled field experiments. Without such field manipulations it is impossible to adequately assess the relative importance of competition, predation, and physical stress in determining the distribution and abundance of species or the intensity of interactions that occur between them.

In this paper I examine experimentally the factors maintaining these separate algal assemblages and contend that the sand-plain species (algae that are almost never found on the reef) would competitively exclude other species from the reef

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slope if they were not selectively removed by reef-associated grazers. Competition and physiological specialization appear to have no effect on excluding sand-plain species from the reef slope.

In the remainder of the paper I test the following hypotheses. (1) Low light and scarcity of attachment sites severely limit the growth of algae on the sand plain. (2) Sand-plain algae are not physiologically restricted to deep waters; they are most fit in the physical regime typical of shallower reef-slope habitats. (3) Reef-associated grazers are responsible for excluding sand-plain species from the reef slope. (4) In the absence of herbivores, sand-plain species competitively dominate reef-slope species. (5) Because of differential competitive ability, sand-plain genera are better adapted for temperate areas than are reef-slope genera.

DESCRIPTION OF STUDY SITE

The study was carried out from December, 1977, through July, 1979, at the Smithsonian Tropical Research Institute's Galeta Point Laboratory (fig. 1), located on the Caribbean coast of Panama at 9° 24'N, 79° 52'W. The reef is representative of the fringing reefs found on the northern coast of Panama (Glynn 1972; MacIntyre and Glynn 1976) and according to W.H. Adey (personal communication), who has extensively surveyed Caribbean reef systems, is similar in formation to about 15% of the Caribbean reefs with which he is familiar.

Encrusting coralline algae cover much of the reef slope. Upright algal forms such as *Halimeda opuntia* and *Amphiroa* spp. cover less total area but produce large aggregates on colonies of the more structured corals such as *Porites* and *Agaricia*. The upright red alga, *Bryothamnion seaforthii*, dominates the areas of rubble between standing coral structures. At a depth of 10–14 m, the reef abuts an extensive sand plain that includes sparse fragments of hard substrate to which upright algae are attached. Red algae, such as *Gracilaria*, *Halymenia*, and *Solieria*, comprise most of the cover and are characteristically attached to small coral fragments partially buried by the sand. Siphonaceous greens such as *Halimeda* and *Udotea* that can anchor directly in the sand are present but relatively uncommon.

During dry season, usually December–April, winds blow consistently from the north at 24–27 km/h (Hendler 1976), which is about three times the mean wet season velocity. Waves generated by these strong, unidirectional winds cause considerable turbidity that reduces light penetration markedly, leaving the sand plain in near darkness for a majority of the time. Wave-induced turbulence also causes sand movement that uproots the weakly attached sea grass *Halophila baillensis* and overturns coral fragments to which upright algae are attached.

Grazing fish (primarily Scaridae and Acanthuridae) and sea urchins (primarily *Diadema*, *Echinometra*, and *Euclidaris*), that occur in abundance on the reef, are rare in the sand-plain habitat. During a typical dive on the reef slope one may see hundreds of herbivorous fish and many sea urchins. If the same time is spent on the sand plain, a diver will usually encounter 0–3 immature herbivorous fish and no sea urchins (in more than 500 h of SCUBA diving on the sand plain, only two sea urchins were seen).

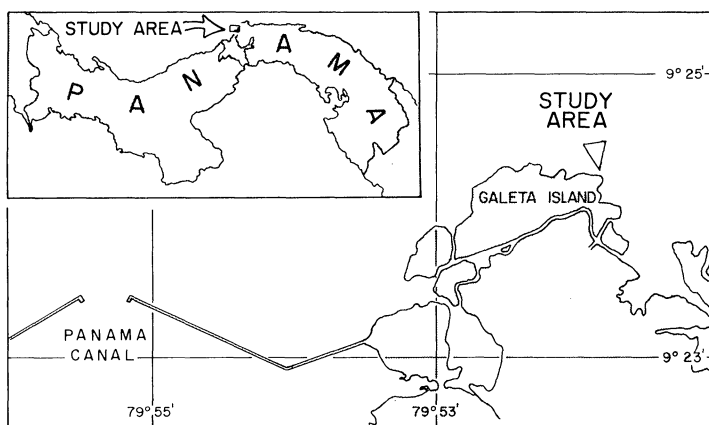


FIG. 1.—The Galeta Point study site and its location within the Republic of Panama.

METHODS AND MATERIALS

To evaluate the importance of hard substrate as an attachment site for sand-plain algae, all algae and hard substrates were collected from 20 1-m² quadrats located randomly within a potential sampling area of 2,000 m². In the laboratory, samples were rinsed quickly in fresh water, sorted to species, and dried to constant weight at 80° C. Attachment site (hard substrate, sand, or another plant) was recorded for each individual.

Using a 0.15 m² vinyl quadrat that contained 100 holes arranged in a stratified random array, the percent cover of hard substrate was assessed by pushing a small steel pin through each hole to a depth of 1 cm. Seventy-eight randomly located samples were taken within the sand-plain study area on July 19, 1979.

To assess the impact of turbulence and turbidity during the dry season, 100 1-m² quadrats were located randomly on the sand plain within a 1,500-m² study area. At approximately monthly intervals, all quadrats were monitored to determine the number of macrophyte species, the number of individuals, and the percentage cover of plants. Percentage cover was assessed by a point intercept method using 100 stratified random points/m². Parallax bias was minimal since the quadrat could be placed flush against the two-dimensional sand plain. Underwater measurements of photosynthetically active light were taken at about weekly intervals with a Li-Cor Model 185-A quantum/radiometer/photometer. Readings were made between 1100–1300 h at 20 permanent stations located randomly within the study area.

