

## Anchor Species and Epiphytes in Intertidal Algal Turf<sup>1</sup>

JOAN G. STEWART<sup>2</sup>

**ABSTRACT:** This study characterizes a turflike vegetation composed of benthic marine algae, in the low intertidal in southern California, by means of quantitative relative abundance data collected over a 2-yr period. The algae comprise a relatively homogeneous assemblage that is fastened to the substrate by one to six "anchor" taxa with thalli that persist throughout the year and become reestablished on exposed surfaces within several months. Two species of *Corallina* together occupy more than 60 percent of the total substrate sampled. Epiphytes attached to these anchor species include 42 species that are consistently found and another 25 that are infrequently or incidentally recorded. Abundances of several of the epiphytes fluctuated during the sampling period, but the number of species present showed no distinct seasonal change. In the northern Gulf of California a similar-appearing turf includes several of the same species in different proportions, but anchor species are different. Many unrelated taxa in both turfs exhibit the same morphological characters. A census of macroinvertebrates associated with the southern California vegetation suggests that grazing is not important in maintaining the relatively uniform height of these plants.

THE TERM "TURF" HAS proved convenient (e.g., Lawson and John 1977, Santelices and Abbott 1978) to refer generally to mats of small algal thalli in warm temperate or tropical regions, although workers describing these associations often explicitly indicate differences in composition and structure. For example, when Littler (1980) commented that turf communities were "prevalent in the middle to low intertidal zones at nearly all sites" in southern California, he was referring to areas covered with single or several filamentous red algae; with *Gigartina canaliculata*; with *Corallina*; with a mixture of *Gelidium pusillum*, *G. coulteri*, coralline species, and filamentous epiphytes; and contrasted with the latter, with coralline algae supporting larger frondose epiphytes.

Neushul and Dahl (1967) equated *parvosilvosa* (in Gislén 1930) with *turf*, which

they defined as a taxonomically complex component of subtidal vegetation comprising an aggregate of species of small algae and developmental forms of larger algae. Over half of the approximately 80 species they list are less than 1 cm high, another 23 species are under 10 cm, and all are primarily attached to rock substrates. Algal thalli in the intertidal turfs described in the present study intertwine and reattach to one another. Borowitzka, Larkum, and Borowitzka (1978), Hay (1978), and Lauret (1974) discuss other turflike formations—each different in species composition, vertical position on the shore, and morphology and persistence of the mat as a whole.

Large portions of flat intertidal rocky beaches in southern California are covered by algal turf, a formation distinct from the better-known vegetation in central California and northward, where larger discrete thalli predominate. Turfs on boulders, on the sides of tidepools, or high in the intertidal on rocks close to sand beaches differ in several features from turfs in the mid-to-low intertidal zone, covering tops of

<sup>1</sup>This study was supported by National Science Foundation grant DEB-78-03562. Manuscript accepted 30 October 1981.

<sup>2</sup>A-002, Scripps Institution of Oceanography, University of California, La Jolla, California 92093.

flat rocks. The study described here was designed to analyze and compare algal turfs that appear to be relatively homogeneous and grow at the same level in the intertidal. The taxonomic and morphologic features shared by vegetation at four sites indicate a framework for comparing other turfs. An opportunity to sample a similar-appearing association in the northern Gulf of California provided data with which to begin testing the supposition that there may be common properties of this form of algal growth that are adaptive responses to physical or biological features of the environment.

Physical and geographical characteristics of southern California coasts are reported in Anon. (1965), Emery (1960), and Jones (1971). Comparable data for the Gulf of California are summarized in Roden (1964).

#### MATERIALS AND METHODS

##### *Study Sites*

The lower limits of the southern California turf described in this study and the upper edges of *Phyllospadix* beds (*P. torreyi* Watson and *P. scouleri* Hooker) meet at approximately the 0.0 tidal level (MLLW). Shoreward, the upper limits of coralline-based turf merge into beds of the chiton *Nuttalina fluxa* or mats of filamentous algae, or boulders and sand replace the flat rock substrate. Representative sampling sites where vegetation appeared to be relatively homogeneous and similar were selected within broad bands of this turf on four flat intertidal platforms (Figures 1, 2). Sites were paired, with sites *a* and *b* 2 km apart near La Jolla, and sites *c* and *d* 6 km apart. Sites *c* and *d* were 15 km north of sites *a* and *b*, and all were at approximately 32°40' N, 117°14' W, in San Diego County.

In the Gulf of California, field work consisted of collecting and examining 200 vial-size samples of turf on a broad intertidal platform (10 from each of 20 transects) during a 1-wk period in March–April 1979 at Playa Estación, near Puerto Peñasco, Sonora, Mexico, 31°17' N, 113°34' W.

##### *Sampling*

Preliminary analyses of species accumulation curves and variances of mean abundance estimates in ten-sample replicates showed that ten fixed 25 × 25 cm quadrats per site per visit provided reliable information about species abundances. A transect was established at each southern California site perpendicular to the water edge, beginning at the *Phyllospadix* boundary and extending 10–20 m over flat unbroken substrate. Sampling (May 1977–June 1979) was undertaken when tide and surf conditions, and daylight, allowed precise field discrimination of anchor taxa by both form and color. Table 1 summarizes the sampling program.

The algal cover in each quadrat was estimated by centering transparent plexiglass plates at fixed points along the transect. Nonepiphytic species beneath the plate were identified, and the amount of substrate surface covered by each was traced onto the plate. Nonalgal cover (bare sand, rock, invertebrates) was marked in the same way. Areas delineated on the plexiglass plates were later traced onto papers which were then laid over graph paper to determine proportional cover.

From just outside each fixed quadrat, a 2 × 5 cm vial was filled with pieces of epiphyte-covered substrate-attached algae representative of thalli within the quadrat. Epiphytic thalli from each vial were sorted and identified with a dissecting microscope, and the most common were ranked by abundance. The presence/absence data recorded for each quadrat-associated vial were converted to frequency-of-occurrence standardized data; arcsine transformation preceded calculation of the Bray–Curtis measure of dissimilarity (Clifford and Stephenson 1975) between sites and sampling dates. Taxonomic diversity was compared with a statistic derived for use with presence/absence data (Herrera 1976).

Representative biomass data were obtained from five randomly selected 12.5 × 12.5 cm quadrats scraped at each site four times during the year.

