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THE FUNCTIONAL MORPHOLOGY OF TURF-FORMING SEAWEEDS: PERSISTENCE IN STRESSFUL MARINE HABITATS¹

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Abstract. Many seaweeds that occur in physically stressful habitats or habitats subject to moderate herbivory grow as colonial turfs rather than as spatially separated individuals. The turf growth form is energetically expensive (the net production per gram ash free dry mass of turfs being 33–61% lower than that of individuals), but turfs suffer less physiological damage during desiccating low tides and lose less biomass to herbivores. The upper portions of turf-forming species show significantly greater rates of apparent photosynthesis and dark respiration than do the lower portions. This spatial partitioning of photosynthetic activity decreases the energetic cost of the turf arrangement and may allow basal portions to function as persistent resting stages during periods of adverse conditions when uprights cannot be maintained. Turf-forming species are specialized for areas that are subject to moderate grazing pressure and physical stresses. They are dependent upon these factors to prevent their competitive exclusion by more productive, but less resistant, seaweeds. Damage to apical portions causes increased branching that results in a more tightly compacted turf. Algae that regenerate in this way can adjust their growth form in accordance with varying levels of disturbance encountered in different habitats and thus incur the minimal cost consistent with survival in that area.

For seaweeds occurring in stressful habitats, selection has favored characteristics that increase persistence in space and time even though these involve considerable losses in competitive ability and productivity.

Key words: *competition; desiccation; Dictyota; fringing reef; Halimeda; herbivory; Laurencia; morphology; productivity; seaweeds; turf.*

INTRODUCTION

Many seaweeds grow as colonial assemblages rather than as spatially separated individuals (see Harper [1977] for a discussion of similar growth characteristics in terrestrial plants). Among them, the turf growth form is abundant worldwide in tropical and temperate intertidal habitats (Stephenson and Stephenson 1972) and is generally the dominant form in shallow reef habitats (Dahl 1972, 1973, Cribb 1973, Benayahu and Loya 1977).

Turf species possess both prostrate and upright branches. The number of uprights is increased primarily by means of vegetative growth, with the compact turf configuration being affected by: (1) the number of uprights per length of prostrate, (2) their degree of branching, and (3) the extent to which lateral connections form between uprights.

Turf-forming species show considerable morphological plasticity. In subtidal habitats with low grazing, fronds tend to be arborescent, sparsely branched, and loosely arranged, while in desiccated or grazed areas they often become shorter, more erect and more highly branched and compacted (Dahl 1968, Stewart 1968, Munda 1972, Gittins 1975, Liddle 1975). The produc-

tivity of a freshwater alga has been shown to vary inversely with the density of uprights (Pfeifer and McDiffett 1975) and packing often occurs to such an extent in these turf-forming species that productivity should be severely decreased due to self-shading and nutrient limitation.

Since many species from the three major divisions of seaweeds (Chlorophyta, Rhodophyta, and Phaeophyta) have shown convergent evolution of this growth form, it would appear that there are adaptive advantages inherent in the turf configuration that compensate for the loss of productivity and enable these species to maintain successful populations in stressful habitats.

The tight packing of uprights should result in: (1) decreased net photosynthesis due to self-shading and nutrient depletion within the turf matrix, (2) concentration of photosynthetic activity in the upper portions of the thallus since lower portions receive little light, (3) decreased dark respiration rates in the lower portions of the assemblage because less energy needs to be allocated to building or maintaining photosynthetic apparatus, (4) reduction of desiccation stress due to the increased water-holding capacity of the turfs, (5) decreased grazing losses because turfs are more difficult for herbivores to manipulate and basal attachment areas are shielded by the tightly packed uprights, and (6) a competitive disadvantage since algae that grow as individuals or as colonies with more loosely

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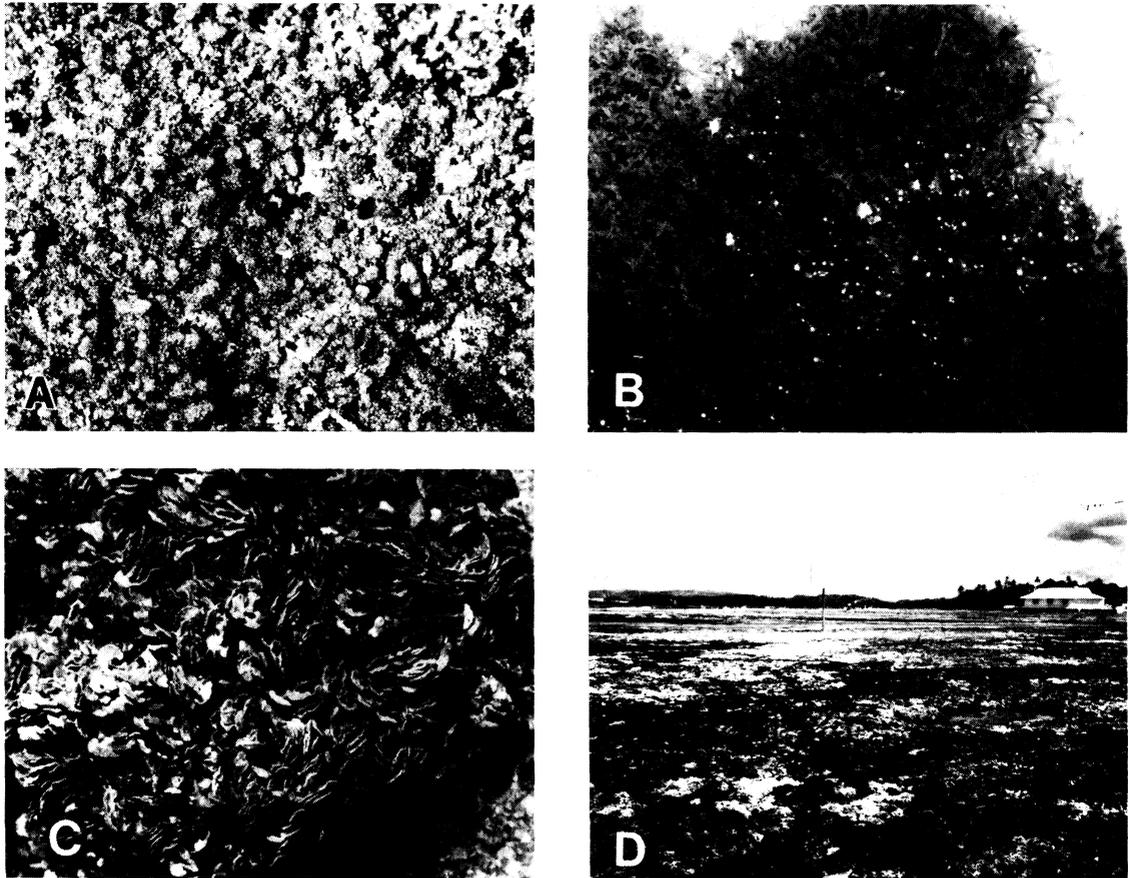


FIG. 1. The reef-flat habitat and major turf-forming species at Galeta Point, Panama. (A) *Laurencia papillosa*, (B) *Dictyota bartayresii*, (C) *Halimeda opuntia*, (D) a reef-flat exposure showing the turf-dominated edge of the flat in the foreground.

arranged uprights require less attachment space, use light more efficiently and grow faster.

