

Intertidal Macrophyte Communities from Pacific Baja California and the Upper Gulf of California: Relatively Constant vs. Environmentally Fluctuating Systems

Mark M. Littler and Diane S. Littler

Department of Ecology and Evolutionary Biology, University of California, Irvine, California 92717, USA

ABSTRACT: The adaptive features of marine macrophyte communities in a markedly fluctuating environment (the northern Gulf of California) were contrasted with those characteristic of a climatically more constant system (the Pacific coast of the Baja Peninsula) in the light of *a priori* predictions. In general, the data suggest the importance of intermediate disturbance in permitting a mosaic of young to mature community types to co-occur in accordance with previous theories. In the less-disturbed (more constant) Pacific coast system, the predominant macrophytes were either calcareous algae or structurally complex vascular plants, with early successional species such as *Ulva californica* and *Gelidium pusillum* being abundant only on recently overturned boulders. The majority of the overall productivity on the Pacific coast was provided by the larger, most abundant species. However, production rates per unit of thallus were highest for small species with high surface area to volume ratios (i. e., *Navicula* sp., *U. californica*, *Chondria californica*) that grew on the overturned rocks. As a group, the macrophytes that dominated the standing stock had considerably lower net productivity and larger thalli which were geometrically complex and formed a layered community that increased spatial heterogeneity. The Pacific site was more diverse (Shannon-Weaver H'), having higher values for both richness (species numbers) and evenness (J'). Conversely, in the seasonally disturbed sites (due to catastrophic environmental fluctuations) annual or opportunistic forms with high reproductive output (e. g., *U. rigida*, various species of *Colpomenia*, as well as eurytopic blue-green algae that are indicative of harsh habitats) were significantly more abundant ($P < 0.05$, Mann-Whitney U-test) than at the Pacific site. These populations rapidly recolonized available substrate following periods of mortality caused by extreme heat, desiccation and insolation during summer low tides. The smaller turf-like growth habits of the dominant macrophytes in the Gulf communities provided little spatial heterogeneity and this appeared to further limit macrobiotic diversity. Forms that contained considerable structural tissue or calcium carbonate as part of their thallus weight were the lowest producers at the Gulf sites and were of moderate to low abundance. Selection in the seasonally disturbed environments appears to have favored a predominance of structurally simple, opportunistic species (e. g., *Ulva*, *Colpomenia*) having high individual net productivity. In the less disturbed Pacific system, photosynthetic rates of the large predominant species (e. g., calcareous forms, thick forms, prostrate crusts, morphologically differentiated flowering plants) were lower because they have evolved structurally complex thalli (at the expense of photosynthetic tissue) in order to withstand the greater pressures of biological interactions. Most of the populational and community features at the Pacific site suggest a relatively long-lived, mature intertidal system containing a mosaic of younger successional stages; whereas, environmental fluctuations beyond the homeostatic capabilities of most marine plants maintain the upper Gulf macrophyte communities in a simpler subclimax condition.

INTRODUCTION

Factors providing and maintaining biological diversity have been longstanding concerns of ecologists and during the past two decades this interest has expanded markedly. Several hypotheses have been proposed to explain trends in diversity within natural systems. These include components of competition (e. g., Dayton, 1975; Buss and Jackson, 1979; Sousa, 1979a), predation (Paine, 1966, 1971), productivity

(Margalef, 1963; Connell and Orias, 1964), environmental constancy (Sanders, 1968, 1969), spatial heterogeneity (MacArthur, 1964; Kohn, 1967; Dayton, 1971) and disturbance (Levin and Paine, 1974; Osman, 1977; Talbot et al., 1978; Connell, 1978; Sousa, 1979b). It has been proposed (Sanders, 1969; Connell, 1975) that species numbers should decrease along a gradient of increasing environmental disturbance (i. e., beyond an optimal level; Fox, 1979), with a corresponding trend towards biological generalization (Slobodkin

and Sanders, 1969). Sanders (1969) defined physically-controlled habitats as those having (1) only a recent history, (2) large environmental amplitudes or (3) unfavorable physical conditions with concomitantly severe physiological stresses (at least some of the time) thereby reducing survival and reproduction. In this paper, we follow Grime (1979) in distinguishing (1) stress as those factors, that limit primary productivity (e. g., shortages of light, nutrients or sub-optimal temperatures) and (2) disturbance as phenomena which destroy plant biomass (e. g., herbivory, disease, desiccation, lethally high temperatures); both of these terms are used in a relative, not absolute, sense.

We used a 'post analytical' technique, whereby the outcome of past phenomena were assessed empirically and interpreted in view of intuitive *a priori* predictions (Littler and Littler, 1980). We took advantage of a natural phenomenon to examine the role of environmental disturbance; i. e., the design involved comparing the adaptive features of marine macrophyte populations in a physically-fluctuating disturbed environment (i. e., the upper Gulf of California) with those in a climatically more constant system at about the same latitude (i. e., the northern Pacific coast of the Baja Peninsula).

The rocky intertidal habitat was chosen for study because of its relatively pristine nature in Baja California, its workability and the existing taxonomic and ecological data base. We tested the *a priori* prediction that macrophyte communities would be more physically controlled in the northern Gulf with seasonal environmental disturbances (i. e., beyond the normal homeostatic capabilities of most marine plants) playing a major role in determining abundance patterns and with the predominant species tending to show early successional characteristics (Littler and Littler, 1980), while the less disturbed Pacific communities would contain more biologically-accomodated, late successional populations. Specifically, we contrasted macrophyte communities at three sites, two in the upper Gulf of California and one on the west coast of the Baja California Peninsula, in terms of natural-history attributes, distribution, abundance, evenness, richness, Shannon-Weaver diversity and primary productivity.

STUDY AREAS

The upper Gulf of California is separated from the temperature moderating influences of Pacific air masses by a central ridge of mountains (1,800–3,050 m high) that runs the length of the Baja Peninsula; summer temperatures are considerably hotter and winter temperatures colder than on the Pacific side and a desert climate prevails (Roden, 1964). As a result, in

the upper Gulf of California, evaporation exceeds precipitation by 250 cm y^{-1} (Roden, 1964) and salinities are in the range of 36–38 ppt, whereas the peninsula's Pacific waters have a salinity range of about 34–35 ppt. The annual water temperature range in the northern Gulf can exceed 22 °C (from 10 °C in winter to as much as 32 °C during summer; Brusca, 1973), while along the Pacific coast, annual temperature ranges of about 5 °C are more typical (Abbott and North, 1971).

Biebl (1962) has indicated that the physiological tolerance ranges of most marine algae in nature are not broad enough to withstand the water temperature extremes experienced in the upper Gulf, much less endure the lethal temperatures, desiccation and high light flux encountered during exposure by the summer low tides; see Wynne and Norris (1976) for further documentation. Norris (1975) and Brusca (1980) have reported marked seasonal variations in species composition and abundance of intertidal algae and invertebrates, respectively, in the upper Gulf. The algae show a pronounced alternation of winter and summer floras at Playa Estacion south of Puerto Peñasco (Norris, 1975) with two of the predominant brown algal genera (*Colpomenia* and *Cutleria*) restricted to the winter months and dramatic diminutions of two other important genera (*Sargassum* and *Padina*) during summer. Such summer reductions are not so impressive for the more mobile invertebrates (Brusca, 1980), primarily manifested in a loss of stenothermal tropical species during the cold winter periods and a less noticeable loss of warm temperate species throughout the summer and autumn. Because of the similarity of the northern Gulf to a large inland lake (Dawson, 1944), wave action and intertidal splash is slight compared to the Pacific coast which is generally unsheltered from oceanic waves.

The rocky-intertidal study sites, each selected (after several hundred km of reconnaissance) as representative of broad coastal areas in Mexico (Fig. 1), were located at (1) Bahia Santa Rosalia, Baja California, 28° 39' 05"N, 114° 10' 41"W; (2) Punta Bufeo, Baja California, 29° 56' 18"N, 114° 25' 56"W; (3) Punta Pelicano, Sonora, 31° 16' 15"N, 113° 35' 14". All of the shorelines were characterized by shallow slopes and consisted of boulder beaches of medium-sized (mostly about 1.0 m diameter) rocks. Sand was abundant in the subtidal zone at all three areas, but was present in the intertidal region only at Bahia Santa Rosalia where it was trapped by the rhizomatous root system of *Phyllospadix* (surf grass). There were high numbers of large mobile herbivores (e. g., *Haliofis*, *Cyanoplax*, *Tegula*) in the lower-intertidal zone at Bahia Santa Rosalia; whereas, at both Gulf sites the only abundant lower-intertidal herbivore appeared to be the small limpet *Acmaea* (*Collisella*) *dalliana*.