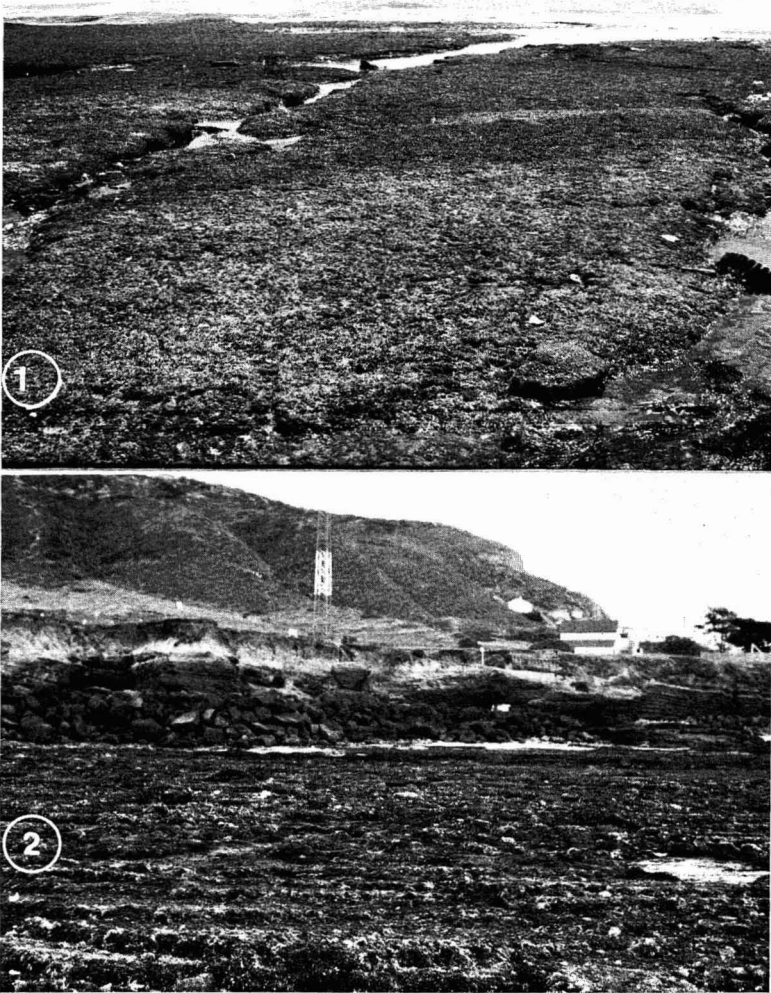


FIGURE 1. *Corallina*-anchored turf in San Diego County, southern California, looking seaward toward *Phyllospadix* bed, site *c*.

FIGURE 2. *Corallina*-anchored turf in San Diego County, looking shoreward to narrow sand and cobble beach, site *d*.

TABLE 1  
SAMPLING SCHEDULE

	MONTH											TOTAL
	J	F	M	A	M	J	J	A	O	N	D	
Number of site visits	4	5	6	1	6	6	2	0	4	8	8	50
Number of quadrats for proportional cover	40	44	53	10	60	50	20	0	40	89	80	486
Number of vials, epiphyte frequency	40	31	32	0	51	53	12	0	40	60	59	378

TABLE 2

SPECIES FOUND IN SAN DIEGO COUNTY *Corallina*-BASED TURF: ALL-YEAR, ALL-SITE MEAN ABUNDANCE ESTIMATES,  $\bar{X}$ 

I. ANCHOR TAXA	PROPORTIONAL COVER
<i>Corallina</i> spp. (see text)	0.433
<i>Pterocladia capillacea</i> (Gmel.) Born. & Thur.	0.164
<i>Hypnea valentiae</i> (Turn.) Mont.	0.022
<i>Lithothrix aspergillum</i> Gray	0.018
<i>Jania crassa</i> Lamour.	0.007
<i>Gelidium pusillum</i> (Stackh.) Le Jol.	0.000
Mixed species	0.120
Sand mat	0.170
Bare rock	0.066
II. MOST ABUNDANT EPIPHYTES	FREQUENCY OF OCCURRENCE
<i>Ceramium eatonianum</i> (Farl.) DeToni	0.619
<i>Ceramium flaccidum</i> (Kütz.) Ardissoni	0.529
<i>Centroceras clavulatum</i> (C. Ag.) Mont.	0.500
<i>Hypnea valentiae</i>	0.433
<i>Lithothrix aspergillum</i>	0.349
<i>Laurencia pacifica</i> Kyl.	0.322
<i>Chondria arcuata</i> Hollenb.	0.251
<i>Binghamia forkii</i> (Daws.) Silva	0.182
<i>Heterosiphonia erecta</i> Gardn.	0.150
III. LESS ABUNDANT EPIPHYTES*	FREQUENCY OF OCCURRENCE
<i>Gelidium pusillum</i>	0.253
<i>Gigartina canaliculata</i> Harv.	0.201
<i>Jania crassa</i>	0.235
<i>Jania tenella</i> (Kütz.) Grun./ <i>J. adhaerens</i> Lamour.	0.222
<i>Polysiphonia simplex</i> Hollenb.	0.113
<i>Sphacelaria furcigera</i> Kütz.	0.113
<i>Ulva</i> sp.	0.317

\*Found in more than 25 percent of vials at one or more sites.

At 3-month intervals in the first year all visible organisms were scraped from the rock surface within three 25 × 25 cm quadrats at one site to monitor reestablishment of algae. As thalli reappeared in these 12 experimental quadrats the area occupied by each species was mapped in the same way that undisturbed quadrats were sampled.

Nomenclature of macroalgae follows Abbott and Hollenberg (1976) except for *Ceramium flaccidum* (Womersley 1978) and *Neogardhiella gaudichaudii* (Abbott 1978). Invertebrates are named according to McLean (1978), Morris, Abbott, and Haderlie (1980), and Ricketts and Calvin (1968).

## RESULTS

*San Diego Turf*

I refer to the coralline algae that attach to rock substrate and support numerous epiphytic species as *anchor taxa*; this name is descriptive of their functional role in this association. Despite striking changes in color and texture of the surface layer from month to month, the 2–7-cm-high turf consisted at all times of the same few anchor species holding a large number of epiphytes (Table 2, Figure 3). The entire mat is an entangled mesh that traps sand, shell, and algal debris. A sea anemone, *Anthopleura elegantissima*,



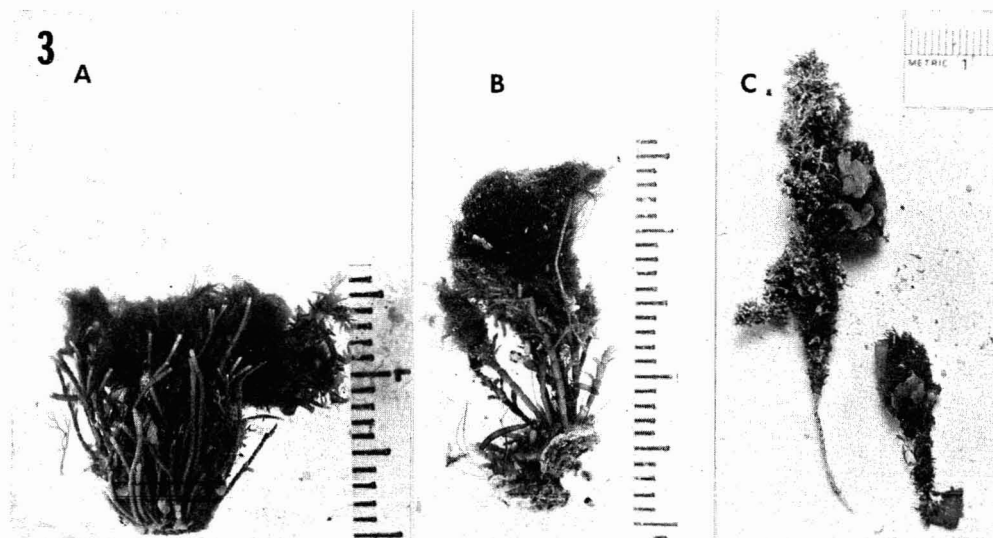


FIGURE 3. Clumps of turf removed from mat to show attached epiphytes. Basiphytes: A, *Jania crassa*; B, *Corallina pinnatifolia*; C, *Corallina vancouveriensis*. Scale in A, B = inches.

was found at all sites throughout the year, but otherwise, invertebrates were small and mostly hidden by algae.