The effect of light quantity on apparent photosynthesis was determined for six common species from the sand plain (*Gracilaria* sp. 1, *Gracilaria* sp. 2, *Gracilaria* sp. 3, *G. domingensis*, *Spyridia aculeata*, and *Solieria tenera*) and for the two most abundant upright species on the reef slope (*Halimeda opuntia* and *Bryothamnion seaforthii*). Determinations of apparent photosynthesis were conducted in a Puffer-Hubbard Uni-Therm Incubator at 27 ± 1° C, with illumination provided by nine Sylvania cool-white fluorescent tubes. Light quantity was

changed by placing the incubation bottles (1.19 liters) at differing distances from the light source and by the use of neutral density filters. To prevent light shock, thalli were brought from the field in darkened containers and successive incubations performed at 13, 35, 75, and 170 $\mu\text{E}/\text{m}^2$ per s. Photosynthetic measurements were made during late November and early December of 1978. Initial O_2 concentration was always at approximately saturation and only those plant portions which were healthy and epiphyte free were used. Plant material was added to each incubation bottle until about 25% of the bottom was covered by nonoverlying thalli. To break down diffusion gradients and keep plants from clumping, constant stirring was provided by magnetic stir bars. Incubations at each light level lasted 1–2 h and consisted of six replicates per species plus one blank bottle. Oxygen determinations were made with a YSI Model 57 oxygen analyzer electrode, the plants dried to constant weight at 80° C, and apparent photosynthesis expressed as mg O_2/g dry wt per h (for the heavily calcified *Halimeda opuntia*, apparent photosynthesis was expressed as mg O_2/g ash free dry wt per h). Dark respiration rates were determined in a similar fashion but incubations lasted for 6 h.

On March 22, 1978, coral fragments containing *Gracilaria* sp. 1 were cleared of other algal species and suspended above the sand plain on eight separate fishing lines made of 90 kg-test monofilament. Each line ran from the sand plain to a small buoy floating about 1 m below the surface of the water. To acclimate individuals to a range of light intensities, eight plants, each on a separate line, were moved from a depth of 12.3 m (the sand plain) to a depth of 9 m where they remained for 7 days. This procedure was repeated at 7-day intervals until there were acclimated plants at 3 m, 6 m, and 9 m deep. On June 8, 1978, this was done again for *G. domingensis* and *Halymenia floresia*. Ten more lines were used that contained one individual of each species at each depth (i.e., now a total of 18 lines).

On September 25, 1978, all plants that were attached directly to the monofilament line were collected and curated. (The original transplanted algae were not collected. Collected algae consisted only of those plants that had settled, germinated, and grown at that depth.) Collections of plants growing between 1.5–4.5 m, 4.5–7.5 m, and 7.5–10.5 m deep were analyzed separately to determine reproductive condition, presence of grazing scars, number of individuals, and two-dimensional surface area. Two-dimensional surface area was calculated by overlaying the pressed specimens with a dot field (8 points/cm²) and counting the points intercepting the plant.

On March 3, 1979, the 11 lines that had withstood the dry season (7 had sunk or been torn out by drifting trees) were brought to the lab and the algae were curated and analyzed as above. All pressed specimens will be deposited in the U.S. National Museum of Natural History, Washington, D.C. Because of rough seas associated with the dry season, entanglement and loss of some larger individuals above a depth of 4.5 m was a problem.

In December, 1977, the importance of grazers was assessed by transplanting algae from the sand plain onto the reef slope. Individuals were collected from the sand plain, taken to the laboratory, shaken free of excess water, weighted three times to the nearest 0.1 g, and fastened between the strands of a marked segment of three-strand rope. The plants were then placed either on the reef slope between

4.5–9 m deep or returned to the sand plain. In both areas, plants were anchored by slipping the rope over small metal rods that had been driven into the substrate. Four species from the sand plain (*Gracilaria* sp. 1, *Solieria tenera*, *G. domingensis* and *Halymenia floresia*) and one that occurs primarily on the reef slope (*Bryothamnion seaforthii*) were transplanted in this manner; for each, 10 individuals were placed on the reef slope and 10 on the sand plain. After 48 h, these were collected, reweighed, and the thallus examined for signs of fish or urchin grazing. Although great care was taken in the transport of all samples, some fragments of the more delicate sand-plain species (primarily *Solieria tenera* and *Halymenia floresia*) were invariably lost. Since sand-plain and reef-slope samples were treated identically, losses of this sort were equivalent for both groups.

This grazing study was conducted during the dry season when strong currents and zero visibility on the sand plain, and poor visibility on the reef made it impossible to locate all of the replicates. This resulted in sample sizes of less than 10 for some species.

During June and July of 1978, eight large white cages (112 cm × 48 cm × 49 cm) made of polyvinyl chloride (PVC) pipe frames and braided nylon netting (1-cm mesh) were placed on the reef at a depth of 5–6 m. Steel rods were driven into the reef, and the cages lashed to them so that the cage floor was 0.5 m above the substrate. This excluded all nonswimming herbivores. Four of the cages were completely enclosed, while the other four served as controls with 41-cm × 83-cm openings in two sides that allowed fish to enter. Two preweighed (as described above) individuals of *Gracilaria* sp. 1 and *G. domingensis* were placed in three-strand ropes and tied to the bottom of each cage, left for 14 days, then collected and reweighed. This procedure was subsequently repeated for *Halymenia floresia* and *Solieria tenera*. To test if fish were attracted or repelled by the cages, eight plants of *Gracilaria* sp. 1 and *G. domingensis* were placed about 10 m away from the cages on thin metal rods that held them 0.3 m above the substrate. All cages were cleaned daily to minimize shading.

To evaluate the proportion of sand-plain and reef-slope algae that have successfully established in temperate areas (hypothesis 5), genera listed in Taylor's (1937) text *Marine Algae of the Northeastern Coast of North America* were compared with those occurring on the sand plain and reef slope at Galeta. (Species comparisons could not be made because many of the sand-plain species at Galeta are undescribed.) When making the comparison, only those genera that occur primarily in one habitat or the other were used. Those few genera that regularly occur both on the reef slope and sand plain were not included in either category.