These hypotheses were tested using the three most common turf-forming species at Galeta Reef, Panama; the brown *Dictyota bartayresii* Lamouroux, the green *Halimeda opuntia* (Linnaeus) Lamouroux and the red *Laurencia papillosa* (Forsskal) Greville.

METHODS AND MATERIALS

Terminology

In this paper the term turf refers to situations where upright branches are more than 0.5 cm tall and are packed so that each is in contact with its neighbors (Fig. 1A–C). In tightly packed turfs this occurs to such an extent that the upper sections of the branches form a continuous, stiff matrix with each upright firmly attached to others with which it comes in contact. Small (<0.5 cm tall) filamentous species that trap sediment and have uprights that are arranged in both vertical and horizontal positions are called mats. The term runners is used for plants that produce scattered uprights along their stoloniferous prostrate axis. Algae that have a single attachment site and do not grow in tight

clumps are referred to as individuals. Thin flat forms that adhere tightly to the substrate are called crusts.

These terms are useful for discussing algal growth forms, but most seaweeds are phenotypically plastic and not all fit well into a single category. Some species have both crustose and upright portions or alternate between these forms during different periods of their life history (see Lubchenco and Cubitt 1980), while others may grow as runners, individuals, loose turfs or tight turfs depending upon the habitat in which they occur.

Study site and organisms

The reef at Galeta Point is typical (Glynn 1972) of fringing reefs on the Caribbean coast of Panama. On the reef flat, hard substrate is dominated by compact turfs consisting primarily of *Laurencia papillosa*, *Halimeda opuntia* and several species of *Dictyota*. Severe exposures to air occur on the reef flat when low tides coincide with calm weather (Fig. 1D). These exposures can be of long duration (Fig. 2) and may kill most nonswimming herbivores (Glynn 1968, Meyer et al. 1975, Hendler 1977) as well as significantly reduce algal cover.

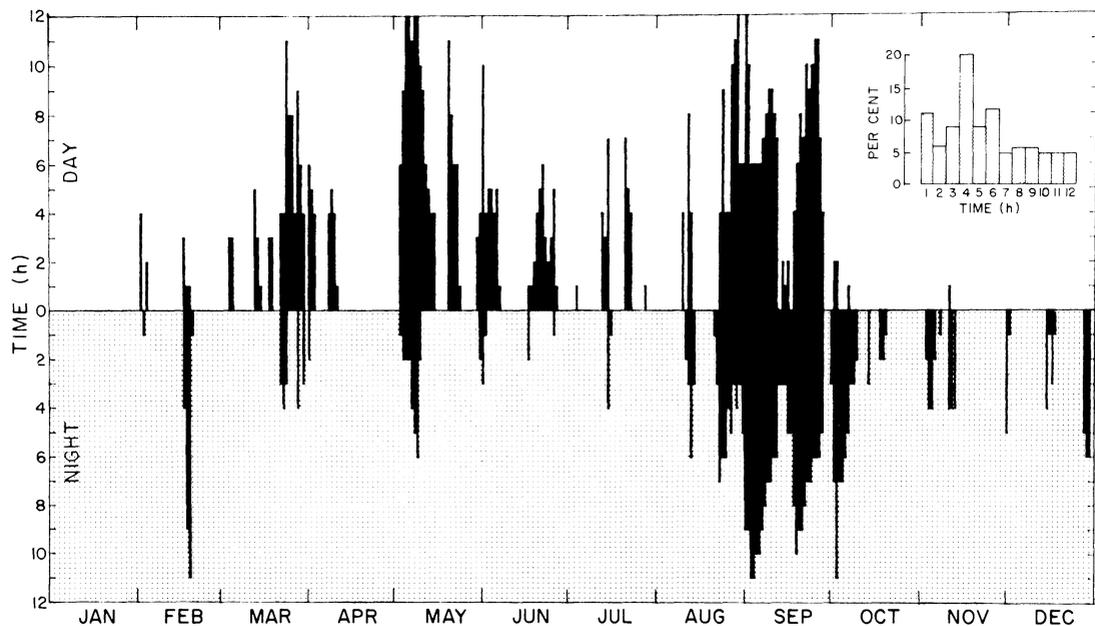


FIG. 2. The number of hours per day during which the turf-dominated reef edge was exposed by low tides for the year 1974. Times above the X-axis represent daylight hours (between 0600–1800), lines below the X-axis represent nighttime hours (before 0600 or after 1800). The histogram in the upper right corner gives a breakdown of the duration of daytime exposures according to their frequency of occurrence. (Tidal data are from the mid-reef tide gauge at the Galeta Point Marine Laboratory of the Smithsonian Tropical Research Institute.)

For a subtidal tropical habitat, the reef slope supports a relatively lush growth of seaweeds (exceeding 100% cover of upright species in some areas). Shallower areas are populated primarily by encrusting coralline algae and turf-forming species, while plants growing as individuals or as loosely arranged aggregates become more abundant with increasing depth. Turf-forming species at Galeta occur from 1–10 m deep, but form tightly compacted assemblages only in the shallower areas.

Laurencia papillosa is a fleshy red alga that grows in coarse turfs from 2–10 cm tall (Fig. 1A) and occurs only on the platform. It is excluded from the reef slope by grazing fishes and urchins (M. E. Hay, *personal observation*). Unlike many other members of the genus (Fenical 1975, Fenical and Norris 1975), it does not appear to have large amounts of secondary metabolites which might act as herbivore deterrents (Fenical and Norris, *in press*).

Dictyota bartayressii, a thin brown alga that forms dense, hemispherical clumps (Fig. 1B), is most abundant in tide pools and channel areas of the reef flat but can also occur on the reef slope. The lower portions of the fronds form extensive lateral connections that make the turf fairly rigid and only the uppermost portions move with the current. It has a high concentration of polyphenol substances (Norris and Fenical, *in press*) and is often abundant in areas subject to moderate grazing pressure.

Halimeda opuntia is abundant on many portions of the reef slope above ≈ 5 m of depth and also occurs in moderate abundance on the reef flat in pools and beneath other algae or sea grasses. It is a calcified, articulated, green alga that forms tightly compacted turfs on the reef flat (Fig. 1C) and moderately compacted ones on the shallow reef slope. It occurs as a lax aggregation of nonlaterally connected uprights in the deeper parts of its range. *H. opuntia* often occurs in areas subject to high grazing rates and appears to be a low preference item for most herbivores. Work on the natural product chemistry of *H. opuntia* is now in progress (W. Fenical, *personal communication*) and it appears to contain compounds related to those found in other members of the Codiaceae, for example *Rhipocephalus* (Sun and Fenical 1979).