**ANCHOR TAXA:** Figures 4A–D and 5 show, respectively, the monthly proportions of substrate covered by *Corallina* and sand mat, and mean values for each of 11 cover categories at each site over the sampling period. *Corallina* spp. includes *C. pinnatifolia* (Manza) Daws. and *C. vancouveriensis* Yendo. “Sand mat” records sand showing emergent tips of *Corallina* axes and sand covered with filamentous or repent epiphytes, of which diatoms, ectocarpoid filaments, *Binghamia forkii*, filamentous red algae, *Coeloseira parva*, *Colpomenia sinuosa*, and *Ulva* species were most common. When samples of sand mat were removed and washed, clumps of *Corallina* thalli remained (Figure 3). Additional evidence that sand mat and *Corallina* occupy the same space at different times is found in data from individual quadrats in successive months that showed a change from 100 percent sand mat to 100 percent *Corallina* within 2–6 wk. Sand mat and *Corallina* data combined account for approximately 60 percent of the total area sampled at all sites (Figure 4E); at separate sites, *Corallina* and sand mat occupy between

90 percent (Figure 4C) and 42 percent (Figure 4A) of the surface area.

*Gelidium pusillum* and *Hypnea valentiae* (Figure 5) were infrequently found attached directly to the substrate. *Lithothrix aspergillum* and *Jania crassa* occur in temporary patches, covering less than 8 percent of the quadrat areas at any time. These four species were also recorded as epiphytes when attached to *Corallina*. *Pterocladia capillacea* is a major component of turf at two sites (Figure 5A, B), but it is virtually absent from the other two (Figure 5C, D).

**EPIPHYTIC TAXA:** At any single time, 15–30 species were found fastened to anchor species at every site. Relative frequencies of the nine most abundant epiphytes (Table 2, part II) are shown in ranked order in Figure 6. Of these, six were common and abundant at all sites, while each of the other three was absent or rare at one site. Most of the ubiquitous epiphytes are too small to recognize easily in the field. Among the larger species, *Laurencia pacifica* and *Gigartina canaliculata* occurred on underlying rock substrate as well as on *Corallina*. At times, each was relatively abundant, but the thalli did not persist in individual quadrats from month to month. Single or a few specimens

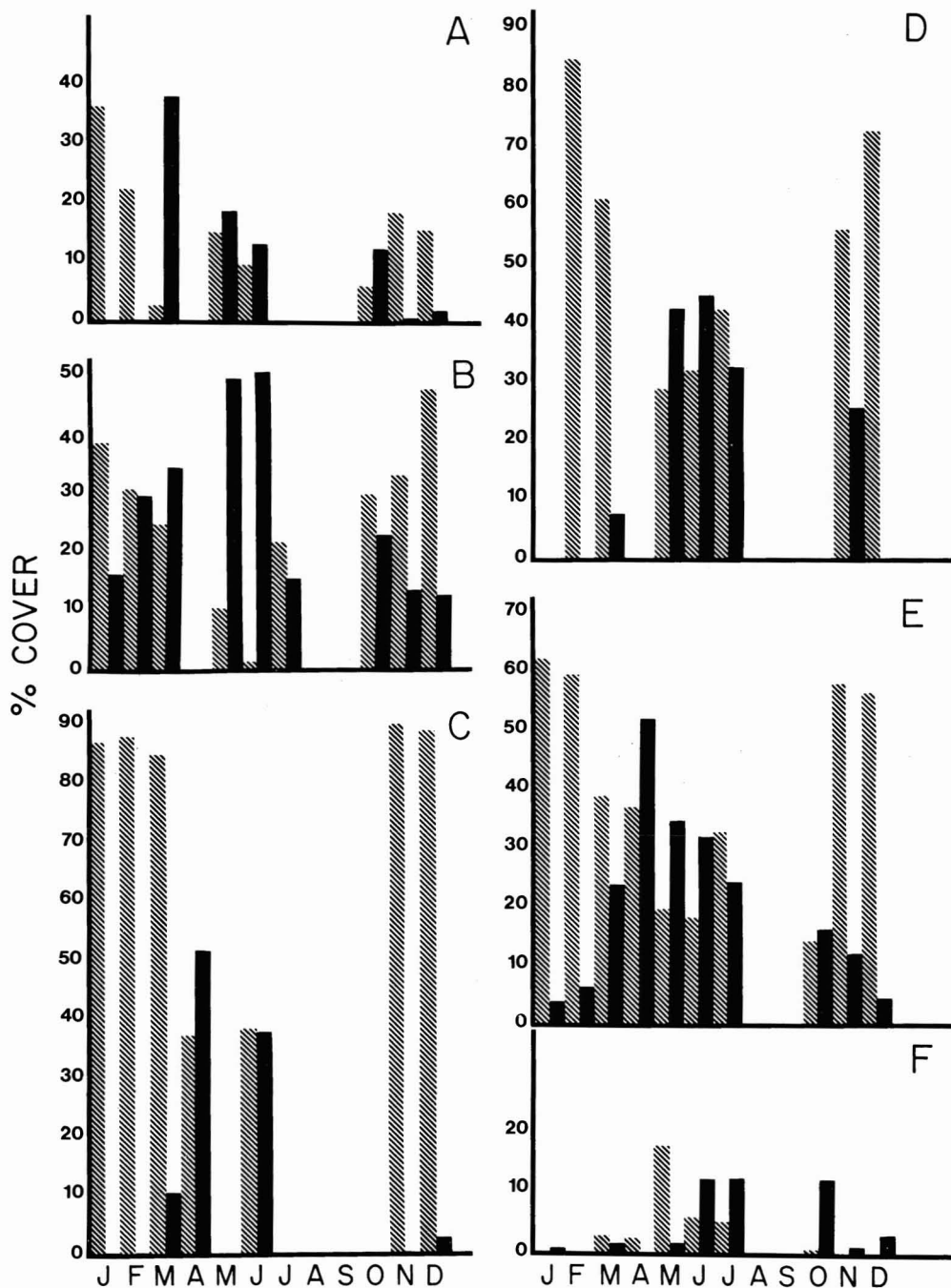
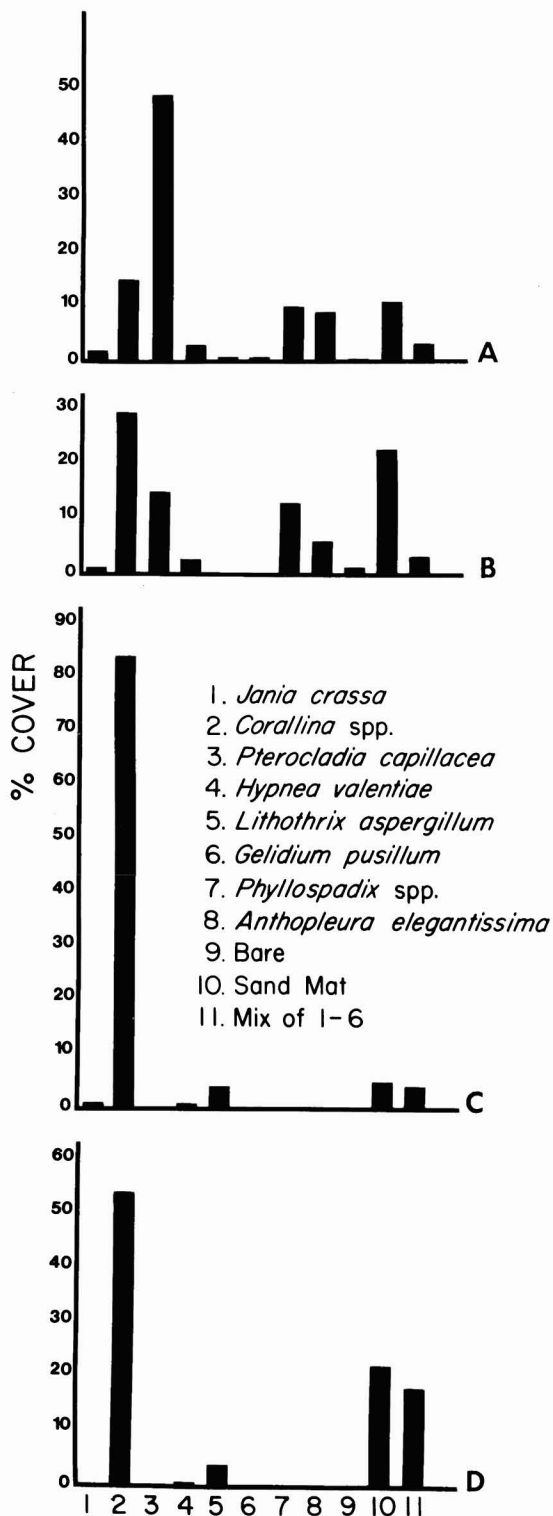


