**The Functional Morphology of Turf-Forming Seaweeds: Persistence in Stressful Marine Habitats**

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

*MARKE. HAY' Stnitlz.tonirrrr Tropic.(rI Re.tetrrc.11 Instirrrre, Post Qffic,e Bo.t 2072, Btrlhon, P~rrtrnltr, trrrti*

*L)epcir-ttnet~t of'Ec,ology rrnd Evolrrriot~nrl\. Biolo,gy. Ut~iversitj of' C~rlforrritr trt Irr,it~e,*

*Ir-i,ine, Ctrliforrritr 92717 USA*

Ah.\trrrc,t. Many \eaweed\ that occur in physically stressful habitats or habitats subject to mod- erate 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 turf$ suffer less physiological damage during desiccating low tides and lose less biomass to herbivores. The upper portion? of turf-forming 4pecie.i $how significantly greater rates of apparent photosynthesis and dark respiration than do the lower portions. This spatial partitioning of photo\ynthetic 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 stresse?. They are dependent upon these factors to prevent their competitive exclusion by more productive, but less resijtant, seaweeds. Damage to apical por- tions causes increased branching that results in a more tightly compacted turf. Algae that regenerate in thi\ 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 rvords: cotnpetition; tie.vic,c,ntiorr: Dictyota: ,fiit~git~~reqf: Halimeda; herhi~,op;Laurencia; tnorpllolo,qy; prodrrc.ti~,ity; .setr\t.eetl.\; turf.*

INTRODUCTION

Many seaweeds grow as colonial assemblages rather than as spatially separated individuals (see Harper [I9771 for a discussion of similar growth characteris- tics in terrestrial plants). Among them. the turfgrowth 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 Lays 1977).

Turf species possess both prostrate and upright branches. The number of uprights is increased pri- marily by means of vegetative growth, with the com- pact turf config~lration being affected by: (I) the num- ber of uprights per length of prostrate, (2) their degree of branching, and (3) the extent to which lateral con- nections form between uprights.

Turf-forming species show considerable mor-pholog- ical 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 high- ly branched and compacted (Dahl 1968, Stewart 1968, Munda 1972, Gittins 1975, L,iddle 1975). The produc-

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accepted ad~re,s: 17 July D~~~~~~~~~ 1980. 310, Smithsonian Institution, of Washington. paleobioloQv. D.C. L 20560 ,

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tivity of a freshwater alga has been shown to vary inversely with the density of uprights (Heifer 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 Phaeo- phyta) have shown convergent evolution of this growth form, it would appear that there are adaptive advantages inherent in the turf configuration that com- pensate for the loss of productivity and enable these species to maintain successfill 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) concen- tration of photosynthetic activity in the upper portions of the thallus since lower portions receive little light, (3) decreased dark respiration rates in the lower por- tions 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 t~lrfs are more dif- ficult for herbivores to manipulate and basal attach- ment 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.I . The reef-flat habitat and major turf-forming species at Galeta Point, Panama. (A) Lnurrncitr pripillo.st~. (B) Dic,tyotci httrtciyresii. (C) Halirnedo oprrnriri. (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 tul-f-forming species at Galeta Reef, Panama: the brown Dic~yottr hartnyresii Lamouroux, the green Hnlimeda oprrrlrici (Linnaeus) Lamouroux and the red Lalirencici pnpillosci (Forsskal) Greville.

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. IA-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 at- tached 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 run- ners 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 Cubit 1980), while oth- ers may grow as runners, individuals, loose turfs or tight turfs depending upon the habitat in which they occur

The reef at Galeta Point is typical (Glynn 1971,) of fringing reefs on the Caribbean coast of Panama. On the reef flat. hard substrate is dominated by compact turfs consisting primarily of La~lrencitr ptrpillosci

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Htil- irnedtr oprrrlritr and several species of Dictyort~.Severe exposures to air occur on the reef flat when low tides coincide with calm weather (Fig. ID). These expo- sures can be of long duration (Fig. 1,) and may kill most nonswimming herbivores (Glynn 1968. Meyer et al. 1975, Hendler (977) as well as significantly reduce algal cover.