Tests of the hypotheses

To examine hypothesis 1: (turfs should have decreased photosynthetic rates), turfs of *Laurencia papillosa*, *Halimeda opuntia*, and *Dictyota bartayressii* were collected from the reef flat or shallow reef slope and incubated as aggregates and as "individuals" (individuals consisted of separated aggregates) in 1.19 L light and dark bottles. Six replicates were used in each experiment and all incubations (1–3 h) were conducted between 1000 and 1400 in a shallow seawater tank (30°–31°C) immediately adjacent to the reef flat. Stirring was provided at 10–15 min intervals by magnetic

stirrers and all O₂ determinations were made with a Yellow Springs Instrument Company Model 57A O₂ meter and electrode. Blank bottles were used to control for phytoplankton production and all O₂ determinations were made under sunny skies on 10 April 1978.

Hypotheses 2: (photosynthesis should be concentrated in the upper portions of the thallus) and 3: (respiration should be reduced in the lower portions) were tested by cutting off the upper and lower thirds of turfs with a razor blade and incubating them as described above. (Preliminary tests using cut and uncut thalli showed no detectable effect of cutting on respiration or photosynthesis.)

To test hypothesis 4: (the turf form should decrease desiccation stress), a reef-flat exposure was simulated by placing turfs and individuals of each species on pieces of damp coral rock that were located in moist sand on the edge of the Galeta reef flat. The rate of water loss was measured by periodically subsampling uprights from the different treatments and determining their wet mass to dry mass ratios. Thalli from the two treatments were collected at hourly intervals, placed in running seawater for 0.5–1 h, then incubated as above. Because the turf configuration significantly affects production rates, all turfs were separated and incubated as individuals to facilitate comparison between treatments. Tests were conducted during late June and early July 1978; however, since species were tested on separate days, no comparisons will be made between different species. Experiments using *Dictyota bartayresii* and *Halimeda opuntia* were done on hazy, overcast days, while those using *Laurencia papillosa* were done on a bright, sunny day. Since these experiments were carried out during the wet season when wind speed and solar radiation are low (Hendler 1976) and relative humidity is high, conditions prevailing during reef flat exposures that occur during the dry season are probably much more severe.

Hypothesis 5: (turfs should be less vulnerable to grazing) was evaluated by pairing aggregate and individual arrangements of each species by wet mass, mounting them in numbered sections of three-strand rope and placing them where the sea urchin *Diadema antillarum* Philippi or the parrot fish *Sparisoma rubripinne* Cuvier and Valenciennes could graze them. Ten aggregate-individual pairs were used in each experiment.

Grazing experiments with urchins were performed in a shallow, sandy lagoon where *Diadema* densities were 10.4 urchins/m² (SE = 2.2, N = 10) and herbivorous fish were not active (throughout 2.0 h of observation during each test, no herbivorous fish were seen in the experimental area). Urchin experiments lasted 12–24 h. Fish grazing experiments were performed in a large (depth = 1.0 m, diameter = 3.0 m), continuous-flow seawater tank and all tests lasted 24 h.

The suitability of turf-dominated areas for urchins was assessed by measuring urchin densities in turf

centers, at turf margins, and in nearby areas that were structurally similar but devoid of turfs. A 0.15-m² (30 × 50 cm) quadrat was flipped end-over-end along six transects randomly located within a bed of *Porites* (finger coral) that was partially overgrown by turfs (primarily *Halimeda opuntia*, with *Dictyota bartayresii* and *Amphiroa* spp. being present but much less abundant). All transects were between 1 and 2 m deep and the coral structure below turfs appeared identical to that which was nearby but not overgrown. Quadrats with >80% cover of turfs were considered turf centers, those with 25–50% turf margins, and those with <5% were considered to be devoid of turfs. All urchins within each quadrat were counted regardless of species or size.

Several different approaches were used to evaluate hypothesis 6: (turfs should be poor competitors). The apparent photosynthetic rate of each common species (*Acanthophora spicifera* [Vahl] Borgesen; *Centroceras clavulatum* [C. Agardh] Montagne; *Dictyota bartayresii*; *Gelidiella acerosa* [Forsskal] Feldmann and Hamel; *Halimeda opuntia*; *Hypnea musciformis* [Wulfen] Lamouroux; *Laurencia papillosa*; and *Spyridia filamentosa* [Wulfen] Harvey) within the *Laurencia*-dominated area of the reef flat was measured as described above.

The susceptibility of each of these species to desiccation was measured by simulating a 2-h reef-flat exposure and comparing photosynthetic rates of desiccated plants with nondesiccated controls. Plants of each species were simultaneously placed on a damp concrete slab located by the reef flat and allowed to dry for 2 h. The plants were then allowed to recover in running seawater for 48 h before measurements of apparent photosynthesis were made. Control plants were also held in running seawater for 48 h prior to incubation.

To assess the effect of prolonged low tides, 13 0.15-m² quadrats were located on the algal-dominated edge of the reef flat and the percentage cover of each species of algae monitored before and after a prolonged exposure that occurred during April and May of 1978.

Between periods of prolonged low tides, *Acanthophora spicifera*, *Hypnea musciformis*, *Spyridia filamentosa*, and *Centroceras clavulatum* often overgrow reef-flat populations of *Laurencia papillosa* and *Halimeda opuntia*, but these facultative epiphytes were exceedingly rare or absent on the reef slope. To determine whether grazers were responsible for restricting these species from the reef slope, 16 individuals of each species were blotted dry, weighed, placed in numbered sections of three-strand rope and these ropes placed in four sets of paired cages (1.0 × 1.5 cm mesh). For each pair of cages, one was completely closed while the other had one side removed; all were located between 1.0 and 1.5 m deep. After 72 h the algae were collected and reweighed.

TABLE 1. Apparent photosynthetic and dark respiration rates of three turf-forming algal species when incubated as turfs and as individuals. $N = 6$ for each treatment.

Species	Type	Apparent photosynthesis in $\text{mg O}_2 \cdot \text{g}^{-1}$ ash-free dry mass $\cdot \text{h}^{-1}$ and 95% confidence limits	P value by the Mann-Whitney U test	Dark respiration in $\text{mg O}_2 \cdot \text{g}^{-1}$ ash-free dry mass $\cdot \text{h}^{-1}$ and 95% confidence limits	P value by the Mann-Whitney U test
<i>Laurencia papillosa</i>	turf	6.87 ± 1.60	$P = .005$	-0.98 ± 0.09	$.10 > P > .05$
	individual	9.92 ± 0.91		-1.15 ± 0.14	
<i>Halimeda opuntia</i>	turf	1.43 ± 0.52	$P < .0025$	-0.96 ± 0.08	$P < .0025$
	individual	2.54 ± 0.31		-1.33 ± 0.08	
<i>Dictyota bartayresii</i>	turf	11.38 ± 1.54	$P < .0025$	-3.16 ± 0.39	$.02 > P > .01$
	individual	22.95 ± 5.37		-3.74 ± 0.23	

The basic distribution, by habitat and depth within habitat, of tight turfs, loose turfs, mats, runners, crusts, and individuals was determined by running five transect lines from the seaward edge of the reef flat to the base of the reef slope and recording the algal form that fell beneath the end point of each 0.5-m interval. Algal cover on the sand plain (depth of 14 m) is low, so in this habitat, 100 randomly placed 1.0-m² quadrats with 100 stratified random points within each quadrat were used to assess the abundance of algal types. Determinations of sand-plain composition were made 70–150 m away from the reef base to eliminate the effects of reef-associated grazers.