RESULTS

The majority of algal species on the sand plain require hard substrate for attachment. Of the 40 species present in the 20 samples, only six were ever found anchored directly in the sand (table 1). Ninety-three percent of the biomass and 88% of the individuals collected were attached to hard substrates (table 1), although only 4% of the sand plain has solid substrate within 1 cm of the surface

TABLE 1

NUMBER OF INDIVIDUALS, BIOMASS, AND ATTACHMENT SITES FOR MACROPHYTE SPECIES COLLECTED IN TWENTY 1-m² QUADRATS LOCATED RANDOMLY ON THE SAND PLAIN
(Species are arranged in order of decreasing biomass.)

SPECIES NAME	ATTACHED TO HARD SUBSTRATE		ATTACHED IN SAND		ATTACHED TO OTHER PLANTS	
	No. of Plants	Dry Wt (g)	No. of Plants	Dry Wt (g)	No. of Plants	Dry Wt (g)
<i>Gracilaria</i> sp. 1	349	10.140				
<i>Gracilaria</i> sp. 2	72	4.373				
<i>Halimeda copiosa</i> *	23	2.635	10	1.589		
<i>Gracilaria cuneata</i>	24	2.273				
<i>Cryptonemia luxurians</i>	5	1.812				
<i>Gracilaria domingensis</i>	57	1.782				
<i>Solieria tenera</i>	34	1.511			6	.187
<i>Spyridia aculeata</i>	44	1.657	1	.001	2	.007
<i>Gracilaria</i> sp. 3	49	1.114				
<i>Dictyota</i> spp. & <i>Dictyopteris</i> spp.	48	.806	1	.001	38	.109
<i>Chondria tenuissima</i>	14	.716				
<i>Bryothamnion seaforthii</i>	13	.489				
<i>Udotea conglutinata</i>	2	.001	9	.462		
<i>Gracilaria</i> sp. 4	9	.302				
<i>Gracilaria</i> sp. 5	33	.267				
<i>Gracilaria cylindrica</i>	4	.228				
<i>Halimeda simulans</i> *			3	.138		
<i>Nitophyllum</i> sp.	7	.096				
<i>Halophila baillonis</i>			3	.068		
<i>Chondria baileyana</i>	30	.044	41	.021		
<i>Halymenia rosea</i>	20	.058				
<i>Dictyurus occidentalis</i>	1	.051				
<i>Halymenia floresia</i>	6	.041				
<i>Cryptonemia crenulata</i>	1	.027				
<i>Botryocladia occidentalis</i>	4	.026				
<i>Corallina subulata</i> *	2	.025				
<i>Jania adherens</i> *	9	.009			9	.016
<i>Hypoglossum tenuifolium</i>	13	.020			1	.001
<i>Delessariaceae</i>	1	.021				
<i>Gelidiella acerosa</i>	1	.016				
<i>Laurencia intricata</i>	2	.010			1	.003
<i>Botryocladia</i> sp.	5	.012				
<i>Eucheuma</i> sp.	2	.010				
<i>Neoagardhiella</i> sp.	2	.010				
<i>Bryopsis plumosa</i>	14	.007				
<i>Neoagardhiella ramosissima</i>	1	.004				
<i>Acanthophora spicifera</i>	1	.004				
<i>Microdictyon boergesenii</i>	1	.001			3	.002
<i>Hypnea cervicornis</i>	3	.002			1	.001
<i>Halymenia hancockii</i>	4	.002				
<i>Gracilaria damaecornis</i>					1	.001
Totals	910	30.601	68	2.280	61	.139
% of total sample	88	93	6	7	6	<1

NOTE.—Collections were made during June, 1979.

* Biomass of calcified species is given in g ash free dry wt.

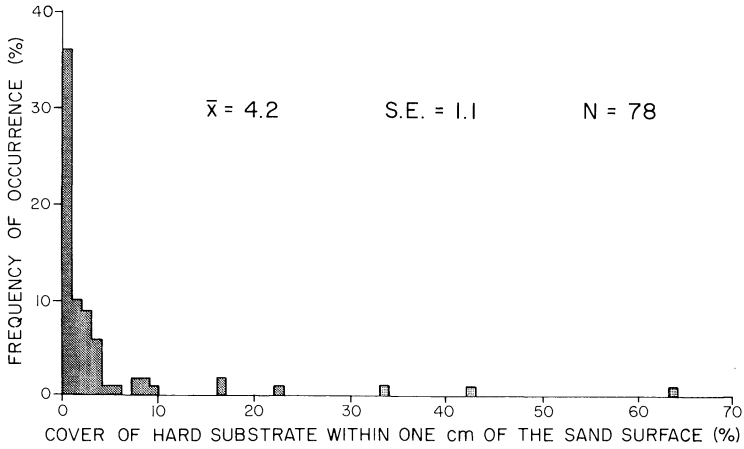


FIG. 2.—Abundance-frequency diagram for the percent cover of hard substrate within 78 0.15-m² quadrats located randomly on the sand plain. Measurements were made on July 19, 1979.