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FIG.2. Ihe number of hours per day during which the turf-dominated reef edge was exposed by low tides for the year 1974. Times ohove the X-axis represent daylight hours (between 0630-1800). lines below the X-axis represent nighttime hours (before 0600 or after 1800). The histogram in the upper right corner gives a hreakdown 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 sup- ports a relatively ILIS~growth of seaweeds (exceeding IOWA cover of upright species in some areas). Shal- lower areas are populated primarily by encrusting cor- alline algae and turf-forming species, while plants growing as individuals or as loosely arranged aggre- gates 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.

Lnrrrencirr pnpi/lo.vri is a fleshy red alga that grows in coarse turfs from 3-10 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. persorlril ob.servrrtiotz). Unlike many other members of the ge- nus (Fenical 1975. Fenical and Norris 1975). it does not appear to have large amounts of secondary me- tabolites which might act as herbivore deterrents (Fen- ical and Norris, in pre.~.~).

Dicryotri brrrrc~yrc~.vsi, a thin brown alga that forms dense, hemispherical clumps (Fig. IB), is most abun- dant 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 por- tions move with the current. It has a high concentra- tion of polyphenol substances (Norris and Fenical. in prc..vs) and is often abundant in areas subject to mod- erate grazing pressure.

Hrrlirnedtr opcrtzric~ 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. IC) and moderately com- pacted ones on the shallow reef slope. It occurs as a lax aggregation of nonlaterally connected uprights in the deeper parts of its range. H . opcrntiri 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 . opcrntici is now in progress (W. Fenical, persorlril cornn~crnicc~tion) and it appears to contain compounds related to those found in other members of the Codiaceae, for example Rhi- pocc~phrrlers (Sun and Fenical 1979).

Tc~sts of the hypothc~.ve.v To examine hypothesis 1: (turfs should have de- creased photosynthetic rates), turfs of Lrrerrc.tzcirr pcip- illosc~, Hr~linledrr oprrnticl, and Dictyotrr bartciyresii were collected from the reef flat or shallow reef slope and incubated as aggregates and as "individuals" (in- dividuals 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"-3 1°C) immediately adjacent to the reef flat. Stir- ring was provided at 10-15 min intervals by magnetic

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stirrers and all 0, determinations were made with a Yellow Springs Instrument Company Model 57A 0, meter and electrode. Blank bottles were used to con- trol for phytoplankton production and all 0, determi- nations were made under sunny skies on I0 April 1978. Hypotheses 2: (photosynthesis should be concen- trated in the upper portions of the thallus) and 3: (res- piration 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 ~rprightsfrom 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 t~rrf configuration significantly af- fects production rates, all t~rrfs were separated and incubated as individuals to facilitate comparison be- tween 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 Dictyo- tcr htrrttryrcsii and Htrlin~edtr oprrrztitr were done on hazy, overcast days, while those using Ltrrircrzcitr ptrp- illo.str 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 pre- vailing 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 indi- vidual arrangements of each species by wet mass. mounting them in numbered sections of three-strand rope and placing them where the sea ~rrchin t)icrdc~rntr trrztilltrrrrm Philippi or the parrot fish Sptrri.sornc~ rub- ripinne Cuvier and Valenciennes could graze them. Ten aggregate-individual pairs were used in each ex- periment.

Grazing experiments with urchins were performed in a shallow, sandy lagoon where t)irrdc~mtrdensities were 10.4 urchinsim' (st;.

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centers, at turf margins, and in nearby areas that were structurally similar but devoid of turfs. A 0.15-m' (30 x 50 cm) quadrat was flipped end-over-end along six transects randomly located within a bed of Poritc..~ (finger coral) that was partially overgrown by t~rrfs (primarily Htrlin~edtr oprtnricl, with Dictyottr hnrttry- resii and Arnphiron spp. being present but much le\s abundant). All transects were between I and 2 m deep and the coral structure below turfs appeared identical to that which was nearby but not overgrown. Quadrats with >8(% cover of turfs were considered turf cen- ters. those with 25-5m turf margins, and those with <5% were considered to be devoid of turfs. All ur- chins 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 (Actrrzthophorc~ spicif'c.t.tr [Vahl] Borgesen: Cerztroc,cv-

***(1.7***

***cltr~~rtltrtrrrn[C. Agardh] Montagne: t)ictyottr htrr- t t ~ ~ r e ~ :Gelidielltr i i trc,c~rostr [Forsskal] Feldmann and Hamel: Htrlinzedtr oprrrztirr : Hypnerr nzrt.scifi)rrni.c [Wulfen] Lamouroux: Ltrrrrc.nc.itr ptrpillo.vcr : and Spyr- idic1~51trmento.scr[Wulfen] Harvey) within the Larrrrrz- cirr-dominated area of the reef flat was measured as described above.***

The susceptibility of each of these species to des- iccation was measured by simulating a 2-h reef-flat exposure and comparing photosynthetic rates of des- iccated 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- m' 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 pro- longed exposure that occurred during April and May of 1978.