FIGURE 4. A-E, monthly proportions of substrate covered by *Corallina* species (striped bar) and sand mat (solid bar). A, B, La Jolla sites; C, D, Point Loma sites; E, four-site pooled data; F, monthly proportion of turf surface occupied by *Colpomenia sinuosa* (striped bar; axis units represent mean values in square centimeters), and *Hypnea valentiae* in discrete clumps or entangled with other species (solid bar; axis indicates percent cover), four-site pooled data.



of an additional 49+ species either were occasionally found in samples or were observed near the transect. Most of these species are more often associated with habitats other than this midintertidal turf (Table 3).

**TEMPORAL FLUCTUATIONS:** No definite seasonal trends were found in the total number of species observed, the number of species per vial, or the mean abundances of most taxa. Calculated diversity coefficients ( $D/D_{max}$ ; Herrera 1976) for combined site data suggest less diversity during May–October. *Corallina*, including data recorded as sand mat, persisted throughout the year at similar levels (Figure 4). Among the abundant epiphytes, *Ceramium flaccidum* was most frequently found in October, while *Ceramium eatonianum* and *Centroceras clavulatum* were most often seen in winter–spring months. *Heterosiphonia erecta* and *Ulva* sp. showed maximum abundances in January and March, respectively, but were present throughout the year. At site *b*, 19–30 percent of the quadrat surface was occupied by *Pterocladia capillacea* between November and February, then less than 10 percent during March–July. Algal biomass, which consisted largely of *Corallina* species and, on two sites, of *Pterocladia capillacea*, was greater at all sites (1930–3584 g/m<sup>2</sup> dry wt) during July–October than December–March (1288–1582 g/m<sup>2</sup> dry wt).

*Lithothrix aspergillum* was occasionally observed in large conspicuous patches within the study areas, but according to data, its appearance was intermittent and followed no clear temporal cycle, both as an epiphyte on *Corallina* and as an anchor species. For example, between November 1977 and February 1978, 16–23 percent of the surface in one quadrat (site *c*) was covered, but very little or none was recorded in the same quadrat either before or after this period. At site *d* in May 1977 the ten quadrats together contained 1040 cm<sup>2</sup> (of 6250), while in May 1979 no *Lithothrix* was found in any.

FIGURE 5. Relative abundance of algae and nonalgal categories recorded by percent cover data. A, B, La Jolla sites; C, D, Point Loma sites.