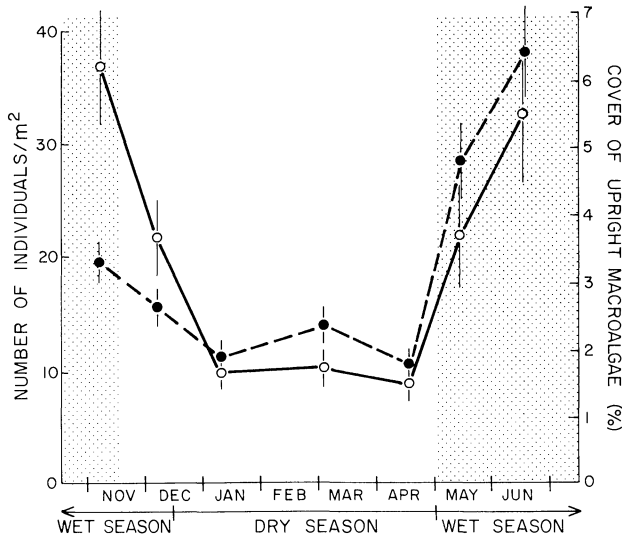


FIG. 3.—Seasonal change in mean density and percent cover of upright macroalgae on the sand plain. Estimates were obtained from one hundred randomly located 1.0-m² quadrats. Open circles represent mean % cover/m² and closed circles represent mean number of individuals/m². Vertical bars show 95% confidence intervals.

(fig. 2). A correlation analysis of total algal biomass per quadrat against the weight of hard substrate per quadrat (a rough estimate of attachment site availability) was significantly positive ($r = .45$, $.05 > P > .025$) in slope.

Mid-day light levels ($\mu\text{E}/\text{m}^2$ per s) on the sand plain during the dry season ($\bar{X} = 33$, $\text{SE} = 12$, $N = 29$) were about 60% below those for the wet season ($\bar{X} = 81$, $\text{SE} = 26$, $N = 12$). Dry season conditions of low light and sand movement result in the

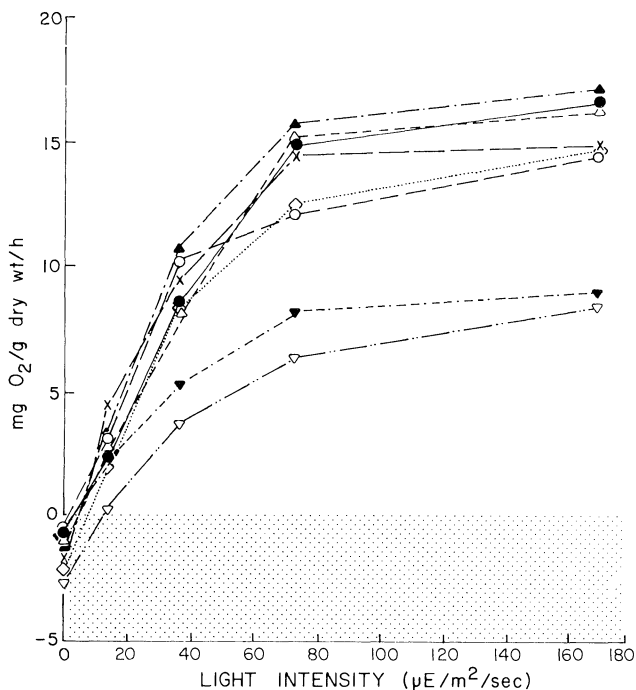


FIG. 4.—Apparent photosynthesis ($\text{mg O}_2/\text{g dry wt/h}$) as a function of light quantity for two common reef-slope algae, *Bryothamnion seaforthii* (\blacktriangledown) and *Halimeda opuntia* (∇), and six common sand-plain algae, *Gracilaria* sp. 1 (\bullet), *Gracilaria* sp. 2 (\circ), *Gracilaria* sp. 3 (\blacktriangle), *G. domingensis* (\triangle), *Solicria tenera* (\diamond) and *Spyridia aculeata* (\times). $N = 6$ for each determination and significant ($P < .05$ by analysis of variance and Newman-Keuls) differences are as follows: At 35, 70, 170 $\mu\text{E}/\text{m}^2/\text{s}$ *Bryothamnion* and *Halimeda* are lower than all other species and are not different from each other. At 13 $\mu\text{E}/\text{m}^2/\text{s}$ *Halimeda* is lower and *Spyridia* is higher than all other species, and at 0 $\mu\text{E}/\text{m}^2/\text{s}$ *Halimeda* is lower than all other species.

reduction of percent cover and number of plants on the sand plain (fig. 3). Both of these increase rapidly in early May when winds decrease and turbidity is reduced.

For the range of light levels tested (fig. 4), species from the sand plain are more productive than those from the reef and both become light saturated at about 75–100 $\mu\text{E}/\text{m}^2$ per s. This is approximately the mean light level recorded at mid-day on the sand plain during the wet season but is triple that of the dry season mean. Both the light saturation curves (fig. 4) and the greater abundance and size of algae colonizing the monofilament lines at shallower depths (table 2A, 2B, fig. 5) show that light limitation occurs during most of the year. Recruitment (densities), growth (size), reproduction (proportion of fertile thalli), and species numbers on the lines at the 1.5–4.5 m depth greatly exceeded that at the deeper stations during both wet and dry seasons (fig. 5), and show that sand-plain algae can complete their entire life history in shallow water subject to high light intensities. Plants at the shallower depths were often much larger and much more densely branched than those at deeper levels or those occurring naturally on the

<i>Gracilaria domingensis</i>	9	44.2	22	2♀								
<i>Spyridia aculeata</i>	1	30.1	0									
<i>Hypnea cornuta</i>	5	44.2	20	1♀								
Dry season												
<i>Gracilaria</i> sp. 1	17	27.0	12	2♀	22	6.5	4	1♀	18	5.2	0	
<i>Gracilaria</i> sp. 3	9	25.2	77	2♀5*1♂	7	18.3	42	1♀2*	1	.8	0	
<i>Gracilaria domingensis</i>	6	8.5	0		3	2.5	0		2	3.7	0	
<i>Chondria tenuissima</i>	27	24.9	7	2♀	1	.2	0					
<i>Boryocladia</i> sp.	7	2.4	86	1♀5*	2	.2	100	1♀1*				
<i>Euclima</i> sp.					1	.5	0					
<i>Gracilaria cylindrica</i>	1	58.1	100	1♀	1	2.0	100	1♀				
<i>Gracilaria cuneata</i>	3	10.8	0		1	.7	0					
<i>Spyridia aculeata</i>	3	1.8	0	1♀	1	4.9	0					
<i>Bryothamnion seaforthii</i>	2	42.0	100	2♀	2	.3	0					
<i>Solieria tenera</i>	5	28.0	0		4	44.1	0					
<i>Hypnea cervicornis</i>	1	8.1	0									
<i>Gracilaria</i> sp. (foliifera?)	3	24.0	33	1♀1*								
<i>Gracilaria</i> sp. 2	1	.6	0									
<i>Botryocladia pyriformis</i>	4	1.0	25	1♀								
Unidentified red	1	.1	0									