***Between periods of prolonged low tides, Acnntho- phortr .spicifPrtr, Hypnetr nlrrsc,ifbrn~is, Spyriditr***

$/ti- n~erzto.sn,and Centrocc~rcr.~c~lnvrrlrrrrtmoften overgrow reef-flat populations of Ltcrtrerzcicr pcrpilloscc and Httl- irnedtr oprrnticr, but these facultative epiphytes were exceedingly rare or absent on the reef slope. To de- 2.2. .Y

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10) and herbiv-

termine whether grazers were responsible for restrict- orous fish were not active (throughout 2.0 h of obser-

ing these species from the reef slope, L6 individuals of \lation during each test, no herbivorouc fish were seen

each species were blotted dry, weighed, placed in in the experimental area). Urchin experiments lasted

numbered sections of three-strand rope and these 12-24 h. Fish grazing experiments were performed in

ropes placed in four sets of paired cages

( a large (depth

=

1.0 x 1.5 cm 1.0 m, diameter

=

3.0 m), continu-

mesh). For each pair of cages. one was completely ous-flow seawater tank and all tests lasted 24 h.

closed while the other had one side removed: all were The witability of turf-dominated areas for urchins

located between I .O and 1.5 m deep. After 72 h the was assessed by measuring ~rrchin densities in turf

algae were collected and reweighed.

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TABL~Apparent I .

photmynthetic and dark respiration rates of three turf-forming algal species when incubated as turfs and as individuals. .Y

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6 for each treatment.

Apparent Dark photosynthesis in mg O,.g respiration

in mg O,.g

' ash-free dry ash-free dry mass.h-' and P value by the mas\.h-' and P value by the Species J ' Y P ~ 95% confidence limit\

Mann-Whitney 95% confidence Mann-Whitney

*Loirrenc.icr turf 6.87*

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U test limits

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test

*pcipillo,\*

*(I*

individual 1.60 9.92 -+ 0.91

P

=

,005

-0.98 t 0.09 . l o > P > .05 1.15

-C Htrlinled(c turf 1.43 -+ 0.52 oprrn tirr individu:il 2.54 -+ 0.31 Dictyotti t u ~ f 11.38 t 1.54

harttryre.t ii individual 22.95

-C

0.14

P -:,0025

-0.96 t 0.08 -

1.33 2 0.08

P ,0025

5.37

P -< .0025

3.16 -+ 0.39 ,002 > P > .01 -3.74 -+ 0.23

The basic distribution. by habitat and depth within

water column despite moderate to heavy water mo- habitat, of tight turfs. loose tutfs, mats, runners,

tion. crusts, and individuals was determined by running five

Hypothe.se.s 2 rrtzd 3.-The upper portions of all transect lines from the seaward edge of the reef flat to

species showed apparent photosynthetic rates that the base of the reef slope and recording the algal form

were much greater (P < ,0025) than those of lower that fell beneath the end point of each 0.5-m interval.

portions (Table 3). and the lower portions of all species Algal cover on the sand plain (depth of 14 m) is low.

showed significantly ( P < .01) decreased rates of dark so in this habitat. 100 randomly placed 1 .O-m' quadrats

respiration. Therefore, those portions of the plant that with 100 stratified random points within each quadrat

receive adequate light and water flow are highly pro- were used to assess the abundance of algal types. De-

ductive but also costly to maintain, while lower por- terminations of sand-plain composition were made 70-

tions which are subject to near darkness and overlap- 150 m away from the reef base to eliminate the effects

ping diffusion gradients have little photosynthetic of reef-associated grazers.

capacity but also have maintenance costs that are re- duced by 18-5376.

