Analysis of seaweed communities in a disturbed rocky intertidal environment near Whites Point, Los Angeles, Calif., U.S.A.

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Introduction

Recently, our understanding of the effects of severe disturbances such as sewage pollution (e.g., Borowitzka 1972; Munda 1974; Littler & Murray 1975; Murray & Littler 1977a, 1978a), sand scouring and sediment burial (e.g., Daly & Mathieson 1977; Seapy & Littler 1982; Taylor & Littler 1982; Littler *et al.* 1983), substratum instability (e.g., Sousa 1979, 1980) and extreme aerial exposure (e.g., Seapy & Littler 1982) on the population dynamics and diversity of intertidal seaweeds has been greatly advanced. Under conditions of extreme disturbance, communities show reduced species diversity and increased standing stocks of opportunistic seaweeds, with the caveat that, as noted by Sousa (1979, 1980) and Littler *et al.* (1983), localized disturbance can produce mixed patches of organisms undergoing different stages of succession resulting in an overall increase in community diversity.

A synthetic functional-form hypothesis has been advanced recently by Littler & Littler (1980) whereby different hypothetical survival strategies are outlined for seaweeds representative of stressed and nonstressed environments. Aspects of this functional-form model have been successfully employed to interpret population dynamics of seaweeds in severely disturbed rocky intertidal habitats (Littler & Littler 1981; Seapy & Littler 1982; Littler *et al.* 1983) and to establish relationships between seaweed primary productivity and thallus morphology (Littler 1980a, 1981; Littler & Arnold 1982).

As a continuation of our interest in seaweed communities of disturbed environments, we chose to study the rocky intertidal zone near Whites Point, Los Angeles, California, USA. This region of the southern California coast has been a site of major sewage discharge for more than 40 years and historically has received heavy human usage due to its accessibility. Previous research (Dawson 1959, 1965; Widdowson 1971; Thom & Widdowson 1978) has characterized the seaweed flora near Whites Point as depauperate in terms of species numbers, and has implicated sewage as a causative factor; additionally, the exposure of the Whites Point shoreline to human traffic and air pollution has been emphasized (Widdowson 1971; Thom & Widdowson 1978). Earlier, we reported (Murray & Littler 1977b, 1978b, 1979a) substantial alterations in macroorganism standing stocks near Whites Point associated with periodic movements of sand, gravel and loose cobbles.

The purpose of this paper is to provide an overview of the seasonal dynamics in the standing stocks of the seaweeds inhabiting the disturbed rocky intertidal shoreline near Whites Point. Additionally, we present an analysis of the composition of the Whites Point seaweed communities based upon ecologically related functional-form groups.

Study area

The study area (33°43.0′N, 118°19.1′W) is located along a southwest-facing portion of the southern California shoreline, ~4.0 km northwest of the port of Los Angeles breakwater and ~0.6 km northwest of Whites Point (Fig. 1). Prior to and during our research, two ocean outfalls were operated by the Los Angeles County Sanitation Dis-

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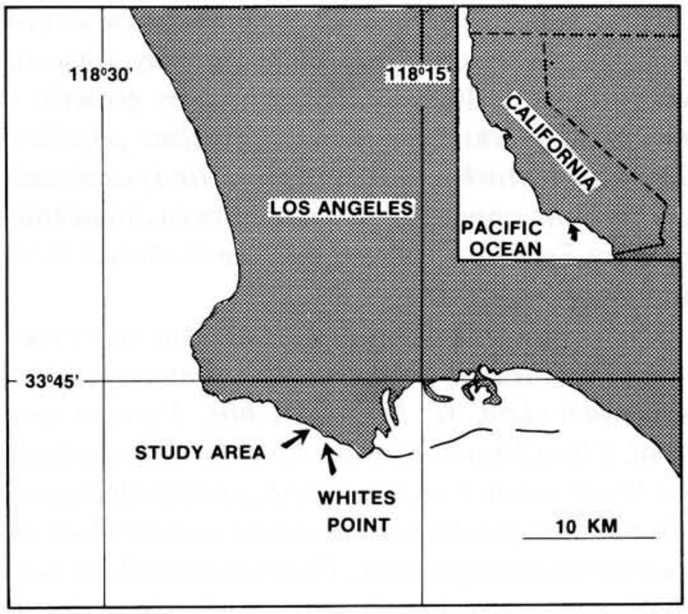

Fig. 1. Location of the study area near Whites Point, Los Angeles, California.

tricts near Whites Point, discharging occasionally chlorinated, primary-treated effluent into 50- to 60-m depths at an average annual flow rate ranging from 1.27 to 1.34×10^9 l d^{-1} (Schafer 1976, 1977, 1979, 1980). The discharged sewage, which consists of both municipal and industrial wastes, generally flows parallel to the shoreline in a northwesterly direction, spreading out from the 60-m depth contour (J. Stull, Los Angeles County Sanitation Districts, pers. commun.). Although the majority of sewage effects are currently thought to be focused in deeper water, Grigg (1979) has reported reduced diversity and abundance of algae, invertebrates and fishes in rocky bottom communities at 6-m depths around the Whites Point outfalls, as well as increased rates of light attenuation and elevated concentrations of DDT, trace metals and flocculent material.