NOTE.—Wet-season collections were taken on Sept. 25, 1978 from 18 monofilament lines that had been available for settlement for 15–25 weeks. Dry-season collections were taken on March 3, 1979 from 11 of the original 18 lines; seven lines were destroyed during the dry season. Since reproductive male (♂) plants are often difficult to detect, only reproductive female (♀) and tetrasporic (*) plants were considered in determining the percentage of reproductive plants. If reproductive males were seen, this was noted under reproductive type.

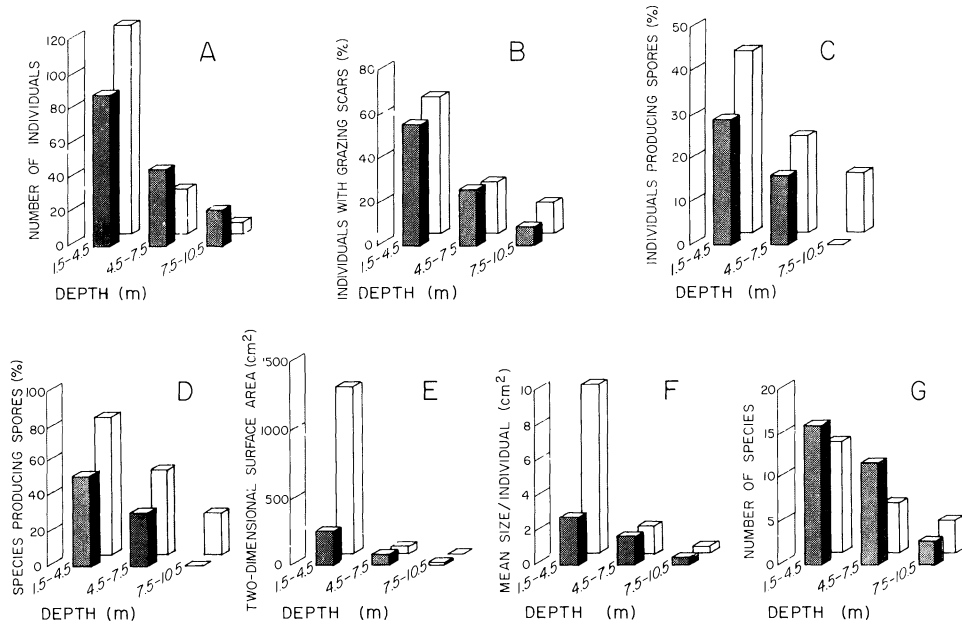


FIG. 5.—The effect of depth on the sand-plain algal assemblage during the wet and calm (light bars) and dry and turbid (dark bars) season. Data are from table 2 with all species pooled at each depth.

sand plain. Plants at 1.5–4.5 m deep were not photoinhibited since these grew to a larger size (fig. 5) and had higher reproductive output than those at deeper levels. Small herbivorous fishes settled out among the large algal clumps at the shallower stations and this resulted in greater evidence of grazing at these depths (fig. 5).

When plants from the sand plain were moved to the reef slope during the early dry season (table 3), they lost significantly (Mann-Whitney U test, $P < .0005$) more biomass than control plants transplanted back onto the sand plain. Crescent-shaped scars resulting from fish grazing were evident on all sand-plain species that were placed on the reef slope, with four of the 30 plants showing the more ragged marks of sea urchins as well. The reef-slope alga, *Bryothamnion seaforthii*, had several grazed tips but showed no measurable loss in wet weight.

Caging experiments conducted during the wet season showed that the sand-plain species could increase their wet weight by about 70% in 2 wk when placed on the reef slope at 4.5 m deep (fig. 6), and that fish grazing alone could account for their exclusion from the reef-slope habitat. Plants placed at a distance of at least 10 m from the cages showed considerable losses of wet weight in only 24 h (*Gracilaria domingensis*, $\bar{X} = -64\%$, $SE = 13\%$, $N = 8$; *Gracilaria* sp. 1, $\bar{X} = -100\%$, $SE = 0\%$, $N = 8$), while plants in the open cages showed only minor damage after this same period. This suggests that the cages inhibited herbivorous fish to some extent and that grazing rates in the open-sided cages were artificially low. During the experiment, new individuals of *Gracilaria* sp. 1 and *G. domingensis* recruited onto coral fragments in the closed cages and onto several of the metal

TABLE 3
EFFECT OF GRAZING ON ALGAE FROM THE SAND PLAIN WHEN PLACED IN REEF-SLOPE OR SAND-PLAIN HABITATS
(All transplants were conducted during December 1977.)

	<i>Solieria tenera</i>	<i>Gracilaria</i> sp. 1	<i>Gracilaria domingensis</i>	<i>Halimenia floresia</i>	<i>Bryothamnion seaforthii</i>
Primary habitat	sand plain	sand plain	sand plain	sand plain	reef slope
Mean wet wt/plant	15 g	3 g	8 g	13 g	10 g
Mean change of plants on the sand plain (N)	-10.7% (6)	-7.2% (10)	-2.7% (10)	-20.5% (9)	+3.2% (10)
Mean change of plants on the reef slope (N)	-79.8% (8)	-93.9% (10)	-37.5% (10)	-78.9% (10)	+11.3% (10)
P value by the Mann-Whitney U test	P < .0005	P < .0005	P < .0005	P < .0005	P > .20
No. of reef plants showing scars from fish grazing*	unable to differentiate				
No. of reef plants showing scars from urchin grazing*	unable to differentiate	0	4	0	0

* Samples placed on the sand plain never showed urchin scars and only two fish scars were observed, both on *Halimenia floresia*.