Hypothesis 4.-In each species, the aggregate form Hyporhc~.si.s I.-As shown in Table I. all of the

significantly decreased the rate of water loss and the species tested had significantly (Mann-Whitney U

rate at which apparent photosynthesis declined (Fig. te\t; P < ,005) greater productivitle\ a\ lnd~v~duals

3). In the case of individuals, apparent photosynthesis than a\ turf\. The Increase in mean apparent photo-

dropped to zero or below after only 2 h of exposure. \ynthe\i\ vaned from 44% for Lnrrrentirr to 102% for

Since many reef-flat exposures last longer than this Dictyotrr. Mean dark respiration rates were also sig-

(Fig. 2) and result in more severe environmental con- nificantly (Mann-Whitney U test; P < .01) higher for

ditions than simulated here, it appears that nonaggre- Hrrlinzedrr and Z)icryorci individuals. Because of the

gated individuals of these algae would often be killed lesser relative increases in these rates and the rela-

on the reef flat. tively low magnitude of dark respiration, this does not

Hypothesis 5.-When subjected to grazing fish and offset the increase in apparent photosynthesis. Using

urchins, significantly (P < .05) more biomass was lost these production measurements and conversion fac-

by individuals than by aggregates (Table 4). Under tors proposed by Wanders (1976) for the shallow reef

these test conditions, the turf growth form decreased algae at Curacao, Netherlands Antilles, a rough esti-

losses by 15-50%. mate of the net production per 24 h was calculated for turfs and individuals (Table 3).

The decreased productivity of the turfs results from both self-shading and increased diffusion gradients. When turfs were pulled from the substrate and placed

TABLE2. Net production (mg O,.g-' ash-free dry mas5.d

of turfs and individuals for a 24-h period (using conversion factors proposed by Wander\ [I9761 for the shallow reef algae at Curacao. Netherlands Antilles). above a light sensor, only about 0.3% of the ambient. photosynthetically a c t ~ v e l ~ g h t ( a m b i e n t

=

1400 pE.m-L.\-l) penetrated to the ba\e\ of Hnlirnedrr

Net production124 h oprrnrltr, about 0.1% to the ba\e\ of Lnrrrent irr prrpil- loscr, and about 0.05% to the bases of Dictyotrr hrir-

Species rtryrcvii: and when liquified fluorescent dye was squirt- ed into the lower sections of turfs on the reef flat, it often took 2-5 min to disperse completely into the

% increase of indi- viduals

*Halitnrdtr oprrnticr Larirrnc,itr ~~crpillosti Dictyotci hrrrtrryrc~sii*

as

a\ turf

individuals

4.6 57.7 80.6

11.8 86.0 188.3

156 49 134

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3.

Apparent .Y =

6 for photosynthetic each treatment.

and dark re\piration rate5 of the upper and lower portions of three turfiforming algal

.Apparent photosynthesis mg O,.g

'

in ash-free dry mass. h-I and

Dark respiration in mg O,.g-l a\h-free P value dry ma\\. h-' and P value Specie5 Type 95% confidence

limits

Whitney by the Mann- U test 95% confidence limit\ Whitney hy the Mann-

U test

l o p Bottom 12.63

*2*

1.48 4.50 i 1.11

P -: ,0025

Top Bottom

-

1.60 t 0.13 -

1.39 t 0.18

P

=

P -< .0025 -

1 .32

*2*

0.08 -0.72

i

.01

5.78 I .6l t t Dic,tyottr htrrttryrc,\ii 0.41 0.40 TOP 36.84 i 4.86 Bottom 4.30

*2*

P

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.0025 P

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,0025

3. I6

0.09 -4.13 i 0.18 -

P

.:

,0025

Observations on feeding behavior in the field sug- ge\t 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 or large turf patches they invariably moved rapidly back to the margin. A few urchins were oc- casionally seen near the center of turf patches, but only after extended periods of very calm seas. When- ever current velocity or wave action increased, they quickly moved off the turfs. When urchins did graze turfs, they ~rsually removed only the uppermost por- tion of the fronds without harming lower plant por- tions. No ~rrchins 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 sec- tions of the algae and were never seen to eat through to the substrate.

Sea urchin densities are significantly (P< .01) low- er in areas dominated by turfs (Table 5), with densities at turf centers being 98% lower and those at turf mar- gins being 70% lower than those in nearby areas with- out turf cover.

Hypothesi.~6.-Fig. 4 shows the di:;tributions 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 impor- tant factors. The turf growth form is gradually re- placed 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 Lrrrrrenc.itr pup- illo.str

1.94 t 0.21

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 Accintl~ophorti, Hypnaci, Cenfrocerrr.~, Spyridin and Dic,ryottr 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-re- sistant turfs such as H(i1itnedn oprrntirr, Dictyotrr htrr- tcryre.vii 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 exclo- sure cages) but suffered large losses in open cages.