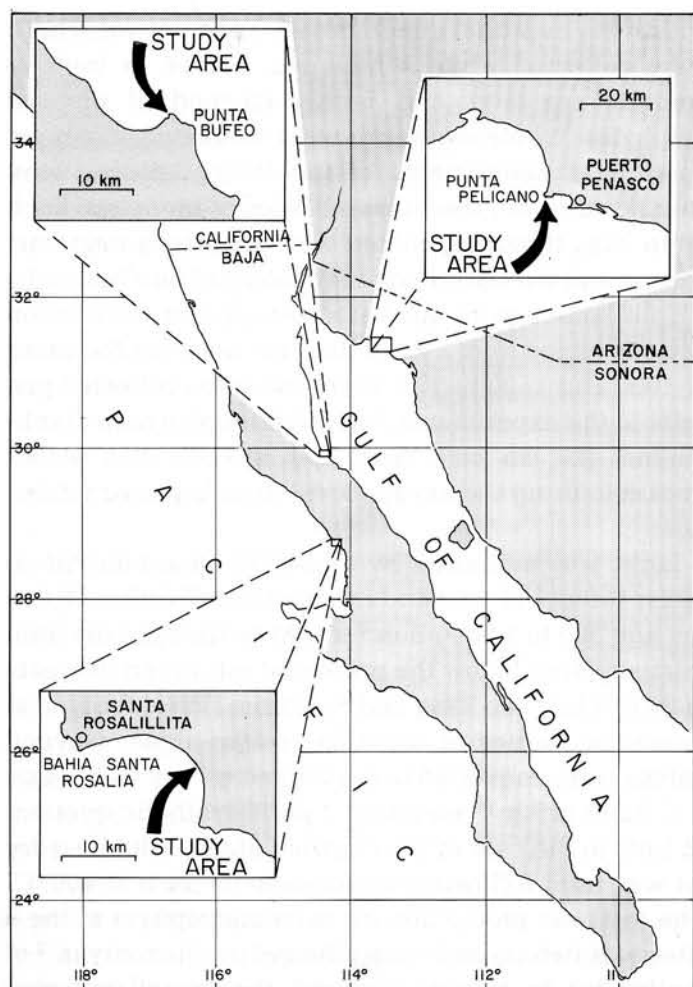


Fig. 1. Locations of the 3 study sites

The Bahia Santa Rosalia site (Fig. 1), sampled during 8–11 February 1975, represents an area of relatively low disturbance where physical conditions are somewhat ameliorated by frequent morning fog and summer coastal upwelling, which generates narrow annual water temperature ranges of 15° to 20 °C (Ricketts et al., 1968). Annual precipitation is approximately 80 mm (Hastings and Humphrey, 1969). The intertidal boulder beach at this site (–0.5 to +1.2 m, 0 datum, mean lower low water = MLLW) is part of a large open embayment with relatively heavy swell and semi-diurnal tides that have an annual extreme range of about 2.2 m (US Department of Commerce, 1975). The boulder shoreline of the embayment is structurally and biologically monotonous with little variation in zonal assemblages from the fishing village of Santa Rosalilita to the southern rocky point of the bay (Fig. 1).

The Punta Bufeo study site (Fig. 1), sampled on 22–25 February 1975, lies approximately 1° in latitude and 140 km to the north across the Baja Peninsula from Bahia Santa Rosalia. The terrestrial climate of this area is desert-like (Roden, 1964) with only 49 mm of rainfall per year (Hastings and Humphrey, 1969). More importantly, water temperatures vary from 15° to 30 °C yearly

(Brusca, 1973) and the Gulf experiences little fog to buffer the high insolation, heat and desiccating disturbances. Fluctuations in the maximum yearly tidal amplitude were estimated at approximately 5.2 m, the range for Tapoca Bay across the Gulf from the study site (University of Arizona, 1973). Although occurring twice daily, the tides are somewhat irregular (Dawson, 1944); the intertidal boulder shoreline ranges from –0.3 to +3.7 m (MLLW).

The Punta Pelicano study site, surveyed from 2–5 March 1973, is located about 180 km northeast and 1.5° in latitude north of Punta Bufeo on the south side of a granitic promontory that extends westward into the Gulf of California approximately 8.5 km north of the town of Puerto Peñasco, Sonora, Mexico. Water temperatures range seasonally from 14° to 31 °C (University of Arizona, 1973). This site, like Punta Bufeo, is exposed to disturbing summer desert conditions with only 50 mm of rainfall per year. The tidal amplitude can be exceptionally large (7.5 m maximum range) and, except for occasional storms that cause local wave turbulence, this site is hydrographically quite calm. The intertidal boulder shoreline ranges from –1.2 to +5.5 m relative to MLLW.

MATERIALS AND METHODS

The methods employed to determine macrophyte standing stocks have been evaluated and presented in detail elsewhere (Littler, 1971; Littler, 1980b). The techniques used to measure primary productivity were essentially the same as those described by Littler and Arnold (1980). A brief synopsis of these methods, including modifications used in the present study, is given below.

Standing Stock Assessments

Because space and light have been documented (Dayton, 1975) to be limiting resources in rocky-intertidal habitats and marine macrophytes compete for these using their cover, we felt that per cent cover would be the most appropriate estimate of the standing stock. During each assessment, photographs of 30 × 50 cm quadrats (0.15 m²) were taken during low tide at right angles to the substrata with 35 mm cameras equipped with electronic flash units; also, detailed field notes were recorded of species location, composition and abundance for later use in the laboratory. At each study site, two transects were used to position the quadrats in an unbiased systematized (uniform) pattern over the entire intertidal zone (i. e., from the high-water mark to the lowest level exposed during low

tide). At Bahia Santa Rosalia, transects 120 m in length containing 50 quadrats were sampled, at Punta Bufo, 50 m-long transects were used to locate 78 quadrats, while the Punta Pelicano site was assessed by means of 45 m-long transects containing 90 quadrats.

A minimum of two photographic transparencies were taken for each sample quadrat, one using color film (Kodachrome 64) and the other Ektachrome infrared film. Infra-red photographs increased the accuracy in measuring the abundances of certain macrophytes, particularly the blue-green algae, and revealed the presence of unhealthy or bleached thalli. In cases where sampling included multilayered canopies, additional photographs were taken to measure stratification after upper layers were carefully moved aside.

Species composition and cover were determined in the laboratory for each quadrat from analyses of the photographs and detailed field notes; cover estimates of the macrophyte standing stocks were made by the point-intercept method described by Littler (1980b). Species observed in quadrats but not encountered by point-intercepts were assigned a cover value of 0.1 %. The mean cover was determined for the major species in each 0.3-m tidal interval and used to plot distribution and abundance patterns over all intervals sampled. The data were summed and averaged to yield mean cover values for each macrophyte population, which were then used to compare between sites and to calculate Pielou's (1975) evenness index (J'_e) and Shannon and Weaver (1949) diversity (H'_e). The significance of differences in cover of stress-tolerant (i. e., blue-green algae) and opportunistic forms (i. e., *Ulva*, *Colpomenia*, *Gelidium*, *Giffordia*, and colonial diatoms) were determined separately for quadrats from the upper and lower halves of the intertidal zones between all three sites by the Mann-Whitney U statistic (Sokal and Rohlf, 1969).

Primary Production Measurements

The oxygen-electrode method was used to assess functional-morphological relationships by measuring the net primary productivity of the most abundant macrophyte species (see Littler, 1980a; Littler and Littler, 1980). Specimens were incubated at ambient water temperatures (i. e., 15 °C: Pacific Baja, 16 °C: Punta Bufo, 16 °C: Punta Pelicano) in either 300 ml BOD bottles or 1220 ml wide-mouth canning jars, depending upon the size of the thallus. Throughout the experiments, the average thallus concentration per volume of water did not exceed the ratio recommended by Littler (1979). Care was taken to select individuals that were representative of populations occurring

within the intertidal quadrats assessed for cover. Thalli were collected while submerged, placed in trays of ambient seawater and gently cleaned of obvious epiphytes. Whole organisms were incubated whenever possible; measurements of the larger species were conducted on representative blades or branches. Each bottle was thoroughly mixed with air-driven magnetic stirrers and stir bars at approximately 15 min intervals; 4 light bottles were incubated per species. Incubation periods varied from 2 to 4 h duration between the times of 1000 and 1500 h. The water used was collected just prior to the experiments, filtered through a nanoplankton net (10 μ m pore size) then shaken in a sealed bucket to bring the oxygen level to ambient air saturation.

Light was measured by a LI-COR Quantum/Photometer (Model LI 185) and ranged from 25,500 to 66,000 lux and 330 to 1,750 μ E m⁻² s⁻¹. At no time did the light intensity drop below the presumed saturation intensity of 20,000 lux; see King and Schramm (1976) for typical saturation values of intertidal macro-algae. Oxygen values were converted to mg C fixed g⁻¹ dry wt h⁻¹, and g C fixed m⁻² h⁻¹, assuming a photosynthetic quotient of 1.00. In the case of the calcified algae, ash free g dry wt was used following combustion for 24 h at 400 °C. The total net production for each macrophyte at the 3 sites was determined using the net productivity m⁻² of thallus h⁻¹ in conjunction with the overall per cent cover value m⁻² of intertidal substrate.