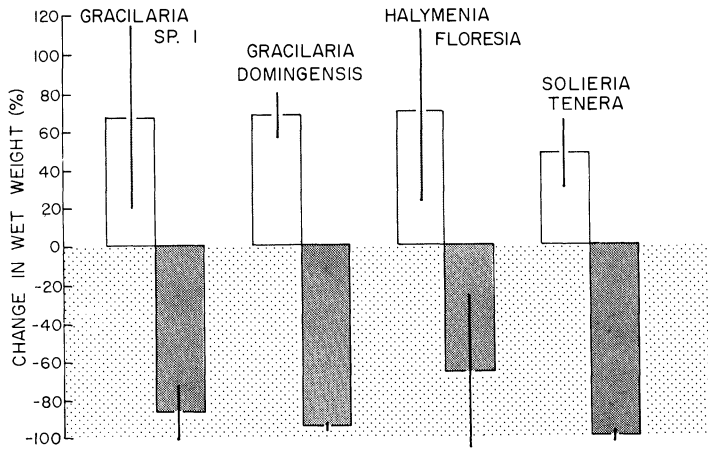


FIG. 6.—Percent change in wet weight of sand-plain algae when placed on the reef slope in closed (lightly shaded) and open-sided (darkly shaded) control cages for 14 days. Vertical bars represent 95% confidence intervals; $N = 8$ for each treatment.

support rods. In a survey of six ropes (some as many as 6 yr old) that anchor marker buoys on the reef, 10 species of sand-plain algae were found along with one species that occurs on both the reef slope and the sand plain (table 4). Together, these observations provide documentation that spores of the sand-plain species do reach the reef and are capable of germinating and growing well in that physical environment, when they are protected from herbivores.

When *Halimeda opuntia* and *Amphiroa* spp. were transplanted onto the sand plain, they showed no sign of either damage from herbivores or active growth. These species would either gradually lose their pigment and appear to decompose or become covered by sand and die.

Forty percent (10 of 25) of the nonfilamentous, upright genera of algae that occur on the sand plain also occur on the northeastern coast of North America (table 5) while only 14% (4 of 28) of such reef-slope genera are found at that latitude. This difference is significant ($P = .035$, Fisher's exact test) and is consistent with the hypothesis that sand-plain algae have a competitive advantage over reef-slope species.

DISCUSSION

Hypothesis 1: Limiting Resources

Although hard substrates were patchy (fig. 2) and comprised only 4% cover, they supported 93% of the biomass and 88% of the individuals (table 1) occurring on the sand plain in June, 1979. Thus, further expansion of the algal assemblage was limited over 96% of the sand-plain surface area by the lack of adequate attachment sites. In addition, light limitation occurred throughout much of the year (fig. 5) and further restricted growth on the hard substrates. Marked decreases in algal cover and density (fig. 3) occurred when dry-season winds in-

TABLE 4
MACROALGAE FOUND GROWING ON ROPES WHICH ANCHORED BUOYS TO THE REEF

SPECIES	DISTRIBUTION		
	Sand Plain Only	Sand Plain and Reef Slope	Reef Slope Only
<i>Bryothamnion seaforthii</i>		+	
<i>Botryocladia occidentalis</i>	+		
<i>Gracilaria</i> sp. 1	+		
<i>Gracilaria</i> sp. 3	+		
<i>G. cylindrica</i>	+		
<i>Gracilaria</i> sp. 6	+		
<i>Nitophyllum</i> sp.	+		
<i>Delesseriaceae</i>	+		
<i>G. cuneata</i>	+		
<i>Spyridia aculeata</i>	+		
<i>Weberella pelta</i>	+		

NOTE.—The ropes had been on the reef for 1–6 yr.

TABLE 5
COMPARISON OF THE NUMBER OF REEF-SLOPE AND SAND-PLAIN GENERA FROM GALETA, PANAMA, ALSO FOUND ON THE NORTHEASTERN COAST OF NORTH AMERICA

	Total No.	No. Found on Northeastern Coast of North America	No. Not Found on Northeastern Coast of North America
Sand-plain genera	25	10	15
Reef-slope genera	28	4	24

SOURCE.—Only nonfilamentous, upright genera are included and Taylor (1937) is used as the reference for North America genera.

NOTE.— $P = .035$, Fisher's exact test.

creased sand movement and turbidity, and resulted in extremely low (often $0 \mu\text{E}/\text{m}^2$ per s) light levels on the sand plain. Thus, during the benign wet season, the habitat is severely resource limited (i.e., light and substrate) and during the stressful dry season it is unsuitable for growth. The nearby reef slope offers an abundance of attachment sites with higher light levels; however algal species from the sand plain rarely occur there.

Hypothesis 2: The Extent of Physiological Specialization

It has been suggested (Dobzhansky 1950; Klopfer 1959; Williams 1964; Janzen 1967) that many tropical organisms have become physiologically specialized to the extent that they are physically restricted to the environments in which they occur. Many of the algal species present on the sand plain have been characterized (Taylor 1960) as "deep water" species; therefore they could conceivably be excluded from the reef slope because of photoinhibition leading to reduced growth

and reproduction. Photoinhibition has been suggested (Jones 1959; Littler and Doty 1975) as a primary factor in restricting the distribution of some algae in other systems.