The turf growth form causes a large decrease in ap- parent photosynthesis and a small decrease in dark respiration (Table 1). The effect on net photosynthesis per 24 h is large. with individuals being 50-15m more productive than turfs (Table 2). This figure is probably low for two reasons. First, these turfs usually occur in clumps that are 70 cm to several metres in diameter and, therefore, have relatively little edge area where light can reach basal portions and where diffusion gra- .

*Htrlin~c.dtr oprrn titi, and Gc.lidiellrr rrcero.srr are*

dients can be easily broken down by water- movement. The turf sections used in these incubations were <4 often heavily overgrown by more productive species

cm in diameter and therefore had a much greater pro- (Fig. 5) such as Hypnc~r rntrscifornzis, Actrnrhophorci

*portion of exposed edge. Secondly. fronds within t~rrfs .spic,ifi~rtr, I)ic,r?.otci htrrtc~yre.vii, Spj,riclitr $filri~tlolro.sti,*

are usually much more deeply pigmented in the upper and Colrroc,orti.s c~l(i~~rrltitio~~. Although some of these

sections than in the lower portions and these lower species can also form turfs, they are more easily dam-

portions have less photosynthetic potential (Table 3). aged by desiccation than are the less productive turfs

Individual thalli should not show this spatial differ- (Fig. 6) and their abundance is often drastically re-

entiation of pigmentation and photosynthetic activity duced following severe low tides (Table 6). An ex-

and should have higher rates of production than "in- tended low tide that occurred during late April and

dividuals" made by separating turfs. These biases may

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TIME (h) TIME (h)

FIG.3. The mean rnte of water loss and decrease in apparent photosynthe\is of turf\ (open circles) and of individuals (triangle4 when exposed to desiccating low tide condition\. The vertical bars give 95% confidence interval\. .Y

=

6 for all points.

be offset to some extent by the stirring regime used Decreased productivity results from both self-shad- for productivity determinations. since wave action in& and inequitable nutrient distribution. Light reach- should be more effective at breaking down diffusion ing the lower sections of the turf matrix is only 0.05- gradients within the turf. During the rough, dry sea- 0.2% (0.7-2.8 ~ E . m - ~ . s - at l midday) of that reaching son. diffusion gradients may not be large but lower the uppermost portions. and dye studies conducted in sections of the turf would still be below light compen- the field indicate that water exchange between the in- sation. During the calm, wet season, nutrient depletion ternal turf matrix and the water column is slow. will be a much greater problem since wave action is Rates of apparent photosynthesis and dark respira- very slight. (On many days breakers are only a few tion are spatially separated within the thalli of turf centimetres tall.) formers, with upper portions having higher rates than

TABLE4. The differential impact of grazers on turfs and individuals.

Approximate Mean amount

initial lost by individuals P value mean wet mass in excess of that by the Wilcoxon Species N of algae (g) lost by turfs paired-sample test

.A. Percent wet mass lost by individuals as compared with turfs due to the grazing activity of the parrot fish, Spori.sotno

***rrrhripintzc,. Htrlitnetltr ol~rrt~rttr 10 45 -20.8% i 13.4 P < ,0025 Ltrrrretzc~irr ptrr~illo.\tr 10 30 -46.1% t 16.8 P < .0025 Dic,r~otc~harrtr~rr.sii 10 I0***

-

15.1% i 22.4 P

=

.05

B. Percent wet ma\s lost by individuals a\ compared with turfs due to the grazlng activity of the sea urch~n. Ditrtlenztr

***~~ntill~~rrrtn.***

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TABL.E5. Mean sea ~~rchin density in 0.15-m' quadrats as a function of turf abundance. All means are significantly dif- ferent at P < .01 (Analysis of Var~ance).