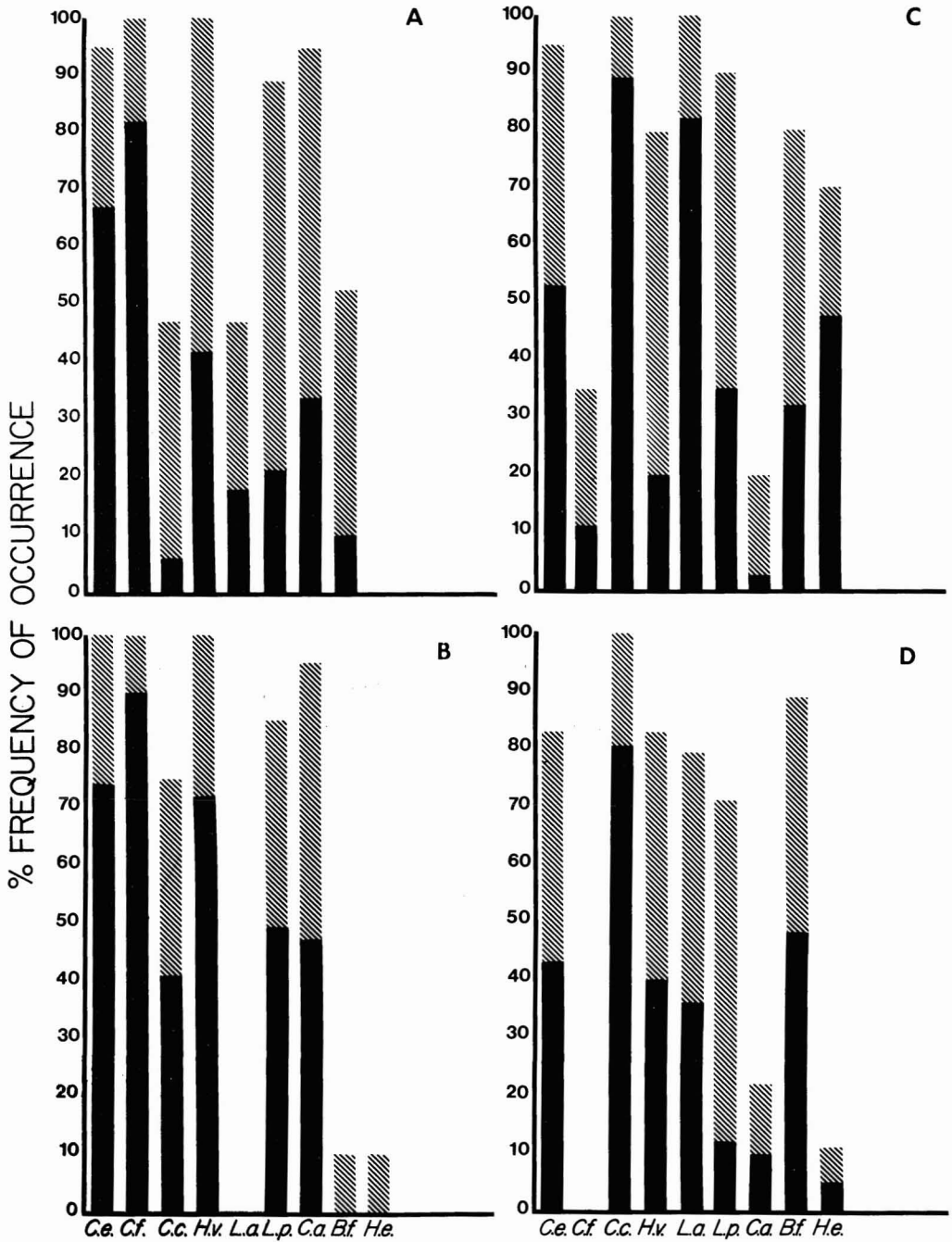


FIGURE 6. Relative abundance of the nine most abundant epiphytes. *A, B* La Jolla sites; *C, D* Point Loma sites. Solid bars show percent frequency of occurrence in individual vial samples. Striped bars show percent occurrence in site samples (ten vials per sample). Species are those listed in Table 2, part II.

TABLE 3

ALGAE INFREQUENTLY FOUND IN SAMPLES OR ONLY OBSERVED NEAR TRANSECTS

<i>Acrosorium uncinatum</i> (Turn.) Kyl.	<i>Gastroclonium coulteri</i> (Harv.) Kyl.
<i>Anisocladella pacifica</i> Kyl.	<i>Gracilaria andersonii</i> (Grun.) Kyl.
<i>Bossiella</i> sp.	<i>Haliptylon gracile</i> (Lamour.) Johans.
<i>Bryopsis hypnoides</i> Lamour.	<i>Herposiphonia plumula</i> (J. Ag.) Hollenb.
<i>B. pennatula</i> J. Ag.	<i>H. verticillata</i> (Harv.) Kyl.
<i>Callithamnion rupicolum</i> Anders.	<i>Hypnea valentiae</i> var. <i>gardneri</i> Hollenb.
<i>Ceramium clarionense</i> S. & G.	<i>Laurencia spectabilis</i> Post & Rupr.
<i>C. sinicola</i> S. & G.	<i>Leathesia difformis</i> (L.) Aresch.
<i>Chaetomorpha californica</i> Coll.	<i>Lomentaria hakodatensis</i> Yendo
<i>C. spiralis</i> Okam.	<i>Macrocystis pyrifera</i> (L.) C. Ag.*
<i>Chondria californica</i> (Coll.) Kyl.	<i>Neogardhiella gaudichaudii</i> (Mont.) Abb.
<i>C. nidifica</i> Harv.	<i>Nienburgia andersoniana</i> (J. Ag.) Kyl.
<i>Cladophora albida</i> (Huds.) Kütz.	<i>Ophiodocladus simpliciusculus</i> (Crouan & Crouan) Falk.
<i>C. columbiana</i> Coll.	<i>Plocamium cartilagineum</i> (L.) Dix.
<i>Codium fragile</i> (Sur.) Har.*	<i>P. violaceum</i> Farl.
<i>Coeloseira parva</i> /C. <i>compressa</i> Hollenb.	<i>Pogonophorella californica</i> (J. Ag.) Silva
<i>Colacodasya californica</i> Hollenb.	<i>Polysiphonia hendryi</i> Gardn.
<i>Colpomenia peregrina</i> (Sauv.) Ham.*	<i>P. scopulorum</i> var. <i>villum</i> (J. Ag.) Hollenb.
<i>C. sinuosa</i> (Roth) Derb. & Sol.	<i>Porphyra</i> ( <i>perforata</i> J. Ag.?)
<i>Corallina officinalis</i> L.	<i>Pterosiphonia baileyi</i> (Harv.) Falk.
Crustose taxa	<i>P. dendroidea</i> (Mont.) Falk.
<i>Cryptopleura</i> spp.	<i>Sargassum muticum</i> (Yendo) Fensh.*
<i>Dictyota</i> sp.	<i>Scytosiphon lomentaria</i> (Lyngb.) J. Ag.*
Ectocarpoids	<i>Tenarea</i> sp.
<i>Egregia menziesii</i> (Turn.) Aresch.*	<i>Tiffaniella snyderae</i> (Farl.) Abb.
<i>Enteromorpha</i> sp.	

\*Only observed near transects.

Cover data were seldom recorded for *Hypnea valentiae* independently, because most thalli grew attached to other algae. Mix categories recorded combinations of anchor taxa that could not be separately estimated (Figure 5). Data that included *Hypnea*, added to data for the species alone, substantiate (Figure 4F) the observation that large *Hypnea* thalli were numerous in late summer and fall but were difficult to find in winter and spring. However, small thalli must persist, since they were found in 37–50 percent of the vial samples in every month; the species was the fourth most often found epiphyte overall (Figure 6).

Figure 4F also documents the changes in abundance of *Colpomenia sinuosa*.

VARIABILITY AMONG SAN DIEGO COUNTY SITES: Resemblances among sites, shown in Figures 4 and 6, are substantiated by several statistical treatments of the data which indicate similarities in composition, with pairs of sites in the two areas being most

similar. Differences among sites were largely in relative abundances; anchor and associated taxa at each site included the same dominant taxa with the exceptions of *Pterocladia capillacea* (rare at Point Loma sites) and three of the nine most abundant epiphytes as noted above. Diversity ( $D/D_{\max}$ ) for pooled data is 0.47, and for individual sites, 0.45–0.56. Site *d* had both fewer total species and fewer species in single samples:  $\bar{x} = 4.9$  species per vial in contrast with  $\bar{x} = 5.38$ –7.98 species per vial at the other three sites.

Algal biomass (mean dry weight) for combined samples at each site ranged between 30 g and 36 g for the  $12.5 \times 12.5$  cm quadrats. For purposes of comparison with data gathered in other habitats and reported by other workers, this converts to a calculated mean dry weight of 2048 g/m<sup>2</sup> for the algae in this habitat.