RESULTS

Bahia Santa Rosalia

Standing Stocks

Macrophyte cover averaged 60.2 % over the entire rocky intertidal shore (Table 1) with 51.8 % (Table 2) contributed by forms other than blue-green algae. Blue-green crusts tended to be maximal on the upper intertidal zone. The larger morphologically complex forms reached peaks lower on the shore and formed a layered community that often exceeded 100 % cover. Two articulated calcareous species, *Haliptylon gracile* (18.7 % cover) and *Corallina officinalis* var. *chilensis* (12.1 %), dominated the overall mean cover, followed by *Gelidium pusillum* (7.0 %) and *Ulva californica* (3.7 %); 2 other calcified species and 2 species of surf grass – *Lithothrix aspergillum* (2.0 %), *Phyllospadix torreyi* (1.7 %), *Corallina pinnatifolia* (1.5 %) and *P. scouleri* (1.0 %) – were also major forms. With the exception of the opportunistic forms *G. pusillum* and *U. californica*, which occurred predominantly on newly overturned rocks, all of these species are either heavily calcified

Table 1. Richness, evenness, species diversity, mean cover and productivity of macrophytes occurring in sample plots

Study areas	Rich- ness (No. of major taxa)	Even- ness (J'_e)	Diver- sity (H'_e)	Mean cover (%)	Total pro- duc- tivity (mg C m ⁻² h ⁻¹)
Bahia Santa Rosalia	36	0.59	2.12	60.2	81.7
Punta Bufo	29	0.46	1.56	75.5	56.2
Punta Pelicano	19	0.55	1.62	62.8	47.9

coralline algae or highly structured (relative to most marine plants) surf grasses containing vascular tissue.

The distributional patterns of macrophyte cover are shown as a function of 0.3-m tidal intervals in Figure 2. Although not abundant, *Peyssonnelia* sp. and *Pseudolithoderma nigra* are crustose forms that were extremely widespread within the mosaic of crevice and rivulet habitats formed by the boulders. *Gelidium pusillum* and *Ulva californica* were predominant on newly overturned small boulders throughout the intertidal but were most abundant in the mid-intertidal range sampled (MLLW to + 0.6 m). There was a broad perennial turf community predominant in the mid to lower intertidal comprised of *Haliptylon gracile* and *Corallina officinalis* var. *chilensis*, the former being more abundant somewhat lower in the intertidal. The surf grass *Phyllospadix scouleri* formed a tight band from + 0.2 to + 0.6 m, whereas *Phyllospadix torreyi* continued from + 0.4 m to the lower levels sampled with peaks at + 0.1 m and -0.4 m. *Codium fragile* was present as scattered clumps between + 0.2 and -0.1 m,

while *Lithothrix aspergillum* reached its maximum (12.3 % cover) at +0.4 m but declined sharply as *H. gracile* and *C. officinalis* var. *chilensis* increased lower on the shore.

Shannon-Weaver diversity ($H' = 2.12$), richness (36 taxa exceeding 0.01 % cover, and evenness ($J' = 0.59$) were all relatively high at Bahia Santa Rosalia (Table 1).

Primary Productivity

Overall macrophytic community productivity per square meter of intertidal substrate at Bahia Santa Rosalia (Table 1) totaled 81.7 mg C h⁻¹ with the majority of this (94 %) due to forms other than blue-green algae which provided only 4.8 mg C h⁻¹ or 6 % of the total (Table 2). The greatest contributor to community productivity was *Haliptylon gracile* (31.9 mg C m⁻² h⁻¹), followed by *Corallina officinalis* var. *chilensis* (20.6), *Gelidium pusillum* (12.0), *Ulva californica* (2.4), *C. pinnatifolia* (2.2), *Lithothrix aspergillum* (1.8), *Navicula* sp. (1.4) and *Phyllospadix torreyi* (1.0).

An examination of the individual macrophyte productivity rates per gram dry weight of thallus per hour (Fig. 3) reveals that at Bahia Santa Rosalia the highest producers, by far, were *Navicula* sp. (3.78 mg C), *Ulva californica* (2.98) and *Chondria californica* (2.75), all of which were prevalent on recently overturned rocks (as evidenced by dead or dying calcareous tube worms such as *Spirorbis*). The perennial macrophytes that dominated the standing stock at this site (e. g., calcareous macroalgae and vascular plants) all formed a group with considerably lower hourly rates of production per unit dry weight of thallus (0.41 to 0.88 mg C)

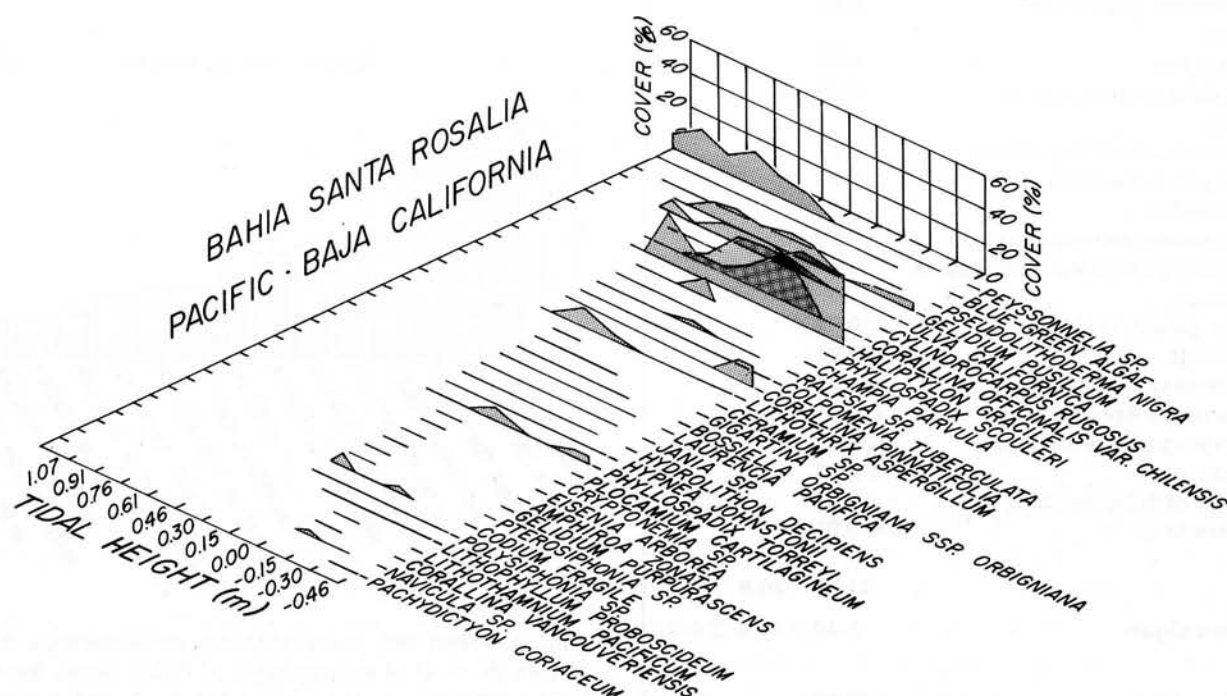


Fig. 2. Cover patterns of major macrophytes at Bahia Santa Rosalia as a function of tidal height

than did the less abundant sheet-like or finely-filamentous forms.

Punta Bufeo

Standing Stocks

Macrophyte cover at Punta Bufeo (Table 1) totaled 75.5 % with 32.1 % contributed by frondose algae and

Table 2. Mean cover (%) and net production rates (mg C fixed h^{-1}) of dominant macrophytes m^{-2} intertidal substrate at Bahia Santa Rosalia. Cover of macroinvertebrates not included

Macrophytes	Cover	Productivity (\pm S.E.)
<i>Haliptylon gracile</i> (Lamour.) Johans.	18.70	31.9 (0.41)
<i>Corallina officinalis</i> var. <i>chilensis</i> (Dec.) Kütz.	12.10	20.6 (4.24)
<i>Gelidium pusillum</i> (Stackh.) Le Jol.	6.96	12.0 (4.24)
<i>Ulva californica</i> Wille	3.70	2.4 (0.27)
<i>Lithothrix aspergillum</i> Gray	2.00	1.8 (0.59)
<i>Phyllospadix torreyi</i> Watson	1.74	1.0 (0.20)
<i>Corallina pinnatifolia</i> (Manza) Daws.	1.50	2.2 (0.35)
<i>Phyllospadix scouleri</i> Hook	1.00	0.7 (0.21)
<i>Codium fragile</i> (Sur.) Har.	0.70	0.8 (0.08)
<i>Pseudolithoderma nigra</i> Hollenb.	0.70	0.9 (0.18)
<i>Navicula</i> sp.	0.49	1.4 (0.05)
<i>Colpomenia tuberculata</i> Saund.	0.40	0.3 (0.08)
<i>Hypnea johnstonii</i> S. & G.	0.30	0.2 (0.03)
<i>Hydrolython decipiens</i> (Fosl.) Adey	0.30	0.2 (0.15)
<i>Peyssonnelia</i> sp.	0.24	0.3 ($> \bar{x}$)
<i>Jania</i> sp.	0.22	0.2 (0.10)
<i>Cylindrocarpus rugosus</i> Okam.	0.14	
<i>Ralfsia</i> sp.	0.11	
<i>Laurencia pacifica</i> Kyl.	0.08	
<i>Lithothamnium pacificum</i> (Fosl.) Fosl.	0.08	
<i>Polysiphonia</i> sp.	0.07	
<i>Lithophyllum proboscideum</i> (Fosl.) Fosl.	0.07	
<i>Champia parvula</i> (C. Ag.) Harv.	0.03	
<i>Pachydictyon coriaceum</i> (Holmes) Okam.	0.03	
<i>Corallina vancouveriensis</i> Yendo	0.02	
<i>Bossiella orbigniana</i> ssp. <i>orbigniana</i> (Dec.) Johans.	0.01	
<i>Amphiroa zonata</i> Yendo	< 0.01	
<i>Ceramium</i> sp.	< 0.01	
<i>Cryptonemia</i> sp.	< 0.01	
<i>Eisenia arborea</i> Aresch.	< 0.01	
<i>Gelidium purpurascens</i> Gardn.	< 0.01	
<i>Gigartina</i> sp.	< 0.01	
<i>Plocamium cartilagineum</i> L. (Dix.)	< 0.01	
<i>Pterosiphonia</i> sp.	< 0.01	
Totals	51.78	76.9
Blue-green algae	8.40	4.8 (2.60)
Bare rock	33.80	

crustose corallines. Of the upright forms (Table 3), the opportunistic *Ulva rigida* (11.6 %) had the highest cover followed by *Digenia simplex* (5.6 %), *Corallina frondescens* (3.8 %), *Ralfsia* sp. (2.8 %), *Gigartina tepida* (1.9 %), *Sargassum johnstonii* (1.7 %) and *Gelidium pusillum* (1.4 %). The eurytopic blue-green algae were predominant at this site with 43.4 % cover.