Mean number of sea urchins1 Number of 0.15 m' and

quadrats 95% confidence surveyed interval

Turf centers

(>80C/r turf cover) 46 0.09

i

REEF 0.08

)SLOPE

T11r.f margins

(25-50Z turf cover) 29 I .38 i

0.55 .Areas without turfs

(<5% turf cover) 32 4.62 i

1.48

*i*

*lower portions (Table 3). The decreased respirative demand of the t u f s basal portion lowers the energetic*

SAN3 ,/PLAIN

*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*

*MATS NDlVIDLlLLS RUNNERS FIG.4. The relative percent cover of algal growth forms on the reef flat. reef slope and sand plain at Galeta Point, 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 pho-*

Panama. Very tightly compacted turfs are shown as darker on the diagram. The reef-flat habitat is subject to considerirble desiccation stress and slight herbivory. The reef slope i\ nev- er desiccated but herbivory is intensive in the shallower area\ and decreases somewhat with depth. The sand-plain habitat tosynthesis since low light levels and slow nutrient

is characterized by low light levels and very little herbivore exchange already limit production within this portion

*activity. of the turf.*

*The growth form of most turf-forming species is very plastic and the pattern of photosynthetic and res- piration 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 de- crease with depth. turfs at greater depths tend to be much more loosely arranged (i.e.. light can penetrate to basal sections) and pigmentation differences be- tween upper and lower portions appear to be less pro- nounced.*

*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 pack- ing 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 (des- iccation, 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 par- amount importance or to grow as loosely arranged ag- gregates in areas that are not subject to these pressures and where competition is the primary selective factor.*

*rate than turfs (Fig. 3). Using rates of apparent pho- tosynthesis 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 suf- fer severe losses.*

*The turf growth form lost 15-5()% less biomass to grazers than did individuals (Table 4). The turfs re- duced susceptibility 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 dis- lodged 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 attach- ment areas. and (3) the decreased structural hetero- geneity 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 com- pacted uprights than for them to crop loosely arranged uprights or those projecting beyond the colony margin. Since both desiccation and herbivory will affect col- ony margins more than colony centers, the impact of When exposed to desiccating conditions, individual?*

*these factors should decrease with increasing colony lose water and photosynthetic ability at a much faster*

*size (i.e.. with greater area to circumference ratio).*

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rng 02.

4 - dry mass. h-I CHANGE IN APPARENT PHCTOCYIITtiE-I: (So)

0 0 2 0 30 4 0

HALMEDA

OPUIJTIA

GEL'D'E~C~RO~A

I ,- rT 1

I I I

LAURENCIA

PAPLLOSL

ACANTHCPHORA

7- HYPlvtA

HALIMEDA

OPUNTA

GELIDELLA

ACEROSA

LAURENCIA

PAPILLOSA

MUSCIFORh>IIS /

1 7

C ICTYOTA

*7*

HYPNEA

MUSCFORMS GARTAYRESI SPYRIDIA FLAWENTOS A

CEIvTROCERAS

CLAbULATUV

r--+ 1 -l

1 7

SPYR131A

FILAMENTOSA

&-

FIG.5. Mean rates of apparent photosynthesis for the

CENTROCERAS

r ~ most common reef-flat algal species at Galeta Point. Panama.

CLAVULATUM Vertical bars represent 959 confidence intervals. ,V

=

I

j

i

\_J apparent photosynthesis of the

control

when subiected plants

to 2 h of and desiccat. seawater for 48 h before pho. tosynthetic mea5u,.ements were ~ ~ ~ indicate~ ~ i significant differences at P < .05 (Mann-Whitney U test).

*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 pri- mary 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 deter- mining overgrowth appears to be rate of photosynthe- sis. All epiphytes have a higher photosynthetic rate than the plants that they overgrow (Fig. 5) and more productive tut-fs will often overgrow less productive*

*T~BI6. E*

The effect of prolonged low tides on reef-flat populations of turf-forming algae which grow on primary substrate (Hnlin~ella. Ltrrrrencin and Gc~lidic~lltr)and on the facultative epiphytes (Centroc,c~rtr.\. Hypt~rcr. Actrtzthophortr. Spyridin, and Dic,ryora) that overgrow them. Data are from 13 0. 15-mL quadrat\ located on the Lrrrrrc~t~c,itr-dominatededge of the reef flat.

Mean 5? cover t SE

*i\* 6 for all species. Htrlitneda. Gelitlirllri. Lorrret~c.in, and Dicryortr often form compact turfs attached to primary substrate. Actrntlzophortr,, H y n c ~ r i Spyritiitr, , Cet~troc.c,rrrs, and at times Dic,r?ort~overgrow Htrlitnrcltr. Gelitiiello, and Lerrrretlcic~and*

6, common reef.flat algal de\iccating low tide ,d plants were held in

species

can attach to primary substrate or other plants.