REESTABLISHMENT OF TURF: On newly exposed surfaces (site *c*), basal crusts that pro-

TABLE 4  
SPECIES FOUND IN TURF SAMPLES AT PUERTO PEÑASCO, MEXICO  
(percent frequency-of-occurrence in vial samples)

SPECIES	FREQUENCY OF OCCURRENCE (%)	SPECIES WITH <2% FREQUENCY (1-4 OCCURRENCE)
<i>Laurencia</i> "pacific" (see Fenical and Norris 1975) or <i>L. paniculata</i>	75.5	<i>Laurencia johnstonii</i> S. & G.
<i>Ceramium sinicola</i> S. & G.	47.5	<i>Spyridia filamentosa</i> (Wulf.) Harv.
<i>Gelidium pusillum</i> (Stackh.) Le Jol.	36	<i>Sphacelaria (fircigera</i> Kütz.?)
<i>Valoniopsis pachynema</i> (Mart.) Børg.	26	<i>Corallina pinnatifolia</i> (Manza) Daws.
<i>Amphiroa (annulata</i> Lemoine?)	24.5	<i>Enteromorpha</i> sp.
<i>Chondria arcuata</i> Hollenb.	18	Ectocarpoid filaments
<i>Colpomenia tuberculata</i> Saunders	17	<i>Heteroderma gibbsii</i> (Fosl. & Setch.) Fosl.?
Noncoralline crust, in part <i>Hildenbrandia</i> sp.	12	<i>Polyclinum</i> sp.
<i>Polysiphonia simplex</i> Hollenb.	10	Diatoms
<i>Cladophora hesperia</i> S. & G.	9.5	<i>Plectonema</i> sp. (?)
<i>Polysiphonia scopulorum</i> var. <i>villum</i> (J. Ag.) Hollenb.	9	<i>Gigartina (tepida</i> Hollenb.?)
<i>Porolithon sonorensis</i> Daws.	6	
Undetermined coralline crusts	6	
<i>Ceramium flaccidum</i> (Kütz.) Ardissonne	3.5	
Undetermined <i>Polysiphonia</i> spp.	3	

duced erect *Corallina* axes began to reappear after 2-4 months, and *Corallina* again occupied most of the substrate after 6-10 months in areas cleared at each of the four seasons. After 12-14 months the experimental quadrats could be distinguished only because the *Corallina* was less dense and, in some instances, large clumps of *C. vancouveriensis* were absent. After 2 yr, the new growth areas were indistinguishable from surrounding turf—*Corallina* was reestablished on surfaces where it had predominated prior to scraping.

#### Puerto Peñasco Turf

Algae are ranked according to frequency in samples in Table 4. The first six taxa were found on all transects in 18-75 percent of the vials, and of these, four occur in San Diego turf, while two are tropical taxa not found in California. Of the next nine, eight are crustose or filamentous epiphytes. The eleven other infrequently recorded taxa include a sessile colonial ascidian, groups of undetermined species, and easily identified algae that were seldom found in this habitat, but that grow nearby in other communities.

More than half the taxa were also found in California turf.

#### Invertebrates in California Turf

Because grazing by herbivorous invertebrates is a possible means of maintaining the rather uniform height of thalli that gives this vegetation its characteristic even surface, an animal census along the transects at each site was made every time algal data were gathered. During each of the 18-20 visits to each site the macroinvertebrates that could be found without destroying algal cover were counted within a 1-m-wide strip the length of the transect; Table 5 gives standardized data and indicates species considered to be primarily algal grazers. Other invertebrates present but not consistently sampled by this method included various worms, colonial ascidians and sponges, burrowing mollusks, and species smaller than 5 mm in largest dimension.

#### DISCUSSION

*Turf* is derived from roots meaning "a tuft of grass," but I presume that most workers



TABLE 5  
NUMBERS OF INVERTEBRATES PER SQUARE METER

INVERTEBRATE	SITE			
	<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>
<b>Cnidara (Coelenterata)</b>				
<i>Anthopleura elegantissima</i> (Brandt, 1835)	2.028	22.74	0.055	0.472
<b>Mollusca</b>				
<b>Gastropoda</b>				
<i>Alia carinata</i> (Hinds, 1844)	0.128	0.09		0.027
h <i>Aplysia californica</i> Cooper, 1863		0.27	0.016	0.145
h <i>Aplysia vaccaria</i> Winkler, 1955				0.181
h <i>Astraea undosa</i> (Wood, 1828)			0.066	0.068
<i>Ceratosstoma nuttalli</i> (Conrad, 1837)			0.022	0.054
h <i>Collisella limatula</i> (Carpenter, 1864)				0.027
? <i>Collisella ochracea</i> (Dall, 1871)				0.027
h <i>Collisella pelta</i> (Rathke, 1833)	0.128		0.005	0.081
<i>Conus californicus</i> Hinds, 1844				0.027
<i>Crepidatella lingulata</i> (Gould, 1846)		0.018		
<i>Dialula sandiegensis</i> (Cooper, 1862)			0.016	0.004
h <i>Fissurella volcano</i> Reeve 1849	0.242	0.072	0.183	0.527
h <i>Haliotis cracherodii</i> Leach, 1814		0.045		
h <i>Haliotis fulgens</i> Philippi, 1845				0.009
<i>Hermisenda crassicornis</i> (Eschscholtz, 1831)				0.018
<i>Hipponix cranioides</i> Carpenter, 1864			0.033	
<i>Homalopoma baculum</i> (Carpenter, 1864)			0.016	0.009
<i>Hopkinsia rosacea</i> MacFarland, 1905				0.031
h <i>Lacuna unifasciata</i> Carpenter, 1857	0.042	0.045		
<i>Macron lividus</i> (A. Adams, 1855)	0.057		0.011	0.14
<i>Navanax inermis</i> (Cooper, 1862)				0.018
<i>Notoacmea paleacea</i> (Gould, 1853)		0.036	0.055	
<i>Pseudomelatoma penicillata</i> (Carpenter, 1864)			0.016	0.15
<i>Roperia poulsoni</i> (Carpenter, 1864)				0.027
? <i>Tegula aureotincta</i> (Forbes, 1852)			0.022	0.054
? <i>Tegula eiseni</i> Jordan, 1936			0.638	1.9
<i>Volvarina taeniolata</i> Morch, 1860			0.005	0.018
<b>Chitons</b>				
? <i>Lepidozona californiensis</i> (Berry, 1931)			0.011	0.159
h <i>Mopalia muscosa</i> (Gould, 1846)	0.028			0.004
*h <i>Nuttalina fluxa</i> (Carpenter, 1864)			0.011	0.040
? <i>Stenoplax conspicua</i> (Pilsbry, 1892)		0.1	0.261	0.40
<b>Arthropoda (crustaceans)</b>				
<i>Callianassa affinis</i> Holmes, 1900				0.022
? <i>Idotea</i> sp.	0.028	0.009		
*h <i>Pachygrapsis crassipes</i> Randall, 1839	2.85	2.9	2.222	
<i>Pagurus</i> sp.	0.128	0.4		0.122
<i>Portunus xantusi</i> (Stimpson, 1860)				0.09
h <i>Pugettia producta</i> (Randall, 1839)	0.014	0.009		
<b>Echinodermata</b>				
h <i>Lytechinus pictus</i> (Verrill, 1867)				0.009
<i>Ophioderma panamense</i> Lutken, 1859				0.05
<i>Ophionereis annulata</i> (LeConte, 1851)				0.2
<i>Ophiothrix spiculata</i> LeConte, 1851				0.05
h <i>Patiria miniata</i> (Brandt, 1835)			0.005	0.059
<i>Pisaster giganteus</i> (Stimpson, 1857)		0.009	0.005	
<i>Pisaster ochraceus</i> (Brandt, 1835)	0.042	0.109		
h <i>Strongylocentrotus purpuratus</i> (Stimpson, 1857)		0.009		