The most conspicuous macrophyte was *Ulva rigida* (Fig. 4) which formed a distinctive band from + 1.4 to + 0.1 m (peak of 49.9 % at + 0.8 m) with scattered patches above and below the interval. Crustose forms such as *Ralfsia* sp., *Peyssonnelia* sp. and *Lithophyllum proboscideum* were quite widespread due to the mosaic-like distribution of their crevice habitat. At the lower tidal levels there were distinctive turf communities characterized by clumps of *Gelidium pusillum*, *Gigartina tepida*, a continuous belt of *Corallina frondescens* (+ 0.8 to -0.2 m, peak of 31.5 % at +0.1 m) and larger thalli of *Sargassum johnstonii* forming a patchy overstory. The lowest zone was dominated by a distinct belt of the red alga *Digenia simplex* (+ 0.2 to -0.3 m, peak of 58.6 % at -0.2 m).

Shannon-Weaver diversity was quite low at Punta Bufeo ($H' = 1.56$) as was evenness ($J' = 0.46$) and there were 29 major species of algae in the samples (Table 1).

Primary Productivity

The mean macrophyte production per square meter of intertidal substrate at Punta Bufeo (Table 1) totaled

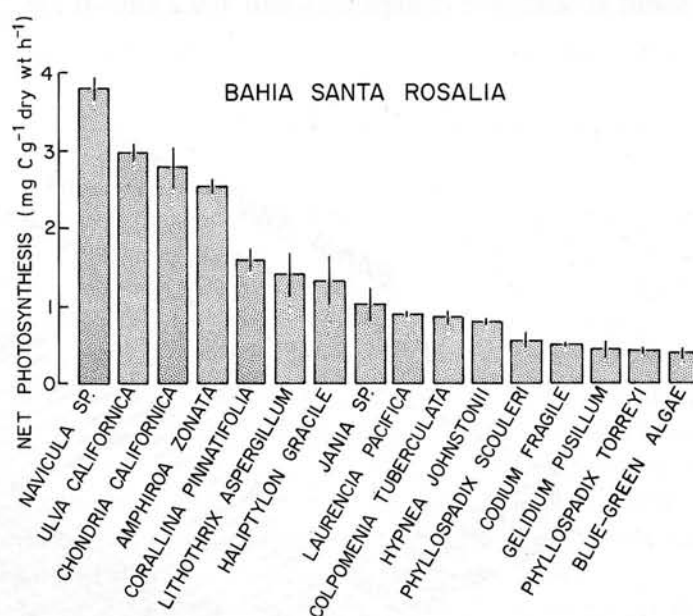


Fig. 3. Mean net photosynthetic performances \pm Standard Errors ($N = 4$) of macrophytes at Bahia Santa Rosalia on the basis of thallus dry weight; ash-free dry wt was used for all calcareous species

Table 3. Mean cover (%) and net production rates (mg C fixed h^{-1}) of dominant macrophytes m^{-2} intertidal substrate at Punta Bufo

Macrophytes	Cover	Productivity (\pm S.E.)
<i>Ulva rigida</i> C. Ag.	11.60	18.8 (3.42)
<i>Digenia simplex</i> (Wulf.) C. Ag.	5.60	6.2 (0.85)
<i>Corallina frondescens</i> Post. & Rupr.	3.80	2.7 (0.25)
<i>Ralfsia</i> sp.	2.80	2.8 ($> \bar{x}$)
<i>Gigartina tepida</i> Hollenb.	1.94	1.1 (0.15)
<i>Sargassum johnstonii</i> S. & G.	1.70	2.6 (0.34)
<i>Gelidium pusillum</i> (Stackh.) Le Jol.	1.35	1.2 (0.13)
<i>Lithophyllum proboscideum</i> (Fosl.) Fosl.	0.90	1.1 (0.86)
<i>Peyssonnelia</i> sp.	0.50	0.5 ($> \bar{x}$)
Diatom	0.40	0.4 (0.01)
<i>Giffordia</i> sp.	0.31	0.3 (0.18)
<i>Amphiroa zonata</i> Yendo	0.20	0.2 (0.12)
<i>Cladophora graminea</i> Coll.	0.20	0.2 (0.04)
<i>Jania capillacea</i> Harv.	0.20	0.2 (0.09)
<i>Laurencia johnstonii</i> S. & G.	0.20	0.2 (0.02)
<i>Eucheuma uncinatum</i> S. & G.	0.15	0.2 (0.04)
<i>Colpomenia tuberculata</i> Saund.	0.09	0.1 (0.01)
<i>Codium simulans</i> S. & G.	0.05	
<i>Gracilaria textorii</i> (Sur.) J. Ag.	0.05	
<i>Gelidium johnstonii</i> S. & G.	0.01	
<i>Colpomenia sinuosa</i> (Roth.) Derb. & Sol.	0.01	
<i>Ishige sinicola</i> (S. & G.) Chihara	0.01	
<i>Champia parvula</i> (C. Ag.) Harv.	< 0.01	
<i>Colpomenia phaeodactyla</i> Wynne & Norris	< 0.01	
<i>Dictyota flabellata</i> (Coll.) S. & G.	< 0.01	
<i>Prionitis abbreviata</i> S. & G.	< 0.01	
<i>Padina durvillaei</i> Bory	< 0.01	
<i>Valoniopsis pachynema</i> (Mart.) Borg.	< 0.01	
Totals	32.13	38.8
Blue-green algae	43.40	17.4 (0.44)
Bare rock	25.50	

56.2 mg C h^{-1} with 69 % (Table 3) due to macrophytes other than blue-green algae (31 %). The majority of carbon fixation was contributed by *Ulva rigida* (18.8 mg C m^{-2} h^{-1}) with much lesser amounts being fixed by *Digenia simplex* (6.2), *Ralfsia* sp. (2.8), *Corallina frondescens* (2.7), *Sargassum johnstonii* (2.6), *Gelidium pusillum* (1.2), *Gigartina tepida* (1.1) and *Lithophyllum proboscideum* (1.1).

Three thin thallus forms produced considerably more (Fig. 5) on an individual thallus weight basis than any of the other macrophytes (i. e., *Colpomenia phaeodactyla*: 3.89 mg C g^{-1} dry wt h^{-1} ; *Porphyra* sp.: 3.25, *Ulva rigida*: 3.19). However, the more highly structured perennial macrophytes, predominant in the lower intertidal (e. g., *Digenia simplex*, *Corallina frondescens*, *Sargassum johnstonii*) had markedly lower

productivities per unit weight of thallus (i. e., 0.19 to 1.24 mg C g^{-1} dry wt h^{-1}).

Punta Pelicano

Standing Stocks

Macrophyte cover at Punta Pelicano totaled 62.8 % (Table 1), over half of which was due to frondose and crustose algal species (Table 4). Of the more three-dimensional forms, *Porolithon sonorense* was the most abundant (12.3 % cover) along with opportunistic species such as *Colpomenia tuberculata* (10.0 %), *Ulva rigida* (4.8 %), *Gelidium pusillum* (2.0 %) and *Giffordia* sp. (1.3 %). *Amphiroa subcylindrica* with 1.0 % cover and *Ishige sinicola* (0.9 %) were abundant in patches. As at Punta Bufo, the two-dimensional eurytopic blue-green algal crusts (29.0 %) were the cover dominants. Cover of blue-green algae in both the upper and lower intertidal zones was significantly greater ($P < 0.05$, Mann-Whitney U-test) than at Bahia Santa Rosalia but was not different ($P > 0.05$) than that at Punta Bufo.

Of the upright forms (Fig. 6), the ephemeral *Giffordia* sp. was abundant (peak of 16.3 % cover at +2.0 m) highest in the intertidal (up to +2.7 m) on newly overturned rocks. Below this, a pronounced belt of *Ulva rigida* (+1.8 m to MLLW, peak of 31.9 % at +1.1 m) appeared overlying the crustose coralline *Porolithon sonorense* (+1.6 to -1.4 m, peak of 76.2 % at -0.2 m). *Gelidium pusillum* occurred patchily in crevice habitats throughout this association. The lower portion of the shore was dominated by a distinct belt of *Colpomenia tuberculata*, which became prominent (peak of 89.8 % at -1.1 m) near the lower limit of *U. rigida* and also covered an understory of *P. sonorense* with small patches of *Amphiroa subcylindrica*, *Ishige sinicola*, *Corallina frondescens* and *Lithophyllum proboscideum* being locally important. The cover of opportunistic species (analyzed as a group) pervading the lower half of the intertidal zone was significantly greater ($P < 0.05$) than at Bahia Santa Rosalia but was statistically similar ($P > 0.05$) to that at Punta Bufo.