The Whites Point shoreline is easily accessible to humans and is regularly subjected to considerable human traffic. Quantitative data depicting human usage are difficult to obtain. However, Widdowson (1971) ranked Whites Point third among fifteen southern California intertidal stations in terms of exposure to human traffic, and we have regularly observed dense recreational usage of the Whites Point shoreline throughout our numerous visits.

Prior to our earlier reports (Murray & Littler 1977b, 1978b, 1979a), the influence of sand, gravel and cobble movement on the Whites Point intertidal communities had been ignored, despite the fact that Cimberg *et al.* (1973) identified sand movement and substratum stability as the two most important factors affecting southern California rocky shore populations. We observed increased winter sand and gravel burial of bedrock substratum along the upper shoreline near Whites Point during 1975–1979 and documented declines in macroorganism standing stocks near surge channels, areas most susceptible to scouring from transported sediment material (Murray & Littler 1977b, 1978b, 1979a).

The specific study site lies at the base of a steep, eroded coastal bluff and consists of a series of eroded bedding planes that run perpendicular to the shoreline. The substratum is composed mostly of Monterey diatomaceous shale of middle Miocene origin. The upper shoreline (+1.5 to +3.0 m) is bounded by aggregations of loose cobbles largely devoid of living macroepibiota. Thus, sampling was limited to the bedding-plane habitats below +1.2 m.

Methods and materials

The methods employed to quantify the standing stocks of epibiotic seaweeds have been described previously (Littler 1980b, c). Therefore, only a brief discussion of site-specific details is presented below.

Two permanent transect lines were established perpendicular to the shoreline along a representative section of the coastline. Quadrats (0.15 m^2 and 1.0 m^2) were positioned at 2.0-m intervals, except along the upper shore where sampling was performed at 1.0-m intervals due to the steeper slope. This sampling array provided an average of 41 0.15-m^2 and 41 1.0-m^2 samples during the study. The 1.0-m^2 quadrats were employed exclusively to sample the larger seaweeds, specifically the larger, lower intertidal brown algae, while the abundances of all other macroalgae were determined using the 0.15-m^2 sample size.

Percent cover was selected as the most meaningful means of quantifying seaweed abundances. Cover data were obtained by photographing each quadrat during low tide with 35-mm cameras equipped with electronic strobes. In addition, the species composition of each quadrat was recorded in the field, along with visual estimates of cover. These field notes were then used in the laboratory along with the photographs to make final determinations of cover using a point-intercept technique.

Quadrat assessments were performed on ten occasions from September 1975 to February 1978. For the first two years of the study, assessments were performed during the months of September, December, February and May, while sampling was restricted to the months of September and February in the last year. During a seasonal assessment, the percent cover of each seaweed population was determined for each 0.3-m tidal interval, from –0.3 m to +1.2 m with reference to MLLW, and the mean cover was calculated for the entire shoreline area sampled. In addition, species diversity was calculated using Shannon's H' index (Shannon & Weaver 1949) and Pielou's J' evenness index (Pielou 1975) using natural logarithms.

Data on seaweed standing stocks were also analyzed in terms of functional-form groupings using the six categories described by Littler & Arnold (1982), i.e., seaweeds were classified by their thallus morphology as belonging to either the sheet-group, filamentous-group, coarsely branched-group, thick leathery-group, jointed calcareous-group or crustose-group, in order to gain greater understanding of the ecology of the Whites Point macroalgal flora.

Results

Seaweed cover averaged 72.5% over the entire rocky intertidal shoreline and ranged from 60.8% to 92.5% during the 2.5 years of study. Generally, cover was greatest during late summer (September) and was least during winter (December, February) (Fig. 2).