NOTE: h = macroalgae included in diet according to published information (*Aplysia californica*—Leighton 1966, Morris et al. 1980; *A. vaccaria*—Morris et al. 1980; *Astraea undosa*—Leighton 1966; *Collisella limatula*—Morris et al. 1980; *C. pelta*—Morris et al. 1980; *Fissurella volcano*—Sousa 1979; *Haliotis cracherodii*—Morris et al. 1980; *H. fulgens*—Leighton 1966; *Lacuna unifasciata*—Sousa 1979; *Mopalia muscosa*—Morris et al. 1980; *Nuttalina fluxa*—Morris et al. 1980; *Pachygrapsis crassipes*—Morris et al. 1980; *Pugettia producta*—Leighton 1966, Morris et al. 1980; *Lytechinus pictus*—Leighton 1966, Morris et al. 1980; *Patiria miniata*—Morris et al. 1980; *Strongylocentrotus purpuratus*—Leighton 1966, Morris 1980).

? = no information for this species, related species are algal herbivores.

\*h = potentially an important herbivore.

who use this word to refer to algal formations understand it to mean a stratum of sediment with a layer of plant growth forming a thick mat—the most applicable definition. Although algal turf is often recorded as a component of intertidal vegetation in many regions of the world, I have found no quantitative information about the composition of any such association. Comparisons between the two turfs of the present study indicate that in these superficially similar associations certain of the taxa are the same while many are different, and most are present in dissimilar relative proportions. However, the structures of both turfs depend on a combination of anchor and epiphytic taxa, and many of the constituent species are either creeping, repent forms or filamentous ceramiacean species. Larger thalli of the same or morphologically similar species of *Gelidium*, *Gigartina*, *Laurencia*, and *Corallina* occur in both areas. In the southern California turf, *Corallina* species occur at similar levels of abundance (measured by substrate covered) throughout the year, although the thalli are intermittently buried in sand.

The persistence of sand within turf and characteristics of the sediment particles presumably influence the composition and morphology of the composite structure of the turf itself and of the individual organisms that are dominant in this habitat. Large, but unmeasured, amounts of sediment were also trapped in the Puerto Peñasco turf at the time of the work there (in late March).

Species lists, or extracted comments from studies of intertidal algae, appear to describe turfs that perhaps share certain features with turf in southern California and in the Gulf of California. For example, in West Africa, Lawson and John (1977) and Lawson, John, and Price (1975) cite species of *Hypnea*, *Ulva*, *Corallina*, *Polysiphonia*, and *Champia* (a taxon comparable in structure and growth habit to *Binghamia* in southern California), and *Gelidium pusillum* and *Centroceras clavulatum* as major components of intertidal turfs. Lawson and Norton (1971) state that in the Canary Islands the lower half of the littoral zone consists of a “rather dirty brownish coloured turf—composed mainly

of small red algae,” including *Centroceras clavulatum*, *Gelidium* and *Laurencia* species, and articulated corallines. On an exposed Brazilian rocky intertidal site, Oliveira and Mayal (1976) found high algal diversity in a narrow band of corallines, mainly *Amphiroa beauvoisii* and *Jania adhaerens* (similar or conspecific with *J. tenella* in California and in the Gulf of California), associated with *Colpomenia sinuosa*, *Centroceras clavulatum*, *Gelidium pusillum*, and species of *Chaetomorpha*, *Ulva*, *Cladophora*, *Hypnea*, *Ceramium*, and *Sphacelaria*, taxa that are included in Tables 2 and 3 of this paper. Feldmann (1938), describing a *Corallina mediterranea* association in the western Mediterranean, states that it is formed of compact tufts (of *C. mediterranea*) associated in extended “lawns,” bearing the same or closely related epiphytic species reported above. Without additional information, conclusions drawn from such observations of any single association cannot be assumed to apply to another.

Most of the algal species in the San Diego turf are also found in different nearby habitats; e.g., adjacent *Phyllospadix* beds contain many of the same taxa but in very different proportional abundances (Stewart and Myers 1980). Because the algal assemblage associated with *Phyllospadix* species at these same four sites has been quantitatively characterized, similarities can be statistically compared. Bray–Curtis dissimilarity indices were calculated for the two different algal assemblages at each site and for the same algal association at different sites. Turf vegetation is more homogeneous (0.26–0.50) than algal vegetation under *Phyllospadix* (0.34–0.68), while the turf algae adjacent to *Phyllospadix* algae at each site were less similar (0.54–0.67). Detailed analyses can be summarized by stating that the most abundant species in each habitat are infrequently seen in the other, but few taxa are excluded from or restricted to either of the two lists.

Abbott and Hollenberg (1976) refer to *Ceramium flaccidum* (as *C. gracillimum* var. *byssoideum* [Harv.] Maz.) and *Chondria arcuata* as rare, and to *Binghamia forkii* as occasional in the California flora. Since

intertidal algal mats had not been studied at that time, the abundance of these species in this habitat apparently had not been observed.

I observed no striking changes in the overall abundance of algal thalli at different times during the 2-yr study, but analysis of percent cover or percent frequency of individual species showed that several fluctuated in cycles coincident with seasonal changes. The same two general conclusions have been drawn from surveys of other intertidal communities in southern California and from studies of the same taxa elsewhere in the world.

At San Clemente Island, off the coast of San Diego, Littler, Murray, and Arnold (1979) documented temporal cycles that coincide with those reported here for three species: (1) *Colpomenia sinuosa* attained a maximum standing crop in summer; (2) *Pterocladia capillacea* was found during most of the year at about 70 percent of the winter maximum, showing a moderate change in abundance; and (3) *Lithothrix aspergillum* occurred at constant levels at all seasons. Littler et al. also concluded that distinct seasonal differences in overall vegetation are lacking at San Clemente.

Wynne and Norris (1976) observed dramatic seasonal fluctuations in the occurrence of *Colpomenia sinuosa* at Puerto Peñasco. Apparently, this species grows in the same seasonal cycle in southern California and in the upper Gulf of California, despite large differences in water and air temperatures during part of the year.