The plants examined here showed no indication of photoinhibition at shallower depths (table 2A, 2B, fig. 5) and grew rapidly on the reef slope (fig. 6) when grazers were excluded. All parameters used to assess habitat preference indicated that sand-plain species are most fit (density, accumulated surface area, and fertility were used as correlates of fitness) in shallow waters and that fitness decreases rapidly with depth. Wet-season comparisons between the station at 1.5–4.5 m deep and the one at 7.5–10.5 m (fig. 5) were striking and revealed the following differences: At the deeper station algal density was 94% less; the proportion of individuals producing spores decreased by 67%; the proportion of species with reproductive individuals was reduced by 71%; two-dimensional surface area declined by over 99%; average plant size was 96% smaller; and the number of species declined by 69%. Samples taken during the dry season showed the same pattern. Throughout both wet and dry season (table 2A, 2B), the algal assemblage on the lines at deeper stations comprised a subset of that present at shallower stations: No deep water or low light specialists were apparent; and all the species studied grew as well or better at the shallower depths and higher light intensities.

Throughout all levels of light quantity tested (13–170 $\mu\text{E}/\text{m}^2$ per s) sand-plain species were about twice as productive (fig. 4) as reef-slope species. Both sand-plain and reef-slope species saturated at about 75–100 $\mu\text{E}/\text{m}^2$ per s. Therefore, sand-plain species were more productive than reef-slope species, and were not harmed by high light intensities (fig. 5) encountered in the field. Their efficiency at low light levels suggests some degree of specialization to the sand-plain habitat but this has not necessitated adaptations that make shallower, brighter areas physiologically unavailable. Conversely, most reef-slope species appear to be unable to tolerate the low light levels and high sedimentation characteristic of the sand plain since algae moved from the reef slope to the sand plain invariably died.

Although surge and wave action were stronger on the shallower reef slope, this did not exclude the fleshy, sand-plain species from the reef. The only times that sand-plain species appeared on the reef slope were during periods of severe wave action, which apparently inhibited herbivore feeding. These algae showed no damage caused by the increased water motion, but as the seas grew calmer all plants began to show the crescent-shaped scars of herbivorous fish and disappeared within a few days.

Hypothesis 3: The Effect of Herbivores on Distribution

Both the dry-season transplants (table 3) and the wet-season caging experiments (fig. 6) showed that grazing pressure is intense enough during both seasons to exclude sand-plain species from the reef. During the dry season, 100% of the sand-plain individuals that were transplanted onto the reef showed evidence of fish grazing (table 3) while only 13% showed evidence of damage from urchin grazing. The wet season caging experiment completely excluded urchins and demonstrated that fish grazing alone could exclude sand-plain species from the

reef slope. This supports Randall's (1961, 1965) contention that herbivorous fishes are the grazers of primary importance on undistributed reefs although urchin grazing has been shown to be a primary factor (Ogden et al. 1973*b*) on reefs that have been overfished.

Herbivores have previously been demonstrated to exclude sea grasses from sandy areas close to reefs (Randall 1965; Ogden et al. 1973*b*) but since these grasses must root into the sand, this affects only a small portion of the available habitat. The interaction of sand-plain algae with reef-associated grazers is fundamentally different in that this assemblage of plants is excluded by herbivores from the habitat to which it is best suited physiologically and is confined to a physically marginal refuge where grazing is much reduced.

Hypothesis 4: The Effect of Herbivores on Competition

The data presented here give predictive insights into potential competitive interactions between reef-slope and sand-plain algae. Tropical reefs are characterized by an abundance of light and hard substrate occupied by corals and crustose coralline algae (Dahl 1972; Taylor 1950; Bakus 1967; Glynn 1976). Intensive grazing by fishes (Stephenson and Searles 1960; Randall 1961, 1965, 1967, 1974; Earle 1972; John and Pople 1973) and sea urchins (Ogden et al. 1973*a*, 1973*b*; Sammarco et al. 1974) prevent the coralline algae from being overgrown by frondose algae (Vine 1974; Wanders 1977). Under such conditions, the primary selective pressure should be for the evolution of antiherbivore defenses, with selection for competitive characteristics that enhance either substrate acquisition and retention or efficient light utilization playing a secondary role. This is in contrast to the sand plain where grazing activity is low (Earle 1972; Dahl 1973; Parrish and Zimmerman 1977) and attachment sites (Dahl 1973, fig. 1) and light (fig. 5) are limiting resources. Consequently, on the sand plain, selection should favor the evolution of competitive characteristics and minimize antiherbivore traits.

Species from the sand plain were more productive and used light quantity more efficiently (fig. 4) than reef-slope species. All sand-plain species grow as upright individuals that can produce a relatively large "canopy" from a single small attachment site, while the most abundant reef-slope species occur as crusts or closely packed aggregates of upright branches (e.g., *Halimeda opuntia*) that produce much less canopy per unit of attachment area. Several of the sand-plain species (*Solieria tenera*, *Neogardhiella ramosissima*, and *Spyridia aculeata*) can attach to both hard substrates and other plants and, on the sand plain, these often attach to, and overgrow, coarser forms such as *Bryothamnion seaforthii* and *Halimeda copiosa*.

The higher productivity of sand-plain species should allow them to grow faster, produce more spores, and colonize newly opened areas faster than reef-slope species. Sand-plain algae are usually tall canopy formers that require less substrate and light and should, therefore, be able to grow above and shade out reef-slope algae. Facultative epiphytes from the sand plain may also overgrow reef-slope species following direct attachment. Therefore, if grazers were re-

moved from the reef slope, allowing competition (either interference or exploitation) for space and light to occur, it is highly probable that the sand-plain species would prevail. Collections from five buoyed ropes (these are unavailable to urchins and fish do not swim up into the water column to graze them) that had been on the reef for 1–6 yr supported this contention since they contained 10 species of algae which occur only on the sand plain, one species present on both the reef slope and the sand plain and none exclusively from the reef slope (table 4).