Shannon-Weaver diversity (H') was 1.62, evenness (J') 0.55 and there were relatively few (19) major algal taxa sampled at Punta Pelicano (Table 1).

Primary Productivity

Mean macrophytic net production rates per square meter of intertidal substrate totaled 47.9 mg C h^{-1} at Punta Pelicano (Table 1), 66 % of which was due to algae other than blue-green forms (34 %). The major contributor to community productivity (Table 4) was

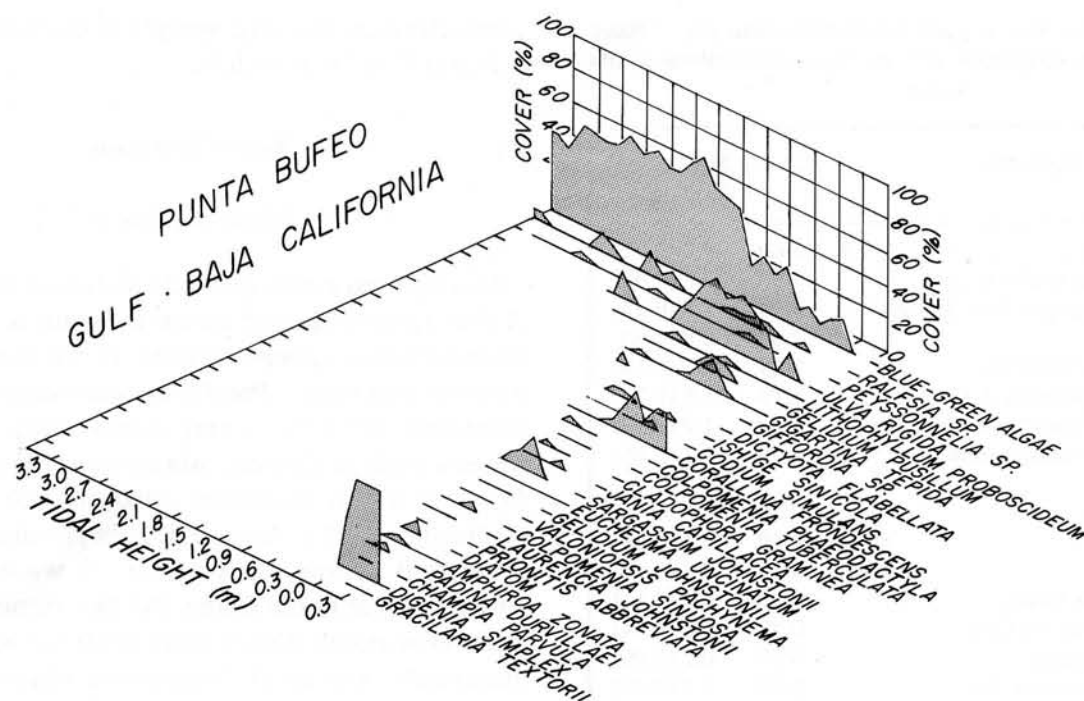


Fig. 4. Cover patterns of major macrophytes at Punta Bufo as a function of tidal height

Porolithon sonorense ($14.1 \text{ mg C m}^{-2} \text{ h}^{-1}$), followed by *Ulva rigida* (7.1), *Colpomenia tuberculata* (4.1), *Gelidium pusillum* (2.0), *Giffordia* sp. (1.7), *Amphiroa subcylindrica* (1.6) and *Ishige sinicola* (1.1).

The opportunistic sheet-like forms (e. g., *Ulva rigida*: $3.25 \text{ mg C g}^{-1} \text{ dry wt h}^{-1}$; *Colpomenia phaeodactyla*: 2.75 ; *Dictyota flabellata*: 2.65) and the fine filamentous *Giffordia* sp. (1.60) again produced much more per gram of thallus (Fig. 7) than the longer-lived macrophytes. The lowest producing forms again contained considerable structural tissue or calcium carbonate as part of their thallus weight.

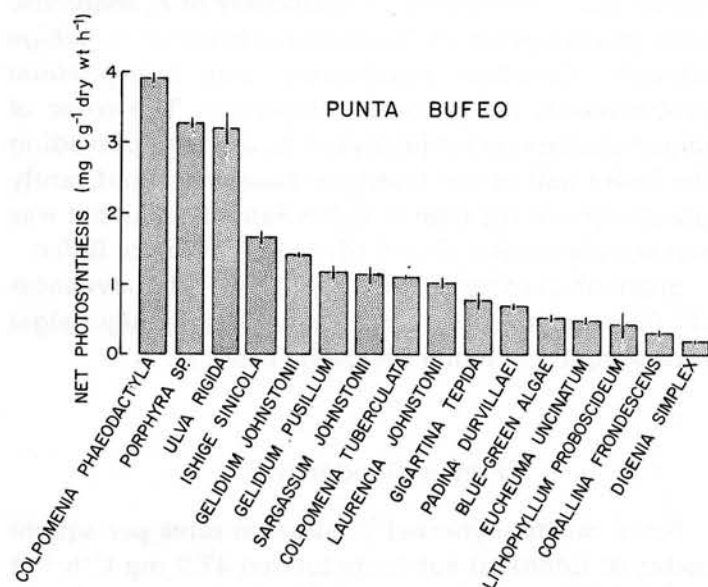


Fig. 5. Mean net photosynthetic performances \pm Standard Errors ($N = 4$) of macrophytes at Punta Bufo

DISCUSSION

The population and community attributes we measured, or determined from the natural history literature, have been summarized in Table 5. In general, the data support the intermediate disturbance hypothesis (Connell, 1978), with biological components of spatial complexity and interference competition (e. g., layering, crowding) appearing secondarily to influence diversity. As Abele and Walters (1979) point out, when testing an hypothesis in this manner, valid comparisons can only be made using similar methodologies and sample sizes for similar habitats and taxonomic entities. In the present study – identical methods were used on the same taxonomic or functional groups – the papers by Katada and Satomi (1975), Littler (1980a) and Littler and Littler (1980) have shown that macrophyte functional-form groups are excellent indicators of selective parameters prevalent in a given habitat. The intertidal habitats sampled in the Gulf were necessarily more extensive (because of greater tidal amplitudes) and this required a larger sample size. However, these differences would tend to bias the data toward falsifying the hypothesis and therefore serve to strengthen further the supportive interpretation as substantiated below.

The predominant macrophytes at Bahia Santa Rosalia were larger perennial forms such as calcareous coralline algae or morphologically complex vascular plants, with the exceptions of *Ulva californica* and *Gelidium pusillum* which occurred abundantly on newly overturned rocks. The taxa and functional groups of macrophytes were generally similar to those

Table 4. Mean cover (%) and net production rates (mg C fixed h⁻¹) of dominant macrophytes m⁻² intertidal substrate at Punta Pelicano

Macrophytes	Cover	Productivity (± S.E.)
<i>Porolithon sonorense</i> Daws.	12.26	14.1 (4.69)
<i>Colpomenia tuberculata</i> Saund.	10.01	4.1 (0.29)
<i>Ulva rigida</i> C. Ag.	4.76	7.1 (2.15)
<i>Gelidium pusillum</i> (Stackh.) Le Jol.	1.96	2.0 (0.70)
<i>Giffordia</i> sp.	1.28	1.7 (0.36)
<i>Amphiroa subcylindrica</i> Daws.	1.04	1.6 (0.57)
<i>Ishige sinicola</i> (S. & G.) Chihara	0.99	1.1 (0.49)
<i>Corallina frondescens</i> Post. & Rup.	0.40	
<i>Lithophyllum proboscideum</i> (Fosl.) Fosl.	0.35	
<i>Gigartina tepida</i> Hollenb.	0.21	
<i>Hydrolithon decipiens</i> (Fosl.) Adey	0.23	
<i>Cladophora graminea</i> Coll.	0.13	
<i>Peyssonnelia</i> sp.	0.10	
<i>Codium simulans</i> S. & G.	0.02	
<i>Cutleria hancockii</i> Daws.	0.02	
<i>Laurencia johnstonii</i> S. & G.	0.01	
<i>Enteromorpha</i> sp.	< 0.01	
<i>Jania capillacea</i> Harv.	< 0.01	
Totals	33.79	31.7
Blue-green algae	29.03	16.2 (8.10)
Bare rock	26.20	

at two other Pacific Baja intertidal habitats several hundred km to the north (Punta Banda; Devlin, 1978) and to the south (Punta Hippolito; Littler, unpublished). This confirms the subjective opinion, based on extensive reconnaissance of the peninsula, that the Bahia Santa Rosalia site is generally characteristic of

northern-central, Pacific Baja boulder-beach habitats. The bulk of the total community productivity at Bahia Santa Rosalia was provided by the same calcareous algae or structurally differentiated surf grasses that dominated the cover. However, in terms of individual macrophyte production rates per unit of thallus, the highest producers were species characteristic of recently overturned small boulders including *Navicula* sp., *U. californica* and *Chondria californica* along with *G. pusillum*. The macrophytes that dominated the standing stock all formed a group with considerably lower net photosynthetic rates per unit weight of thallus which, as discussed below, is attributable to their relatively large proportions of structural to photosynthetic tissues.