RESULTS

Hypothesis 1.—As shown in Table 1, all of the species tested had significantly (Mann-Whitney U test; $P < .005$) greater productivities as individuals than as turfs. The increase in mean apparent photosynthesis varied from 44% for *Laurencia* to 102% for *Dictyota*. Mean dark respiration rates were also significantly (Mann-Whitney U test; $P < .01$) higher for *Halimeda* and *Dictyota* individuals. Because of the lesser relative increases in these rates and the relatively low magnitude of dark respiration, this does not offset the increase in apparent photosynthesis. Using these production measurements and conversion factors proposed by Wanders (1976) for the shallow reef algae at Curacao, Netherlands Antilles, a rough estimate of the net production per 24 h was calculated for turfs and individuals (Table 2).

The decreased productivity of the turfs results from both self-shading and increased diffusion gradients. When turfs were pulled from the substrate and placed above a light sensor, only about 0.2% of the ambient, photosynthetically active light (ambient = $1400 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) penetrated to the bases of *Halimeda opuntia*, about 0.1% to the bases of *Laurencia papillosa*, and about 0.05% to the bases of *Dictyota bartayresii*; and when liquified fluorescent dye was squirted into the lower sections of turfs on the reef flat, it often took 2–5 min to disperse completely into the

water column despite moderate to heavy water motion.

Hypotheses 2 and 3.—The upper portions of all species showed apparent photosynthetic rates that were much greater ($P < .0025$) than those of lower portions (Table 3), and the lower portions of all species showed significantly ($P < .01$) decreased rates of dark respiration. Therefore, those portions of the plant that receive adequate light and water flow are highly productive but also costly to maintain, while lower portions which are subject to near darkness and overlapping diffusion gradients have little photosynthetic capacity but also have maintenance costs that are reduced by 18–53%.

Hypothesis 4.—In each species, the aggregate form significantly decreased the rate of water loss and the rate at which apparent photosynthesis declined (Fig. 3). In the case of individuals, apparent photosynthesis dropped to zero or below after only 2 h of exposure. Since many reef-flat exposures last longer than this (Fig. 2) and result in more severe environmental conditions than simulated here, it appears that nonaggregated individuals of these algae would often be killed on the reef flat.

Hypothesis 5.—When subjected to grazing fish and urchins, significantly ($P < .05$) more biomass was lost by individuals than by aggregates (Table 4). Under these test conditions, the turf growth form decreased losses by 15–50%.

TABLE 2. Net production ($\text{mg O}_2 \cdot \text{g}^{-1}$ ash-free dry mass $\cdot \text{d}^{-1}$) of turfs and individuals for a 24-h period (using conversion factors proposed by Wanders [1976] for the shallow reef algae at Curacao, Netherlands Antilles).

Species	Net production/24 h		% increase of individuals
	as turf	as individuals	
<i>Halimeda opuntia</i>	4.6	11.8	156
<i>Laurencia papillosa</i>	57.7	86.0	49
<i>Dictyota bartayresii</i>	80.6	188.3	134

TABLE 3. Apparent photosynthetic and dark respiration rates of the upper and lower portions of three turf-forming algal species. $N = 6$ for each treatment.

Species	Type	Apparent photosynthesis in $\text{mg O}_2 \cdot \text{g}^{-1}$ ash-free dry mass $\cdot \text{h}^{-1}$ and 95% confidence limits	P value by the Mann-Whitney U test	Dark respiration in $\text{mg O}_2 \cdot \text{g}^{-1}$ ash-free dry mass $\cdot \text{h}^{-1}$ and 95% confidence limits	P value by the Mann-Whitney U test
<i>Laurencia papillosa</i>	Top	12.63 \pm 1.48	$P < .0025$	-1.60 \pm 0.13	$P = .01$
	Bottom	4.50 \pm 1.11		-1.39 \pm 0.18	
<i>Halimeda opuntia</i>	Top	5.78 \pm 0.41	$P < .0025$	-1.32 \pm 0.08	$P < .0025$
	Bottom	1.61 \pm 0.40		-0.72 \pm 0.09	
<i>Dictyota bartayresii</i>	Top	36.84 \pm 4.86	$P < .0025$	-4.13 \pm 0.18	$P < .0025$
	Bottom	4.30 \pm 3.16		-1.94 \pm 0.21	

Observations on feeding behavior in the field suggest that these figures may be low. When urchins were observed in the field, they were rarely seen grazing in the center of turf patches. Their grazing activity was confined to the edges of turfs, and when placed in the center of large turf patches they invariably moved rapidly back to the margin. A few urchins were occasionally seen near the center of turf patches, but only after extended periods of very calm seas. Whenever current velocity or wave action increased, they quickly moved off the turfs. When urchins did graze turfs, they usually removed only the uppermost portion of the fronds without harming lower plant portions. No urchins were seen to crop the turf to the substrate. Grazing fish were not limited to turf margins but, like urchins, did graze only the uppermost sections of the algae and were never seen to eat through to the substrate.

Sea urchin densities are significantly ($P < .01$) lower in areas dominated by turfs (Table 5), with densities at turf centers being 98% lower and those at turf margins being 70% lower than those in nearby areas without turf cover.

Hypothesis 6.—Fig. 4 shows the distributions with depth of algal growth forms at Galeta Point, Panama. Turfs are most common on the reef flat and shallow reef slope where desiccation or herbivory are important factors. The turf growth form is gradually replaced by the individual form on deeper portions of the reef, and on the sand plain individuals are the dominant form and turfs are absent.

On the reef flat, turf formers such as *Laurencia papillosa*, *Halimeda opuntia*, and *Gelidiella acerosa* are often heavily overgrown by more productive species (Fig. 5) such as *Hypnea musciformis*, *Acanthophora spicifera*, *Dictyota bartayresii*, *Spyridia filamentosa*, and *Centroceras clavulatum*. Although some of these species can also form turfs, they are more easily damaged by desiccation than are the less productive turfs (Fig. 6) and their abundance is often drastically reduced following severe low tides (Table 6). An extended low tide that occurred during late April and

early May 1978 caused a 97% reduction in the cover of these more productive species while reducing the cover of the less productive turfs by only 46%. This differential susceptibility to desiccation appears to be primarily responsible for the periodic exclusion of *Acanthophora*, *Hypnea*, *Centroceras*, *Spyridia* and *Dictyota* from the reef flat and for preventing them from excluding the less productive turfs.

Four of these more productive species also show greater susceptibility to herbivory than the grazer-resistant turfs such as *Halimeda opuntia*, *Dictyota bartayresii* and various species of turf-forming coralline algae that occur on the reef slope. When these more productive species were transplanted to the shallow reef slope they showed positive growth rates (Fig. 7) in cages that excluded urchins and large fish (small parrot fish were often seen feeding within the enclosure cages) but suffered large losses in open cages.