*And as turfs increase in size. their central portions also become further removed from unobstructed crev- ices and holes which may serve as refugia for herbi- vores. 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.*

*Cornpetition, suh.vtr(ite retention,*

*rind persiste~zce When competing for space and light with algae that grow as individuals or as less tightly compacted col- onies, the slower growing tut-f formers should be in- ferior. In the absence of physical disturbance or her-*

F~~,, percent change in

Mean 5? cover t

SE before low tides after low tides % Mean Species (3 April 1978) (4 May 1978) change change

~ k

,

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HYPNEA

FILkOSA

I

*These findings can be contrasted with those of Jack- son (1977) who suggests that, for marine invertebrates, MU-MIS CLA\ULATUM 2 0 1 ACAUTHOPHORA*

SDICIFERA 0 - i

FIG.7. Percent change in wet mass of four reef-flat algal specie\ when placed in open cages (light bar\) and exclusion cages (\haded bars) on the \hallow reef slope for 72 h. Ver- tical bars indicate 95% confidence intervals. .V = 8 for each treatment

*ones (i.e.. Dic,rjorrr overgrow4 Lrrrtrrncitr and Hrrli- rnrdtr, Lalrrrncicr overgrow4 Hulitnrdn but not Dic- r~ortr, and Htrlirrlrdrr never overgrows either L)ic.rjorc~ or Lirllret~(,irl). The more productive species are more susceptible to herbivory and desiccation than are the less productive turfs (Figs. 6 and 7). Thus, compen- satory mortality due to herb~vory 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 IOm in some areas. Follow~ng low t~des of long duration, the cover of ep1phyte4 mny drop by 97%. while the cover of t u ~ f s that occupy primary substrate4*

*14*

WROA

C-

*colonial forms are competitively superior to forms that grow as individuals. Reasons for the differing results are unclear but may relate to differences in reproduc- tive options (most solitary animals must rely on sexual reproduction [Jackson 19771 while many solitary sea- weeds may reproduce sexually, asexually or colonize by fragmentation [see Dixon 1965, 19731) or tolerance to physical stresses (solitary invertebrates are often protected by hard exteriors while colonial forms usu- ally have their tissues more exposed). As with the sea- weeds examined here, the impact of predation on sol- itary 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 ap- pears 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 pe- riods. 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, prr.c.ontr1 ohsrr~.c~rior~) (see Buss [I9791 for a discus- sion 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 pop- ulation until conditions are again suitable for growth. By leaving persistent bases, these algae, like colonial animals (Jackson 1977, 1979, Buss 1979) and clonal reduced by only 46%*

*terrestrial plants (Harper 1977, Harper and Bell 1979). (Table 6).*

*are able to: ( I ) avoid the inefficiency of recolonization I f turf formers are competitive inferiors, then they*

*by spores, many of which settle in inappropriate hab- should be restricted to habitats where grazers or phys-*

*itats or are eaten by filter feeders; (2) avoid interfer- ical factors preclude the establishment of more pro-*

*ence competition with other species that settle more ductive, competitively-superior algae. Thus turfs*

*rapidly and interfere with spore settlement or germi- should be most common on the physically stressful*

*nation;(3) avoid complete dependence upon the spore reef flat or the shallow reef slope where herbivorous*

*and sporeling stages that are more susceptible to her- fish and urchins are most active. As light becomes*

*bivory (Burrows and Lodge 1950, D. P. Cheney and limiting (Dayton 1975) and herbivore activity de-*

*E. Sideman, persontrl cornrnrtnictrrion) and physical creases in deeper areas (Gosline 1965, Vine 1974),*

*stress (North 1971. Bird and McLachlan 1974). and turfs should be replaced by individuals.*

*(4)insure the retention of primary substrate in a lo- The distribution o f algal growth forms on Galeta reef*

*cation that has previously proven to be suitable for (Fig. 4) conforms well to this prediction. The relative*

*growth. abundance of turfs and individuals is inversely related,*

*It should also be recognized that the stressful hab- with turfs being most abundant at shallower depths.*

*itats spoken of here are rigorous in a general sense but On the deeper sand plain where grazing pressure is*

*may be relatively benign for turfs. Seaweeds that can very low (Earle 1972. Dahl 1973, Parrish and Zim-*

*form turfs appear to be specialized for physically de- merman 19771, ind~viduals account for about 88% of*

*manding areas or those subject to moderate levels of the algal cover and turf4 are completely absent.*

*herbivory. For turfs, habitats with benign physical re-*

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

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