Conversely, at Punta Bufo and Punta Pelicano, most of the floral components die back and change (Dawson, 1966; Norris, 1975; Wynne and Norris, 1976) in response to the marked increases in seawater temperatures from winter to summer with a resultant predominance of ephemeral forms (i.e., having short or annual life histories). Also, most species, other than Cyanophyta (stress-tolerant strategist sensu Grime, 1977), were more restricted to the lower portions of the intertidal, probably due to desiccation associated with extremely low humidity and high summer temperatures (Hastings and Humphrey, 1969). Because the physiological tolerance ranges of most algae are not sufficiently broad to handle such marked seasonal fluctuations in temperature (Biebl, 1962), an ephemeral life history has adaptive value for avoiding this type of disturbance. The restriction of effective reproduction (directly related to persistence in distribution)

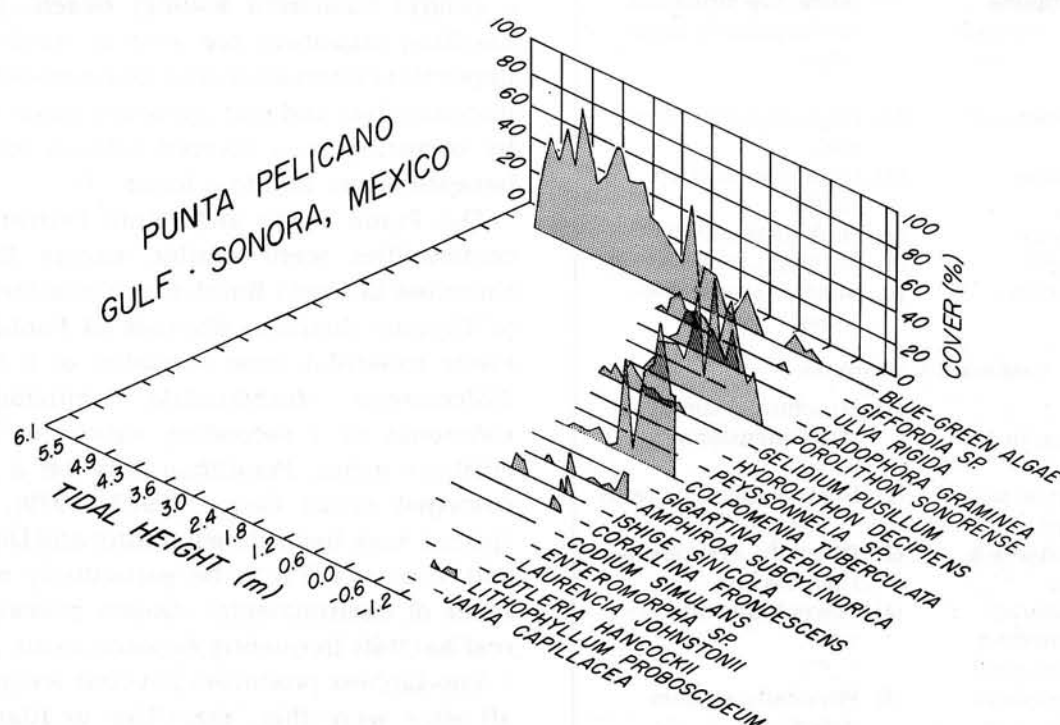


Fig. 6. Cover patterns of major macrophytes at Punta Pelicano as a function of tidal height

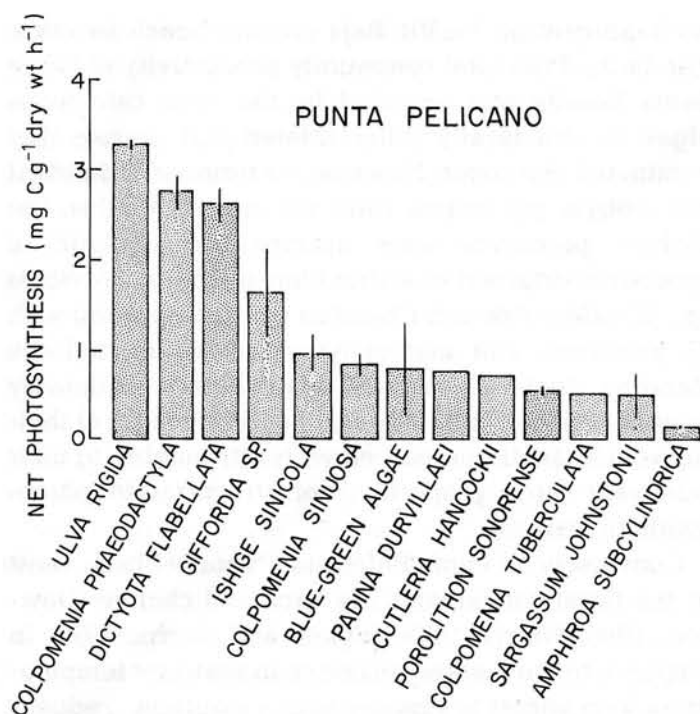


Fig. 7. Mean net photosynthetic performances \pm Standard Errors (N = 4) of macrophyte at Punta Pelicano

Table 5. Summary of populational and community features of abundant macrophytes

Environmentally constant habitat (Pacific Baja)	Environmentally disturbed habitats (Upper Gulf of California)
Populational attributes	
(1) Thalli larger & morphologically complex; low surface/volume ratios; high structural/photosynthetic tissue ratios	(1) Small & simple thalli; high surface/volume ratios; low structural/photosynthetic tissue ratios
(2) Long-lived perennials	(2) Opportunistic ephemerals
(3) Low reproductive output	(3) High reproductive output
(4) Low productivity	(4) High productivity
(5) Stenotopic forms	(5) Eurytopic forms
(6) Mostly late successional	(6) Mostly early successional
Community attributes	
(1) Structurally heterogeneous; three dimensional	(1) Structurally simple; two dimensional
(2) Mosaic pattern of successional seres	(2) Homogeneous patterns
(3) Diversity, evenness & richness high	(3) Diversity, evenness & richness low
(4) More biotic interactions (e.g., crowding, layering of canopies)	(4) Fewer biotic interactions
(5) Biologically accommodated	(5) Physically accommodated

in many marine macroalgae to 5 C° isothermal increments (Setchell, 1920) would support this contention. As a result, both Gulf of California sites contained significantly more ($P < 0.05$) cover of small, highly-reproductive (i.e., long fertile seasons and large numbers of propagules) opportunistic forms such as *Ulva* and various species of *Colpomenia*, as well as eurytopic blue-green algae. Similar to the Gulf habitats, sewage-impact in a southern California rocky-intertidal area (Littler and Murray, 1975) resulted in domination by a low turf of blue-green algae *Gelidium pusillum* and *Ulva californica*. The establishment of such algal turfs in the rocky intertidal appears to be a common feature on shores subjected to other forms of disturbance – e.g., sand abrasion (Daly and Mathieson, 1977) – or substrate instability in the case of the smaller rocks at Bahia Santa Rosalia (cf. Cimberg et al., 1973; Sousa, 1979b). Littler (1980b) has suggested that algal turfs dominated by fine filamentous forms, having high productivities and reproductive capacities along with opportunistic life-history strategies, may be indicative of disturbed intertidal habitats in general.

Blue-green algae generally predominate on upper intertidal shores and are often indicative of harsh or disturbed environments (Littler and Murray, 1975; Golubic, 1970); therefore, it was not surprising that blue-green algae covered significantly ($P < 0.05$, Mann-Whitney U-test) more at Punta Bufo (43.4 %), and Punta Pelicano (29.0 %) than at Bahia Santa Rosalia (8.4 %). For all 3 study areas, turf formers and encrusting species relegated to cryptic habitats between boulders were the most widely dispersed; this agrees with the findings of Seapy and Littler (1978) for a central California boulder beach. These crevice-dwelling organisms are able to avoid desiccation at upper tidal intervals in low, moisture-retaining shaded microhabitats and can sequester space at lower levels by occurring in a layered fashion on the substrate beneath larger frondose forms.

The Punta Bufo and Punta Pelicano macrophyte communities were similar, except that the lower shoreline at Punta Bufo was characterized by a zone of *Digenia simplex*, whereas at Punta Pelicano the lower intertidal zone consisted of a broad band of *Colpomenia tuberculata* utilizing *Porolithon sonorense* as a secondary substrate. The perennial crustose genus *Porolithon* may be a stress-tolerant strategist sensu Grime (1977, 1979); e.g., 2 other species have been shown (Littler and Doty, 1975; Adey and Vassar, 1975) to be particularly resistant to the kinds of environmental stresses prevalent in tropical reef habitats frequently exposed to air.