DISCUSSION

Patterns of photosynthesis and respiration

The turf growth form causes a large decrease in apparent photosynthesis and a small decrease in dark respiration (Table 1). The effect on net photosynthesis per 24 h is large, with individuals being 50–150% more productive than turfs (Table 2). This figure is probably low for two reasons. First, these turfs usually occur in clumps that are 20 cm to several metres in diameter and, therefore, have relatively little edge area where light can reach basal portions and where diffusion gradients can be easily broken down by water movement. The turf sections used in these incubations were <4 cm in diameter and therefore had a much greater proportion of exposed edge. Secondly, fronds within turfs are usually much more deeply pigmented in the upper sections than in the lower portions and these lower portions have less photosynthetic potential (Table 3). Individual thalli should not show this spatial differentiation of pigmentation and photosynthetic activity and should have higher rates of production than "individuals" made by separating turfs. These biases may

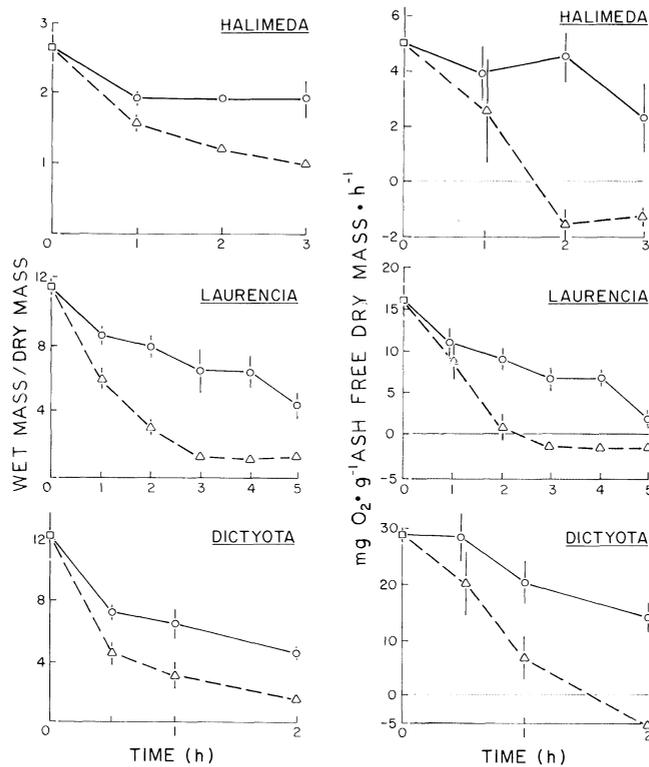


FIG. 3. The mean rate of water loss and decrease in apparent photosynthesis of turfs (open circles) and of individuals (triangles) when exposed to desiccating low tide conditions. The vertical bars give 95% confidence intervals. $N = 6$ for all points.

be offset to some extent by the stirring regime used for productivity determinations, since wave action should be more effective at breaking down diffusion gradients within the turf. During the rough, dry season, diffusion gradients may not be large but lower sections of the turf would still be below light compensation. During the calm, wet season, nutrient depletion will be a much greater problem since wave action is very slight. (On many days breakers are only a few centimetres tall.)

Decreased productivity results from both self-shading and inequitable nutrient distribution. Light reaching the lower sections of the turf matrix is only 0.05–0.2% ($0.7\text{--}2.8 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ at midday) of that reaching the uppermost portions, and dye studies conducted in the field indicate that water exchange between the internal turf matrix and the water column is slow.

Rates of apparent photosynthesis and dark respiration are spatially separated within the thalli of turf formers, with upper portions having higher rates than

TABLE 4. The differential impact of grazers on turfs and individuals.

Species	N	Approximate initial mean wet mass of algae (g)	Mean amount lost by individuals in excess of that lost by turfs	P value by the Wilcoxon paired-sample test
A. Percent wet mass lost by individuals as compared with turfs due to the grazing activity of the parrot fish, <i>Sparisoma rubripinne</i>.				
<i>Halimeda opuntia</i>	10	45	$-20.8\% \pm 13.4$	$P < .0025$
<i>Laurencia papillosa</i>	10	30	$-46.1\% \pm 16.8$	$P < .0025$
<i>Dictyota bartayresii</i>	10	10	$-15.1\% \pm 22.4$	$P = .05$
B. Percent wet mass lost by individuals as compared with turfs due to the grazing activity of the sea urchin, <i>Diadema antillarum</i>.				
<i>Halimeda opuntia</i>	10	52	$-45.5\% \pm 12.2$	$P < .0025$
<i>Laurencia papillosa</i>	10	35	$-35.1\% \pm 19.9$	$.05 > P > .025$
<i>Dictyota bartayresii</i>	10	26	$-27.5\% \pm 14.4$	$.005 > P > .0025$

TABLE 5. Mean sea urchin density in 0.15-m² quadrats as a function of turf abundance. All means are significantly different at $P < .01$ (Analysis of Variance).

	Number of quadrats surveyed	Mean number of sea urchins/0.15 m ² and 95% confidence interval
Turf centers (>80% turf cover)	46	0.09 ± 0.08
Turf margins (25–50% turf cover)	29	1.38 ± 0.55
Areas without turfs (<5% turf cover)	32	4.62 ± 1.48

lower portions (Table 3). The decreased respirative demand of the turf's basal portion lowers the energetic cost of the growth form and may allow this portion to act as a resting stage during periods of severe stress when uprights cannot be maintained (i.e., periods of prolonged low tides, long periods of low light intensity due to turbidity or burial by sediment, or periods of intense grazing). The low photosynthetic potential of basal portions should have little effect on overall photosynthesis since low light levels and slow nutrient exchange already limit production within this portion of the turf.

The growth form of most turf-forming species is very plastic and the pattern of photosynthetic and respiration rates within the thalli, and of thalli packing within the turfs, may be responsive to a wide variety of different situations. As herbivore activity (Gosline 1965, Vine 1974), light intensity and water motion decrease with depth, turfs at greater depths tend to be much more loosely arranged (i.e., light can penetrate to basal sections) and pigmentation differences between upper and lower portions appear to be less pronounced.

Although it has not been shown for these particular seaweeds, many algae branch when the apical cell is damaged or removed (Isaac 1956, Dixon 1958, 1960). Such a regeneration pattern may provide a mechanism by which algae can adjust the degree of upright packing in accordance with the particular pressures they encounter in different areas. Thus, the more often a turf is grazed or killed back by physical factors (desiccation, excessive light or high temperatures during exposures), the more highly compacted it becomes, thereby decreasing the impact of these factors in the future. Seaweeds that regenerate in this manner have the advantage of being able to form compact turfs in areas where physical stresses or herbivory are of paramount importance or to grow as loosely arranged aggregates in areas that are not subject to these pressures and where competition is the primary selective factor.