Greatest algal cover (17.6%) was contributed by encrusting blue-green algae (Table 1). Only four other algal taxa contributed 2.5-yr mean cover values greater than 5.0%. These were two species of turf-forming articulated coralline algae, *Corallina officinalis* var. *chilensis* (13.7%) and *Corallina vancouveriensis* (5.5%), the coarsely branched red alga *Gigartina canaliculata* (6.7%), and encrusting Ralfsiaceae (6.0%). Most of the remaining algal cover was furnished by small, delicately branched red seaweeds (e.g., *Ceramium* spp. *Chondria californica, Herposiphonia littoralis, Polysiphonia* spp., *Centroceras clavulatum*), benthic diatoms and crustose seaweeds (e.g., crustose Corallinaceae, *Cylindrocarpus rugosus*). There was a notable lack of larger, thick-bladed, or coarsely branched seaweeds or sheet-like macroalgae. Larger, fleshy seaweeds were almost exclusively represented by growths of the coarsely branched species *Gigartina papillata, Gigartina leptorhynchos* and *Gigartina canaliculata* along the upper shoreline, and occasional thick leathery *Egregia menziesii* thalli in the lower intertidal zone.

Most seaweeds exhibited variations in percent cover from season to season and year to year, but *na canaliculata, G. leptorhynchos, Egregia menziesii, Chondria californica, Laurencia sinicola* and to a lesser extent *Ceramium* spp., species that generally reached greatest cover in late summer-fall and least cover during winter. The peak periods of overall seaweed cover (Fig. 2) corresponded best with the cover during winter. The peak periods of overall seaweed cover (Fig. 2) corresponded best with the times of greatest abundance of those taxa exhibiting recurrent seasonal patterns. An interesting exception, however, was the small red alga *Centroceras clavulatum*, which showed repetitive cover maxima during the winter months (Table 1).

A total of 67 different algal taxa occurred in our samples, although an average of only 42 seaweeds

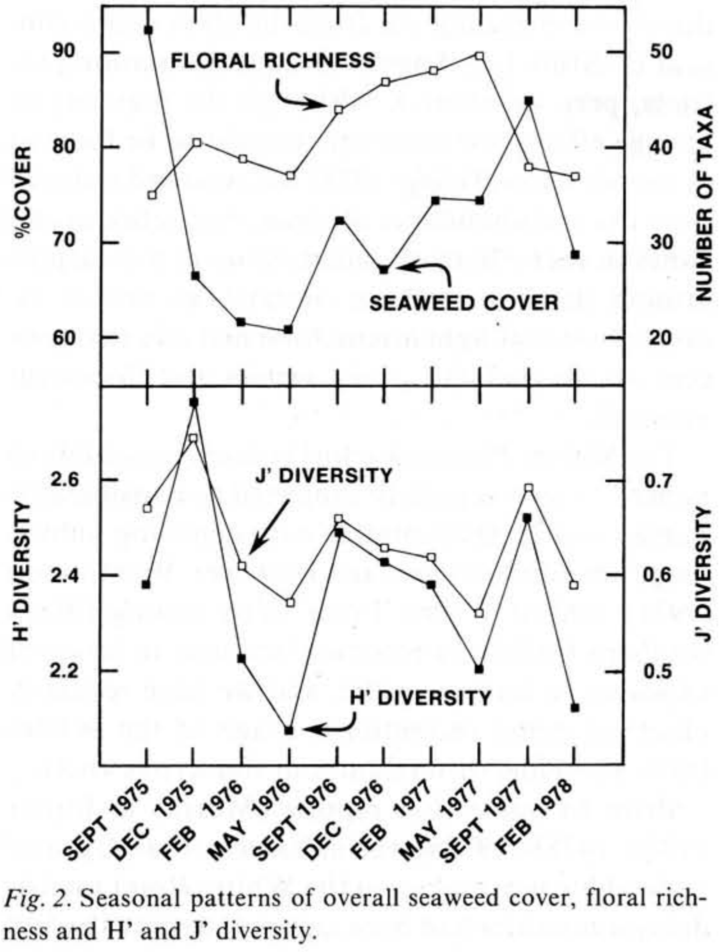

Fig. 2. Seasonal patterns of overall seaweed cover, floral richness and H' and J' diversity.

Table 1. Cover (%) of seaweed populations near Whites Point.