The highest producers per unit weight of thallus at all sites were thin, sheet-like or filamentous forms (including *Ulva rigida*, *Colpomenia phaeodactyla*, *Por-*

phyra sp., *Dictyota flabellata* and *Giffordia* sp.) having high surface/volume ratios, in agreement with the findings of Odum et al. (1958), Kanwisher (1966) and Littler (1980a). These forms have allocated a large percentage of their biomass to photosynthetic tissue (Littler and Littler, 1980) and, therefore, fix a relatively high amount of carbon per unit weight of thallus. Also, the thin construction of these species minimizes self-shading. This thallus form/productivity relationship has been shown to hold over a broad geographic range by the studies of Littler (1980a); a morphology more suited to utilizing light energy and obtaining nutrients could hypothetically account for the higher rates. In partial support, the thin sheet-like *Ulva* has been shown (Ramus, 1978) to have a morphology especially adaptive to high light regimes. Although not predominant, the lowest producers at the Gulf sites were longer-lived species that contained considerable structural tissue or calcium carbonate as part of their thallus weight (comparable to the findings at the Pacific site).

Many of the same highly-productive, sheet-like forms (Figs 3, 5 and 7) have been noted (Bokenham and Stephenson, 1938; Northcraft, 1948; Fahey, 1953; Murray and Littler, 1978; Sousa, 1979b) to be among the earliest colonizers of disturbed rocky-intertidal substrates. Connell's (1975) successional hypothesis states that disturbed patches will most likely be recolonized by species with high reproductive output and that competition should be severe. Our data, and those of Sousa (1979a), are in agreement with this prediction, but primarily in terms of the exploitive form of competition (i.e., more rapid uptake of nutrients and occupation of space), as opposed to interference competition (i.e., overgrowing and physical crowding) which appeared to be more severe on the Pacific side of the peninsula. These data (Figs 4 and 6) and those of Sousa (1979b) suggest that selection in highly disturbed or fluctuating environments has tended to favor structurally simple, opportunistic species – e.g., *Ulva*, *Colpomenia*; shown by Murray and Littler (1978) to be early-successional forms – having high net productivity (Figs 5 and 7), while the large conspicuous species (e.g., calcareous forms, thick forms, prostrate crusts, structurally-complex flowering plants) persist in less physically disturbed, relatively-constant habitats, such as Bahia Santa Rosalia (Fig. 2), at the cost of lower photosynthetic rates (Fig. 3). This cost is no doubt due to the allocation of energy and materials to structural components specialized for competition for light, resistance to predation or resistance to the shearing forces of waves – see Littler and Littler (1980) for costs/benefits data on several of the same forms studied here – which then become unavailable for photosynthesis and reproduction. Additionally, the cover dominants in the Gulf, with their smaller turf-like growth habits,

provide little spatial heterogeneity and this appears to reduce habitats for understory or epiphytic species and to further limit diversity.

Environmental constancy, complex sexual reproduction (i.e., lacking asexual or vegetative short-cuts), intense biotic interactions (e.g., crowding, vertical layering) and the low productivity rates of dominant perennial macrophytic populations at Bahia Santa Rosalia (Fig. 3) suggest a relatively long-established, mature lower-intertidal community. The larger threedimensional macrophytes formed a layered assemblage having complex patterns of spatial heterogeneity. Such augmentations of structural complexity have been shown (Dayton, 1971, 1975) to be intimately related to the number of species that a given habitat can accommodate. In this regard, it is worth noting that Bahia Santa Rosalia (the site with the narrowest intertidal range and fewest samples) had the highest values of richness, evenness and Shannon-Weaver diversity (Table 2); i.e., 19 %, 22 % and 27 % greater than Punta Bufeo and 47 %, 7 % and 24 % higher than Punta Pelicano, respectively.

At Punta Bufeo and Punta Pelicano, yearly environmental disturbances effectively maintain the community in a condition resembling subclimax (Table 5). Productivity values of the dominant macrophytes were high (Figs 5 and 7) compared to those at Bahia Santa Rosalia, indicating a capacity for rapid growth; annual or opportunistic species with simple life histories predominated, emphasizing their ability to proliferate and repopulate quickly following the provision of new substrate due to seasonal (Norris, 1975; Wynne and Norris, 1976) physically induced mortalities. Parallel characteristics have been noted in other macrophyte communities subjected to environmental extremes. For example, the sporadic release of toxic sewage components (Littler and Murray, 1975) selected against all but the most tolerant or rapidly recolonizing organisms (e.g., blue-green algae, *Ulva californica*, *Gelidium pusillum*) in a southern California intertidal boulder habitat.

Thus, we hypothesize that some naturally occurring disturbances (such as extreme temperatures, desiccation and insolation) by providing new space, parallel the effects of other natural disturbances such as sand abrasion (Daly and Mathieson, 1977) and substrate instability (Cimberg et al., 1973; Sousa, 1979b) as well as human-induced perturbations such as sewage pollution (Littler and Murray, 1975); all appear to result in the maintenance of early-successional stages.

Conversely, in accordance with statements by Connell (1972), the less productive dominant macrophytes of the Bahia Santa Rosalia community suggest a relatively mature stage of succession (Table 5). Species diversity and abundance was higher and the predom-

inant populations consisted of perennial forms with more complex sexual reproduction (i.e., reduced vegetative or asexual short-cuts), proportionately more structural components, less photosynthetic tissue (Littler and Littler, 1980) and greater thallus size and complexity (e.g., greater crowding and layering of canopies and, therefore, more secondary substrate levels). These macrophytes are predicted to be slower growing specialists (i.e., biotically competent strategists *sensu* Vermeij, 1978) with their populations hypothetically regulated mainly by biological interactions such as intensive interference competition (as opposed to exploitive competition in the upper Gulf) for space and light.

In summary, the above findings suggest that biological interactions exert greater influences on species diversity as physical gradients become less harsh. The Gulf communities, characterized by physical extremes, appeared to have fewer interference interactions and lower diversity in support of the intermediate disturbance hypothesis of Connell (1978). These habitats were typified by eurytopic and early-successional, opportunistic populations having high productivity. The other end of the spectrum (e.g., Bahia Santa Rosalia) is that of the relatively more benign, constant, biologically-accommodated communities characterized by diverse assemblages of populations with a high degree of evolutionary interaction (Slobodkin and Sanders, 1969) where there is a constant invasion of additional species into the community and long-lived individuals have evolved a high interference competitive ability. Also, while the Pacific site was comparably less disturbed, it did contain numerous patches (overturned boulders) of populations undergoing various stages of succession due to a spatially and temporally complicated background of small-scale, wave-induced disturbances. The mosaic-like nature of these patches contributed substantially to the overall diversity of the system in accordance with the predictions of Levin and Paine (1974), Connell (1978) and Fox (1979) and the findings of Osman (1977) and Sousa (1979b). It should be emphasized in view of the marked contrasts presented above, that most intertidal communities are not so strongly demarcated, but rather are influenced by a continuum of many factors and more typically lie somewhere between these physically disturbed and more benign extremes.

Acknowledgements. The data used in this paper were obtained by re-analyzing photogrammetric samples and taxonomic voucher specimens taken during two 'Marine Super-courses' taught in conjunction with Drs Roger R. Seapy and Paul J. Leviten, who provided expertise on invertebrate taxonomy and ecology. Dr. James N. Norris personally identified or verified each of our macroalgal specimens. This research would not have been possible without the considerable efforts of the following students: Jerry Abajian, Richard Ambrose,

Ernest Christopher, Marjory Clarke, Judith Connors, Richard Cook, Virginia Cooke, Donna Cooksey, Mark Crutcher, Wayne Dorband, Paul Ewald, Jack Fancher, William Fitt, Mark Hay, Maurice Hill, David Jamison, Andrew Kindig, Christopher Kitting, Robert Kleban, Harry Landau, David Martz, Lawrence Miller, Patrick O'Brien, Earl Peattie, Allan Rapp, Robert Rubin, David Rudie, Victoria Sork, James Stretch, Peggy Trabue, Peter Tuck, Scott Verzwylt, Lynnette Vesco, James Watson, Kirk Wentworth, Janet Wheeler and Brian White.