Effects on desiccation and herbivory

When exposed to desiccating conditions, individuals lose water and photosynthetic ability at a much faster

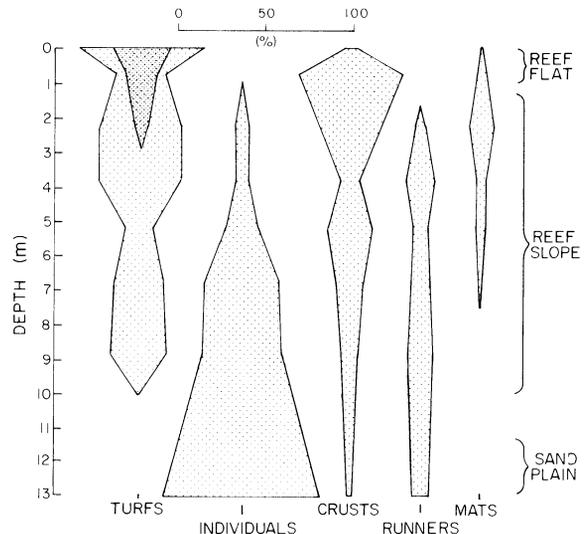


FIG. 4. The relative percent cover of algal growth forms on the reef flat, reef slope and sand plain at Galeta Point, Panama. Very tightly compacted turfs are shown as darker on the diagram. The reef-flat habitat is subject to considerable desiccation stress and slight herbivory. The reef slope is never desiccated but herbivory is intensive in the shallower areas and decreases somewhat with depth. The sand-plain habitat is characterized by low light levels and very little herbivore activity.

rate than turfs (Fig. 3). Using rates of apparent photosynthesis as an indication of physiological damage, it appears that individuals cannot withstand more than about 2 h of exposure to air. The majority of daytime exposures of the reef flat last longer than this (Fig. 2), and nonturf formers growing on the reef flat often suffer severe losses.

The turf growth form lost 15–50% less biomass to grazers than did individuals (Table 4). The turf's resistance to urchin grazing appears to result from: (1) the reluctance of the urchins to climb onto the top of turfs where they are more apt to be dislodged by water motion and probably more prone to predation, (2) urchins being forced to eat from the top down, thus minimizing the number of uprights lost to the water column because of grazing on basal attachment areas, and (3) the decreased structural heterogeneity that results when turfs overgrow corals and fill in crevices and holes that serve as necessary refugia for urchins.

The impact of fish grazing appeared to be reduced for similar reasons; refuge holes are less common in turf-dominated areas, basal attachment sections are shielded by the tightly packed uprights, and it seemed to be much more difficult for fish to bite into the compacted uprights than for them to crop loosely arranged uprights or those projecting beyond the colony margin.

Since both desiccation and herbivory will affect colony margins more than colony centers, the impact of these factors should decrease with increasing colony size (i.e., with greater area to circumference ratio).

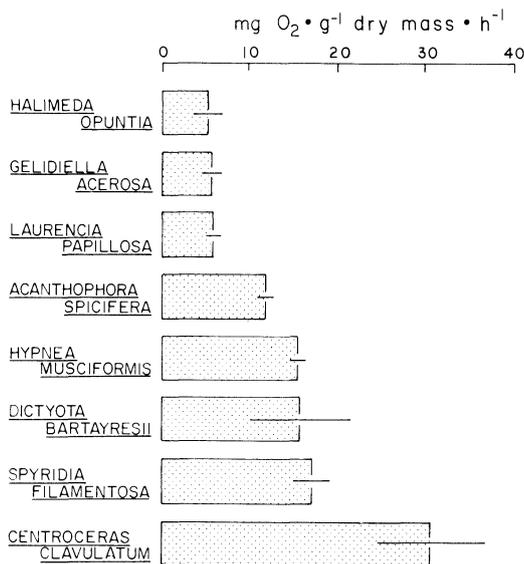


FIG. 5. Mean rates of apparent photosynthesis for the most common reef-flat algal species at Galeta Point, Panama. Vertical bars represent 95% confidence intervals. *N* = 6 for all species. *Halimeda*, *Gelidiella*, *Laurencia*, and *Dictyota* often form compact turfs attached to primary substrate. *Acanthophora*, *Hypnea*, *Spyridia*, *Centroceras*, and at times *Dictyota* overgrow *Halimeda*, *Gelidiella*, and *Laurencia* and can attach to primary substrate or other plants.

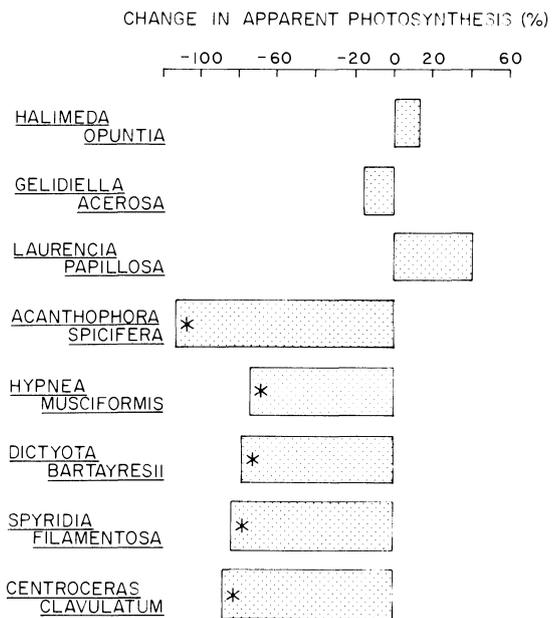


FIG. 6. Percent change in apparent photosynthesis of the common reef-flat algal species when subjected to 2 h of desiccating low tide conditions. Control plants and desiccated plants were held in running seawater for 48 h before photosynthetic measurements were taken. Asterisks indicate significant differences at *P* < .05 (Mann-Whitney *U* test).

And as turfs increase in size, their central portions also become further removed from unobstructed crevices and holes which may serve as refugia for herbivores. Thus, colonies that have sufficiently large area-to-circumference ratios, and which become large enough appreciably to decrease appropriate herbivore habitat may be able to decrease herbivore impact to such an extent that they escape in size.

Competition, substrate retention, and persistence

When competing for space and light with algae that grow as individuals or as less tightly compacted colonies, the slower growing turf formers should be inferior. In the absence of physical disturbance or her-

bivory, faster growing algal species would be more efficient at colonizing newly available substrate by both spore release and vegetative expansion and would also rapidly overgrow and shade out existing turfs. While established turfs may be able to interfere with the settlement and germination of obligate primary substrate species, they are very susceptible to overgrowth by more productive algae that can utilize both primary and secondary substrate.

For the species examined, the primary factor determining overgrowth appears to be rate of photosynthesis. All epiphytes have a higher photosynthetic rate than the plants that they overgrow (Fig. 5) and more productive turfs will often overgrow less productive

TABLE 6. The effect of prolonged low tides on reef-flat populations of turf-forming algae which grow on primary substrate (*Halimeda*, *Laurencia* and *Gelidiella*) and on the facultative epiphytes (*Centroceras*, *Hypnea*, *Acanthophora*, *Spyridia*, and *Dictyota*) that overgrow them. Data are from 13 0.15-m² quadrats located on the *Laurencia*-dominated edge of the reef flat.