Seasonal growth such as is shown for *Hypnea valentiae* in San Diego has been reported for other species of the genus. Mshigeni (1977) suggests that the fluctuating abundances of three species he observed in Hawaii and Lawson's (1957) data for species in Ghana all may be correlated more directly with seasonal occurrences of extreme low tides than with summertime conditions of light and temperature. In San Diego, *H. valentiae* occurs at similar but low frequencies at all times under *Phyllospadix* low in the intertidal zone (Stewart and Myers 1980), while a marked summer increase of

the same species growing higher in the intertidal is recorded in turf data, a contrast consistent with Mshigeni's suggestion.

### Herbivory?

It is tentatively concluded that the numbers of herbivorous macroinvertebrates are too few to support the hypothesis that grazing is an important factor in regulating algal growth at the four San Diego sites. *Aplysia* and *Tegula* species and *Pachygrapsis crassipes*, potentially important in this relationship, were found mostly at single times of the year, or at single sites. *Nuttalina fluxa* is generally restricted to patches at the shoreward edge of the turf.

### ACKNOWLEDGMENTS

I thank the National Park Service, Cabrillo National Monument, for cooperation at site *d*; E. DeMartini for advice concerning sampling designs; R. Hoshaw, of the University of Arizona, for providing the opportunity to work at Puerto Peñasco; and J. Norris for suggesting appropriate nomenclature for Puerto Peñasco taxa. Barbara Myers, of the San Diego Natural History Museum, identified the invertebrates and compiled the data.

### LITERATURE CITED

- ABBOTT, I. A. 1978. Morphological and taxonomic observations on *Neoagardiella* (Gigartinales, Rhodophyta) with emphasis on Pacific populations. *J. Phycol.* 14: 48-53.
- ABBOTT, I. A., and G. J. HOLLENBERG. 1976. Marine algae of California. Stanford University Press, Stanford.
- ANONYMOUS. 1965. An oceanographic and biological survey of the southern California mainland shelf. (California) State Water Quality Control Board Publ. #27. California State Resources Agency, Sacramento, Ca.

- BOROWITZKA, M. A., A. W. D. LARKUM, and L. J. BOROWITZKA. 1978. A preliminary study of algal turf communities of a shallow coral reef lagoon using an artificial substratum. *Aquatic Bot.* 5:365-381.
- CLIFFORD, H. T., and W. STEPHENSON. 1975. An introduction to numerical classification. Academic Press, New York.
- EMERY, K. O. 1960. The sea off southern California. Wiley, New York.
- FELDMANN, J. 1938. Recherches sur la végétation marine de la Méditerranée. *La Côte des Albères. Rev. Algol.* 10:1-339.
- FENICAL, W., and J. N. NORRIS. 1975. Chemotaxonomy in marine algae: Chemical separation of some *Laurencia* species (Rhodophyta) from the Gulf of California. *J. Phycol.* 11:104-108.
- GISLÉN, T. 1930. Epibioses of the Gullmar Fjord. Part 2. Marine sociobiology. *Svensk. Vetensk. Akad. Kongel. Skr.* 4:1-380.
- HAY, M. 1978. The adaptive significance of the turf growth form: An enumeration of the costs and benefits of coloniality in marine macroalgae. *J. Phycol.* 14 (Suppl.):28.
- HERRERA, C. M. 1976. A trophic diversity index for presence-absence food data. *Oecologia (Berlin)* 25:187-191.
- JONES, J. H. 1971. General circulation and water characteristics in the southern California bight. Southern California Coastal Water Research Project.
- LAURET, M. 1974. Étude phytosociologique préliminaire sur les gazons à *Pterosiphonia pennata* (Rhodophycées, Cérariales). *Soc. Phycol. France, Bull.* 19:229-237.
- LAWSON, G. W. 1957. Seasonal variation of intertidal zonation on the coast of Ghana in relation to tidal factors. *J. Ecol.* 45:831-860.
- LAWSON, G. W., and D. M. JOHN. 1977. The marine flora of the Cap Blanc peninsula: Its distribution and affinities. *Bot. J. Linn. Soc.* 75:99-118.
- LAWSON, G. W., and T. A. NORTON. 1971. Some observations on littoral and sublittoral zonation at Teneriffe (Canary Isles). *Bot. Mar.* 14:116-120.
- LAWSON, G. W., D. M. JOHN, and J. H. PRICE. 1975. The marine algal flora of Angola: Its distribution and affinities. *Bot. J. Linn. Soc.* 70:307-324.
- LEIGHTON, D. L. 1966. Studies of food preference in algivorous invertebrates of Southern California kelp beds. *Pac. Sci.* 20:104-113.
- LITTLER, M. M. 1980. Overview of the rocky intertidal systems of southern California. Pages 265-306 in D. M. Power, ed. *The California Islands: Proceedings of a multidisciplinary symposium*. Santa Barbara Museum of Natural History, Santa Barbara, Ca.
- LITTLER, M. M., S. N. MURRAY, and K. E. ARNOLD. 1979. Seasonal variations in net photosynthetic performance and cover of intertidal macrophytes. *Aquatic Bot.* 7:35-46.
- MCLEAN, J. H. 1978. Marine shells of southern California. Los Angeles County Museum of Natural History. Science Ser. no. 24 (rev.), *Zool.* 11 (or: Science Series No. 24, Revised Edition: 1-104).
- MORRIS, R. H., D. P. ABBOTT, and E. C. HADERLIE. 1980. Intertidal invertebrates of California. Stanford University Press, Stanford.
- MSHIGENI, K. E. 1977. Seasonal changes in the standing crops of three *Hypnea* species (Rhodophyta: Gigartinales) in Hawaii. *Bot. Mar.* 20:303-306.
- NEUSHUL, M., and A. L. DAHL. 1967. Composition and growth of subtidal parvosilvosa from Californian kelp forests. *Helv. Wiss. Meer.* 15:480-488.
- DE OLIVEIRA FILHO, E. C., and E. M. MAYAL. 1976. Seasonal distribution of intertidal organisms at Ubatuba, São Paulo (Brazil). *Rev. Brasil. Biol.* 36:305-316.
- RICKETTS, E. A., and J. CALVIN. 1968. *Between Pacific tides*. 4th ed. Stanford University Press, Stanford.
- RODEN, G. I. 1964. Oceanographic aspects of the Gulf of California. Pages 30-58 in T. H. van Andel and G. Shor, eds. *Marine geology of the Gulf of California*. Amer. Assoc. Petrol. Geol., Mem. 3.
- SANTELICES, B., and I. A. ABBOTT. 1978. New records of marine algae from Chile and

- their effect on phytogeography. *Phycologia* 17:213–222.
- Sousa, W. P. 1979. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecol. Monogr.* 49:227–254.
- STEWART, J. G., and B. MYERS. 1980. Assemblages of plants and animals in *Phyllospadix*-dominated habitats. *Aquatic Bot.* 9:73–94.
- WOMERSLEY, H. B. S. 1978. Southern Australian species of *Ceramium* Roth (Rhodophyta). *Austral. J. Mar. Freshw. Res.* 29:205–257.
- WYNNE, M. J., and J. N. NORRIS. 1976. The genus *Colpomenia* Derbes et Solier (Phaeophyta) in the Gulf of California. *Smithsonian Contrib. Bot.* 35:1–18.