LITERATURE CITED

- Abbott, I. A., North, W. J. (1971). Temperature influences on floral composition in California coastal waters. In: Nisizawa, K. (ed.) Proceedings of the seventh international seaweed symposium. University of Tokyo Press, Tokyo, pp. 72-79
- Abele, L. G., Walters, K. (1979). The stability-time hypothesis: reevaluation of the data. *Am. Nat.* 114: 559-568
- Adey, W. H., Vassar, J. M. (1975). Colonization, succession and growth rates of tropical crustose coralline algae (Rhodophyta, Cryptonemiales). *Phycologia* 14: 55-69
- Biebl, R. (1962). Seaweeds. In: Lewin, R. A. (ed.) Physiology and biochemistry of algae. Academic Press, New York, pp. 799-815
- Bokenham, N. A. H., Stephenson, T. A. (1938). The colonization of denuded rock surfaces in the intertidal region of the Cape Peninsula. *Ann. Natal Mus.* 9: 47-81
- Brusca, R. C. (1973). A handbook to the common intertidal invertebrates of the Gulf of California. University of Arizona Press, Tucson, Arizona
- Brusca, R. C. (1980). A handbook to the common intertidal invertebrates of the Gulf of California, 2nd rev. ed., University of Arizona Press, Tucson, Arizona
- Buss, L. W., Jackson, J. B. C. (1979). Competitive networks: nontransitive competitive relationships in cryptic coral reef environments. *Am. Nat.* 113: 223-234
- Cimberg, R. L., Mann, S., Straughan, D. (1973). A reinvestigation of southern California rocky intertidal beaches three and one-half years after the 1969 Santa Barbara oil spill: a preliminary report. In: Proceedings of joint conference on prevention and control of oil spills. American Petroleum Institute, Washington, D. C., pp. 697-702
- Connell, J. H. (1972). Community interactions on marine rocky intertidal shores. *Ann. Rev. Ecol. Syst.* 3: 169-192
- Connell, J. H. (1975). Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In: Cody, M. L.; Diamond, J. M. (eds) Ecology and evolution of communities. Belknap Harvard Press, Cambridge, Massachusetts, pp. 460-490
- Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science, N. Y.* 199: 1302-1310
- Connell, J. H., Orias, E. (1964). The ecological regulation of species diversity. *Am. Nat.* 98: 399-414
- Daly, M. A., Mathieson, A. C. (1977). The effects of sand movement on intertidal seaweeds and selected invertebrates at Bound Rock, New Hampshire, USA. *Mar. Biol.* 43: 45-55
- Dawson, E. Y. (1944). The marine algae of the Gulf of California, University of Southern California Press, Los Angeles, California
- Dawson, E. Y. (1966). Marine algae in the vicinity of Puerto Penasco Sonora, Mexico, University of Arizona, Tucson, Arizona
- Dayton, P. K. (1971). Competition, disturbance, and commun-

- ity organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* 41: 351-389
- Dayton, P. K. (1975). Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecol. Monogr.* 45: 137-159
- Devinny, J. S. (1978). Ordination of seaweed communities: environmental gradients at Punta Banda. *Botanica Mar.* 21: 357-363
- Fahey, E. M. (1953). The repopulation of intertidal transects. *Rhodora* 55: 102-108
- Fox, J. F. (1979). Intermediate-disturbance hypothesis. *Science*, N. Y. 204: 1344-1345
- Golubic, S. (1970). Effect of organic pollution on benthic communities. *Mar. Pollut. Bull.* 1: 56-57
- Grime, J. P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* 111: 1169-1194
- Grime, J. P. (1979). *Plant strategies and vegetation processes*, Wiley, New York
- Hastings, J. R., Humphrey, R. R. (1969). Climatological data and statistics for Baja California. In: Technical reports on the meteorology and climatology of arid regions, No. 18, The University of Arizona Institute of Atmospheric Physics, Tucson, Arizona
- Kanwisher, J. W. (1966). Photosynthesis and respiration in some seaweeds. In: Barnes, H. (ed.) *Some contemporary studies in marine science*. Allen and Unwin, London, pp. 407-420
- Katada, M., Satomi, M. (1975). Ecology of algae. In: Tokida, J., Hirose, H. (eds) *Advance of phycology in Japan*. Gustav Fischer Verlag, Jena, pp. 211-239
- King, R. J., Schramm, W. (1976). Photosynthetic rates of benthic marine algae in relation to light intensity and seasonal variations. *Mar. Biol.* 37: 215-222
- Kohn, A. J. (1967). Environmental complexity and species diversity in the gastropod genus *Conus* on Indo-West Pacific reef platforms. *Am. Nat.* 101: 251-260
- Levin, S. A., Paine, R. T. (1974). Disturbance, patch formation, and community structure. *Proc. Natn. Acad. Sci. U.S.A.* 71: 2744-2747
- Littler, M. M. (1971). Standing stock measurements of crustose coralline algae (Rhodophyta) and other saxicolous organisms. *J. exp. mar. Biol. Ecol.* 6: 91-99
- Littler, M. M. (1979). The effects of bottle volume, thallus weight, oxygen saturation levels, and water movement on apparent photosynthetic rates in marine algae. *Aquat. Bot.* 7: 21-34
- Littler, M. M. (1980a). Morphological form and photosynthetic performances of marine macroalgae: tests of a functional-form hypothesis. *Botanica Mar.* 22: 161-165
- Littler, M. M. (1980b). Overview of the rocky intertidal systems of Southern California. In: Power, D. M. (ed.) *The California islands: Proceedings of a multidisciplinary symposium*. Santa Barbara Museum of Natural History, Santa Barbara, California, pp. 265-306
- Littler, M. M., Arnold, K. E. (1980). Sources of variability in macroalgal primary productivity: sampling and interpretative problems. *Aquat. Bot.* 8: 141-156
- Littler, M. M., Doty, M. S. (1975). Ecological components structuring the seaward edges of tropical pacific reefs: the distribution, communities and productivity of *Porolithon*. *J. Ecol.* 63: 117-129
- Littler, M. M., Littler, D. S. (1980). The evolution of thallus form and survival strategies in benthic macroalgae: field and laboratory tests of a functional-form model. *Am. Nat.* 116: 25-44
- Littler, M. M., Murray, S. N. (1975). Impact of sewage on the distribution, abundance and community structure of rocky intertidal macro-organisms. *Mar. Biol.* 30: 277-291
- MacArthur, R. H. (1964). Environmental factors affecting bird species diversity. *Am. Nat.* 98: 387-397
- Margalef, R. (1963). On certain unifying principles in ecology. *Am. Nat.* 97: 357-374
- Murray, S. N., Littler, M. M. (1978). Patterns of algal succession in a perturbed marine intertidal community. *J. Phycol.* 14: 506-512
- Norris, J. N. (1975). Marine algae of the northern Gulf of California. Ph. D. dissertation, University of California, Santa Barbara, California
- Northcraft, R. D. (1948). Marine algal colonization on the Monterey Peninsula, California. *Am. J. Bot.* 35: 396-404
- Odum, E. P., Kuenzler, E. J., Blunt, M. X. (1958). Uptake of P^{32} and primary productivity in marine benthic algae. *Limnol. Oceanogr.* 3: 340-345
- Osman, R. W. (1977). The establishment and development of a marine epifaunal community. *Ecol. Monogr.* 47: 37-63
- Paine, R. T. (1966). Food web complexity and species diversity. *Am. Nat.* 100: 65-75
- Paine, R. T. (1971). A short-term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat. *Ecology* 52: 1096-1106
- Pielou, R. W. (1975). *Ecological diversity*, Wiley, New York
- Ramus, J. (1978). Seaweed anatomy and photosynthetic performance: the ecological significance of light guides, heterogeneous absorption and multiple scatter. *J. Phycol.* 14: 352-362
- Ricketts, E. F., Calvin, J., Hedgpeth, J. W. (1968). *Between Pacific tides*, Stanford University Press, Stanford, California
- Roden, G. L. (1964). Oceanographic aspects of Gulf of California. In: van Andel, T. H., Shor, G. G., Jr. (eds) *Marine geology of the Gulf of California*. American Association of Petroleum Geologists, Memoir 3, Tulsa, Oklahoma, pp. 30-58
- Sanders, H. L. (1968). Marine benthic diversity: a comparative study. *Am. Nat.* 102: 243-282
- Sanders, H. L. (1969). Benthic marine diversity and the stability-time hypothesis. In: *Diversity and stability in ecological systems*, Brookhaven Symposia in Biology, No. 22, Brookhaven National Laboratory, Upton, New York, pp. 71-81
- Seapy, R. R., Littler, M. M. (1978). The distribution, abundance, community structure, and primary productivity of macroorganisms from two central California rocky intertidal habitats. *Pacif. Sci.* 32: 293-314
- Setchell, W. A. (1920). The temperature interval in the geographical distribution of marine algae. *Science*, N. Y. 52: 187-190
- Shannon, C. E., Weaver, W. (1949). *The mathematical theory of communication*, University of Illinois Press, Urbana, Illinois
- Slobodkin, L. B., Sanders, H. L. (1969). On the contribution of environmental predictability to species diversity. In: *Diversity and stability in ecological systems*, Brookhaven Symposia in Biology, No. 22, Brookhaven National Laboratory, Upton, New York, pp. 82-95
- Sokal, R. R., Rohlf, F. J. (1969). *Biometry*, Freeman, San Francisco
- Sousa, W. P. (1979a). Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecol. Monogr.* 49: 227-254
- Sousa, W. P. (1979b). Disturbance in marine intertidal boulder

- fields: the nonequilibrium maintenance of diversity. Ecol. Monogr. 60: 1225–1239
- Talbot, F. H., Russell, B. C., Anderson, G. R. V. (1978). Coral reef fish communities: unstable, high-diversity systems. Ecol. Monogr. 48: 425–440
- University of Arizona (1973). 1973 tide calendar for the northern Gulf of California, University of Arizona, Tucson, Arizona
- U. S. Department of Commerce (1975). Tide tables 1975, west coast of north and south America including the Hawaiian Islands, National Ocean Survey, Rockville, Maryland
- Vermeij, G. J. (1978). Biogeography and adaptation patterns of marine life, Harvard University Press, Cambridge
- Wynne, M. J., Norris, J. N. (1976). The genus *Colpomenia* Derbes et Solier (Phaeophyta) in the Gulf of California. Smithson. Contr. Botany 35

This paper was presented by Professor J. S. Pearse; it was accepted for printing on September 30, 1980