Species	Mean % cover ± SE before low tides (3 April 1978)	Mean % cover ± SE after low tides (4 May 1978)	% change	Mean change
<i>Halimeda opuntia</i>	12.2 ± 3.4	10.7 ± 2.9	-12	
<i>Laurencia papillosa</i>	42.6 ± 5.2	17.1 ± 2.9	-60	-46%
<i>Gelidiella acerosa</i>	9.9 ± 4.2	3.5 ± 1.1	-65	
<i>Centroceras clavulatum</i>	6.4 ± 4.0	1.0 ± 0.7	-84	
<i>Hypnea musciformis</i>	8.1 ± 4.3	0.1 ± 0.0	-99	
<i>Acanthophora spicifera</i>	0.6 ± 0.3	0.0 ± 0.0	-100	-97%
<i>Spyridia filamentosa</i>	4.7 ± 4.7	0.0 ± 0.0	-100	
<i>Dictyota bartayresii</i>	0.2 ± 0.0	0.0 ± 0.0	-100	

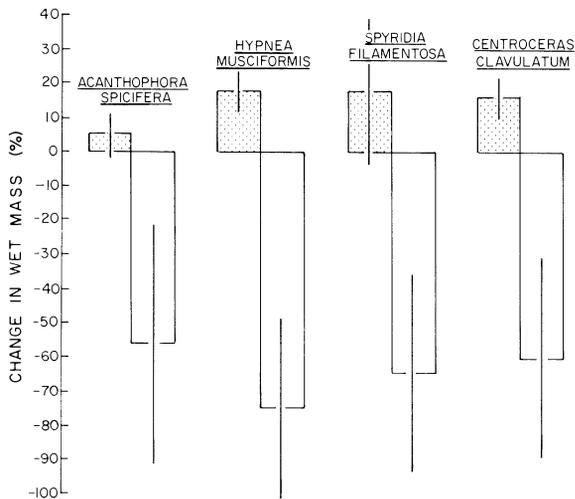


FIG. 7. Percent change in wet mass of four reef-flat algal species when placed in open cages (light bars) and exclusion cages (shaded bars) on the shallow reef slope for 72 h. Vertical bars indicate 95% confidence intervals. $N = 8$ for each treatment.

ones (i.e., *Dictyota* overgrows *Laurencia* and *Halimeda*, *Laurencia* overgrows *Halimeda* but not *Dictyota*, and *Halimeda* never overgrows either *Dictyota* or *Laurencia*). The more productive species are more susceptible to herbivory and desiccation than are the less productive turfs (Figs. 6 and 7). Thus, compensatory mortality due to herbivory on the reef slope and periodic low tides on the reef flat appear to be, in large part, responsible for the maintenance of abundant turf formers in these areas. When the turf-dominated edge of the reef flat remains submerged for long periods, cover of epiphytes may reach 100% in some areas. Following low tides of long duration, the cover of epiphytes may drop by 97%, while the cover of turfs that occupy primary substrates is reduced by only 46% (Table 6).

If turf formers are competitive inferiors, then they should be restricted to habitats where grazers or physical factors preclude the establishment of more productive, competitively-superior algae. Thus turfs should be most common on the physically stressful reef flat or the shallow reef slope where herbivorous fish and urchins are most active. As light becomes limiting (Dayton 1975) and herbivore activity decreases in deeper areas (Gosline 1965, Vine 1974), turfs should be replaced by individuals.

The distribution of algal growth forms on Galeta reef (Fig. 4) conforms well to this prediction. The relative abundance of turfs and individuals is inversely related, with turfs being most abundant at shallower depths. On the deeper sand plain where grazing pressure is very low (Earle 1972, Dahl 1973, Parrish and Zimmerman 1977), individuals account for about 88% of the algal cover and turfs are completely absent.

These findings can be contrasted with those of Jackson (1977) who suggests that, for marine invertebrates, colonial forms are competitively superior to forms that grow as individuals. Reasons for the differing results are unclear but may relate to differences in reproductive options (most solitary animals must rely on sexual reproduction [Jackson 1977] while many solitary seaweeds may reproduce sexually, asexually or colonize by fragmentation [see Dixon 1965, 1973]) or tolerance to physical stresses (solitary invertebrates are often protected by hard exteriors while colonial forms usually have their tissues more exposed). As with the seaweeds examined here, the impact of predation on solitary forms is greater than on colonial ones (Jackson 1977, Buss 1979). If this differential impact is great enough, predation may also play an important role in determining distributional patterns in space and time that have been attributed (Jackson 1977) primarily to competitive interactions.

The primary advantage of the turf growth form appears to be in its ability to persist within areas affected by herbivores and physical stresses that continuously or periodically exclude other more productive algae. Moderate physical stresses or herbivore activity affect turfs very little while causing considerable damage to many other algae, but occasional severe stresses may greatly affect turf formers as well. During such periods, most uprights may be destroyed but many of the prostrate axes or crusts growing in crevices, holes or other refugia remain healthy and are fully capable of regenerating uprights (Dixon 1965, and M. E. Hay, *personal observation*) (see Buss [1979] for a discussion of similar processes in colonial animals). Since basal portions have low rates of respiration (Table 3), they may serve as resting stages that maintain the population until conditions are again suitable for growth. By leaving persistent bases, these algae, like colonial animals (Jackson 1977, 1979, Buss 1979) and clonal terrestrial plants (Harper 1977, Harper and Bell 1979), are able to: (1) avoid the inefficiency of recolonization by spores, many of which settle in inappropriate habitats or are eaten by filter feeders; (2) avoid interference competition with other species that settle more rapidly and interfere with spore settlement or germination; (3) avoid complete dependence upon the spore and sporeling stages that are more susceptible to herbivory (Burrows and Lodge 1950, D. P. Cheney and E. Sideman, *personal communication*) and physical stress (North 1971, Bird and McLachlan 1974), and (4) insure the retention of primary substrate in a location that has previously proven to be suitable for growth.

It should also be recognized that the stressful habitats spoken of here are rigorous in a general sense but may be relatively benign for turfs. Seaweeds that can form turfs appear to be specialized for physically demanding areas or those subject to moderate levels of herbivory. For turfs, habitats with benign physical re-

gimes and few herbivores may be very stressful due to greater pressure from superior competitors.