A second partial test of the hypothesis would be an examination of tropical areas where unusual conditions remove most herbivores. The intertidal area below Gatun Locks, the Caribbean entrance to the Panama Canal, appears to be such an area. Herbivorous fish and urchins are not present there (possibly because of periodic pulses of low salinity water) and the common algal species have been replaced by an assemblage dominated by *Gracilaria cylindrica*. When describing the algae of the Caribbean, Taylor (1960) considered *G. cylindrica* to be a deep-water species restricted in its distribution to below about 15 m, and at Galeta Reef, where grazers are common, the plant occurs only on the sand plain. Although the mouth of the freshwater canal at Panama is an unnatural situation, the abundance in the intertidal there of a so-called deep-water species further supports the contention that such forms could outcompete many of the common shallow water species if herbivore pressures were removed.

Hypothesis 5: Competitive Abilities and Geographic Distribution

If the greater activity of predators or herbivores in the tropics (Doutt 1960; Gillette 1962; Ehrlich and Raven 1964; Paine 1966; Baker 1970; Bouliere and Hadley 1970; Janzen 1970) keep prey populations below the carrying capacity of the physical environment, thus reducing the importance of competitive interactions between prey species (Ricklefs 1979), then competitive ability may be less important than herbivore resistance in explaining the realized patterns of distribution and abundance of tropical plants. In terrestrial systems, the proportion of alkaloid-producing plants is negatively correlated with latitude (Levin 1976), and geographic patterns in efficiency of wood production (Jordan and Murphy 1978) suggest that competition among trees is greater at higher latitudes. Although herbivores clearly play important roles in structuring many temperate, algal assemblages (Paine and Vadas 1969; Dayton 1971, 1975; Lubchenco 1978; Sousa 1979), the large standing crop, limited attachment sites, and multilayered canopies found in many temperate areas strongly suggest that competition is also important. Competition appears to be less important on tropical reefs where, in general, herbivory is intense, standing crops are low, attachment sites are abundant, and canopy formation is usually weak or totally lacking. If competitive interactions are indeed more common or more intense in temperate areas, and if sand-plain species are the better competitors, then they should be relatively well adapted for the more competition-intensive temperate communities. Conversely, the most apparent species on shallow tropical reefs should be excluded by competition from temperate regions where selection is stronger for competitive ability and weaker for antiherbivore characteristics. Therefore, sand-plain species should be distrib-

uted over a wider latitudinal range than reef-slope species and should also become increasingly abundant in shallower habitats in temperate areas because grazing fish have less impact. At present, the incomplete understanding of the taxonomy and distribution of tropical algae (e.g., J. N. Norris estimates that 40% of the species collected from the Galeta Reef area represent new records for Panama) precludes a rigorous test of the hypothesis. A partial test using genera from the reef slope and sand plain at Galeta (table 5) shows that significantly more of the genera found on the sand plain are also found on the northeastern coast of North America. Such correlative findings lend support to the stated hypothesis but should not be viewed as conclusive proof until experimental evidence becomes available to assess the importance of differential competitive ability in generating the pattern.

HERBIVORY, COMPETITION, AND THE MAINTENANCE OF DIVERSITY

Predation (Paine 1966; Janzen 1970; Connell 1971, 1975) and herbivory (Darwin 1859; Harper 1969; Lubchenco 1978) have often been shown or hypothesized to be important in maintaining within-habitat diversity by acting selectively upon abundant species and thus decreasing the probability of competitive exclusion. In the system examined here, the effect of herbivores on within-habitat diversity depends upon both level of activity and selectivity (see Lubchenco 1978). If herbivore pressure or food preference changed in such a manner that sand-plain algae could occur on the reef in low abundances that did not adversely affect the population levels of reef-slope algae, then as many as 75–100 new species could be added to the community without reducing the number of those already present. Conversely, if herbivore impact were reduced drastically, a few sand-plain species might exclude large numbers of reef-slope species causing a marked reduction in diversity. The importance of reef-slope herbivores in maintaining between-habitat diversity is clear since herbivory, not the physical habitat, is directly responsible for maintaining the boundary between two distinctive algal assemblages, one of which should be able to exclude the other.

SUMMARY

An extensive sand plain containing scattered hard substrates dominated by algae adjoins the shallower Galeta reef seaward from a depth of 11–14 m. This sand plain represents a physically marginal habitat where low light and lack of adequate attachment sites limit algal growth and where seasonal physical disturbances (turbidity and sand movement) cause large decreases in algal densities and cover. Light levels are higher and substrate more abundant on the nearby reef slope but species from the sand-plain assemblage rarely occur there. Algae from both reef-slope and sand-plain habitats become light saturated at approximately the same level (75–100 $\mu\text{E}/\text{m}^2$ per s) but those from the sand plain were more productive (i.e., more efficient) throughout the range of light levels tested (13–170 $\mu\text{E}/\text{m}^2$ per s). Efficient utilization of low light levels allows sand-plain species to survive on the dimly lit bottom but does not prohibit them from occupying areas of

high light intensity. During two experimental periods of approximately 6 mo each, plants that settled on monofilament lines at about 3 m deep were 4–20 times more numerous, 6–23 times larger, more than three times as fertile, accumulated 27–400 times as much two-dimensional surface area, and were represented by 3–5 times as many species as algae that recruited at about 9 m deep. Although resources are more plentiful and sand-plain species more fit in shallower reef-slope areas, they are excluded from these habitats by intensive herbivory.

It is hypothesized that in the absence of grazing, sand-plain species would competitively exclude reef-slope species from much of the subtidal reef. If this is valid, then reef herbivores, by limiting competitive dominants to refuge areas, are of primary importance in maintaining the large between-habitat diversity typical of shallow Caribbean reef systems.

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