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LITERATURE CITED

- Benayahu, Y., and Y. Loya. 1977. Seasonal occurrence of benthic algae communities and grazing regulation by sea urchins at the coral reefs of Eilat, Red Sea. Pages 383-389 in *Proceedings, Third International Coral Reef Symposium*. Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida, USA.
- Bird, C. J., and J. McLachlan. 1974. Cold-hardiness of zygotes and embryos of *Fucus* (Phaeophyceae, Fucales). *Phycologia* 13:215-225.
- Burrows, E. M., and S. M. Lodge. 1950. Note on the interrelationships of *Patella*, *Balanus* and *Fucus*, on a semi-exposed coast. Report for 1949 of the Marine Biological Station, Port Erin, Isle of Mann, Annual Report 62:30-34.
- Buss, L. W. 1979. Habitat selection, directional growth and spatial refuges: why colonial animals have more hiding places. Pages 459-497 in G. Larwood and B. R. Rosen, editors. *Biology and systematics of colonial organisms*. Academic Press, New York, New York, USA.
- Cribb, A. B. 1973. The algae of the great barrier reefs. Pages 47-75 in A. O. Jones and R. Endean, editors. *Biology and geology of coral reefs*. Volume II: Biology I. Academic Press, New York, New York, USA.
- Dahl, A. L. 1968. The effect of environment on growth and development of *Zonaria farlowii*. Pages 151-159 in R. Margalef, editor. *Proceedings of the Sixth International Seaweed Symposium*. Subsecretaria de la Marina Mercante, Direccion General de Pesca Maritima, Madrid, Spain.
- . 1972. Ecology and community structure of some tropical reef algae in Samoa. Pages 36-39 in K. Nisizawa, editor. *Proceedings of the Seventh International Seaweed Symposium*. University of Tokyo Press, Tokyo, Japan.
- . 1973. Benthic algal ecology in a deep reef and sand habitat off Puerto Rico. *Botanica Marina* 16:171-175.
- Dayton, P. K. 1975. Experimental evaluations of ecological dominance in a rocky intertidal algal community. *Ecological Monographs* 45:137-159.
- Dixon, P. S. 1958. The structure and development of the thallus in the British species of *Gelidium* and *Pterocladia*. *Annals of Botany*, Volume XXII 87:353-368.
- . 1960. Studies on marine algae of the British Isles: *Ceramium shuttleworthianum* (Kütz) Silva. *Journal of the Marine Biological Association of the United Kingdom* 39:375-390.
- . 1965. Perennation, vegetative propagation and algal life histories, with special reference to *Asperagopsis* and other Rhodophyta. *Botanica Gothoburgensia* 3:67-74.
- . 1973. The biology of the Rhodophyta. Oliver and Boyd, Edinburgh, Great Britain.
- Earle, S. A. 1972. The influence of herbivores on the marine plants of Great Lameshur Bay, with an annotated list of plants. Pages 17-44 in B. B. Collette and S. A. Earle, editors. *Results of the tekite program: ecology of coral reef fishes*. Science Bulletin 14, Los Angeles County Natural History Museum, Los Angeles, California, USA.
- Fenical, W. 1975. Halogenation in the Rhodophyta: a review. *Journal of Phycology* 11:245-259.
- Fenical, W., and J. N. Norris. 1975. Chemotaxonomy of marine algae: chemical separation of some *Laurencia* species (Rhodophyta) from the Gulf of California. *Journal of Phycology* 11:104-108.
- Gittins, B. T. 1975. The biology of *Lithothrix aspergillum*. Dissertation. University of California, Irvine, California, USA.
- Glynn, P. W. 1968. Mass mortalities of echinoids and other reef flat organisms coincident with midday, low water exposures in Puerto Rico. *Marine Biology* 1:226-243.
- . 1972. Observations on the ecology of the Caribbean and Pacific coasts of Panama. *Biological Society of Washington Bulletin* 2:13-20.
- Gosline, W. A. 1965. Vertical zonation of inshore fishes in the upper water layers of the Hawaiian Islands. *Ecology* 46:823-831.
- Harper, J. L. 1977. *The population biology of plants*. Academic Press, New York, New York, USA.
- Harper, J. L., and A. D. Bell. 1979. The population dynamics of growth form in organisms with modular construction. Pages 29-52 in R. M. Anderson, B. D. Turner, and L. R. Taylor, editors. *Population dynamics*. Blackwell Scientific Publications, Oxford, England.
- Hendler, G. L. 1976. Marine studies—Galeta Point. Pages 131-249 in D. M. Windsor, editor. 1975 environmental monitoring and baseline data compiled under the Smithsonian Institution Environmental Sciences Program: tropical studies. Smithsonian Institution, Washington, District of Columbia, USA.
- . 1977. The differential effects of seasonal stress and predation on the stability of reef-flat echinoid populations. Pages 217-223 in *Proceedings, Third International Coral Reef Symposium*. Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Miami, Florida, USA.
- Isaac, W. E. 1956. The ecology of *Grecilaria confervoides* (L.) Grev. in South Africa with special reference to its ecology in the Saldanha-Langebaan Lagoon. Pages 173-185 in T. Braarud and N. A. Sorensen, editors. *Second International Seaweed Symposium*. Pergamon Press, New York, New York, USA.
- Jackson, J. B. C. 1977. Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. *American Naturalist* 111:743-767.
- . 1979. Morphological strategies of sessile animals. Pages 499-555 in G. Larwood and B. R. Rosen, editors. *Biology and systematics of colonial organisms*. Academic Press, New York, New York, USA.
- Liddle, L. B. 1975. The effects of intertidal stress on *Padina sanctaerueis* (Phaeophyta). *Journal of Phycology* 11:327-330.
- Lubchenco, J., and J. Cubit. 1980. Heteromorphic life histories of certain marine algae as adaptations to variations in herbivory. *Ecology* 61:676-687.
- Meyer, D. L., C. Birkeland, and G. L. Hendler. 1975. Marine studies—Galeta Point. Pages 223-409 in D. M. Windsor, editor. 1974 environmental monitoring and baseline data compiled under the Smithsonian Institution Environmental Sciences Program: tropical studies. Smithsonian Institution, Washington, District of Columbia, USA.

- Munda, I. 1972. On the chemical composition, distribution, and ecology of some common benthic marine algae from Iceland. *Botanica Marina* 15:1-45.
- Norris, J. N., and W. Fenical. *In press*. Chemical defence in tropical marine algae. In K. Rutzler and I. G. Macintyre, editors. Atlantic barrier reef ecosystem at Carrie Bow Cay, Belize. Scientific Report 1: structure and communities. Smithsonian Contributions to Marine Science 12. Smithsonian Institution, Washington, D.C., USA.
- North, W. J. 1971. Introduction and background. Pages 1-98 in W. J. North, editor. The biology of giant kelp beds (Macrocystis) in California. Beihefte zur Nova Hedwigia, Heft 32. J. Cramer, Lehre, Germany.
- Parrish, J. D., and R. J. Zimmerman. 1977. Utilization by fishes of space and food resources on an offshore Puerto Rican coral reef and its surroundings. Pages 297-303 in Proceedings, Third International Coral Reef Symposium. Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Miami, Florida, USA.
- Pfeifer, R. F., and W. F. McDiffett. 1975. Some factors affecting primary productivity of stream riffle communities. *Archiv Für Hydrobiologie* 75:306-317.
- Stephenson, T. A., and A. Stephenson. 1972. Life between tide marks on rocky shores. W. H. Freeman, San Francisco, California, USA.
- Stewart, J. G. 1968. Morphological variation in *Pterocladia pyramidale*. *Journal of Phycology* 4:76-84.
- Sun, H. H., and W. Fenical. 1979. Rhipocephalin and Rhipocephalin; toxic feeding deterrents from the tropical marine alga *Rhipocephalus phoenix*. *Tetrahedron Letters* 8:685-688.
- Vine, P. J. 1974. Effects of algal grazing and aggressive behavior of the fishes *Pomacentrus lividus* and *Acanthurus sohal* on coral-reef ecology. *Marine Biology* 24:131-136.
- Wanders, J. B. W. 1976. The role of benthic algae in the shallow reef of Curacao (Netherlands Antilles). I: Primary productivity in the coral reef. *Aquatic Botany* 2:235-270.