Taxa	Functional-form group*	Month										Mean ± S.D.
		Sept 1975	Dec 1975	Feb 1976	May 1976	Sept 1976	Dec 1976	Feb 1977	May 1977	Sept 1977	Feb 1978	
Blue-green algae	C	21.8	10.4	12.4	22.4	10.6	9.9	22.9	23.8	17.1	24.6	17.6 ± 6.2
Corallina officinalis L. var. *chilensis* (Dcne.) Kütz	JC	17.8	6.6	17.9	11.1	16.7	17.6	12.0	12.3	12.6	13.8	13.7 ± 3.6
Gigartina canaliculata Harv.	CB	4.4	2.6	5.0	3.7	7.1	6.7	5.6	12.0	14.1	5.4	6.7 ± 3.6
Ralfsiaceae	C	7.7	7.4	4.1	3.9	5.5	6.4	7.1	7.4	6.0	4.7	6.0 ± 1.4
Corallina vancouveriensis Yendo	JC	7.2	7.6	3.5	2.6	9.0	6.8	5.8	3.0	4.6	4.4	5.5 ± 2.2
Ceramium spp.	F	9.1	3.3	6.1	3.8	4.2	2.6	2.9	3.9	3.4	2.1	4.1 ± 2.1
Gigartina leptorhynchos J. Ag.	CB	7.4	2.2	0.3	1.0	6.0	2.1	0.2	2.5	6.6	0.7	2.9 ± 2.7
Crustose Corallinaceae	C	0.8	3.3	0.8	1.0	0.2	0.5	0.9	1.2	0.5	3.7	1.3 ± 1.2
Herposiphonia littoralis Hollenb.	F	0.1	0.3	0.6	0.4	2.1	3.4	2.8	0.5	0.5	0.8	1.2 ± 1.2
Laurencia sinicola S. & G.	CB	1.1	2.6	<0.1	<0.1	0.9	0.7	0.3	<0.1	3.3	0.5	1.0 ± 1.1
Egregia menziesii (Turn.) Aresch.	TL	5.8	1.4	<0.1	<0.1	0.2	<0.1	<0.1	<0.1	1.3	0.1	0.9 ± 1.8
Chondria californica (Coll.) Kyl.	F	0.2	0.4	<0.1	0.0	4.4	0.2	<0.1	<0.1	3.1	0.0	0.9 ± 1.6
Lithothrix aspergillum Gray	JC	0.2	0.2	0.1	0.2	1.3	0.4	0.6	0.7	4.3	1.0	0.9 ± 1.3
Centroceras clavulatum (C. Ag.) Mont.	F	0.6	1.0	0.8	0.2	<0.1	1.5	1.3	0.1	<0.1	0.2	0.6 ± 0.5
Cryptopleura spp.	S	0.5	0.4	<0.1	0.2	0.8	0.6	0.6	0.6	1.1	0.8	0.6 ± 0.3
Gelidium coulteri Harv. and *G. pusillum* (Stackh.) Le Jolis	CB	1.0	1.1	1.0	0.4	0.2	0.2	0.4	0.9	0.6	0.4	0.6 ± 0.3
Benthic diatoms	F	0.0	0.0	0.2	1.8	<0.1	0.2	1.7	0.2	0.2	<0.1	0.5 ± 0.7
Gigartina papillata (C. Ag.) J. Ag.	CB	0.6	0.5	0.6	0.4	0.5	0.1	0.1	0.1	1.7	0.1	0.5 ± 0.5
Other Seaweeds		6.2	15.2	8.7	7.5	4.5	7.3	9.2	4.6	3.9	5.2	
Total Seaweed Cover		92.5	66.5	62.5	60.8	83.4	67.3	74.6	74.1	85.0	86.6	72.5 ± 9.9

*C = Crustose; JC = Jointed Calcareous; CB = Coarsely Branched; F = Filamentous; S = Sheet; TL = Thick Leathery.

was obtained per seasonal assessment. As the encrusting algae (e.g., blue-green algae, Ralfsiaceae, crustose Corallinaceae) and certain small, red algae (e.g., *Ceramium* spp., *Polysiphonia* spp.) were not identified to the species level, the actual resident flora is somewhat larger. There was no seasonal pattern of floral richness based on numbers of sampled taxa, rather, floral richness varied sporadically from season to season and year to year, ranging from 35 in September 1975 to 50 in May 1977 (Fig. 2). Seaweed diversity, based on both H' and J' indices, was generally greatest during September and December and least during February and May (Fig. 2). H' diversity averaged 2.36 during the study and ranged from 2.77 (December 1975) to 2.07 (May 1976); J' averaged 0.64.

Seaweeds exhibiting mean cover values over the 2.5 yr period ≥0.5% (Table 1, Fig. 3) were categorized according to functional group. The crustose (24.9%) and jointed calcareous (20.1%) functional groups dominated the cover, while moderate cover was furnished by members of the coarsely branched (11.7%) and filamentous (7.3%) groups; less than 1.0% cover was provided by both the sheet and thick leathery seaweeds. These data clearly reveal the striking lack of thick leathery (<1.0% cover) and sheet-like (<1.0% cover) seaweeds near Whites Point and demonstrate the high contributions to seaweed standing stocks of the crustose and jointed calcareous forms. Little seasonal variation from the described general pattern was observable, as for all periods excepting September 1977, the crustose and jointed calcareous seaweeds ranked highest in cover. Interestingly, only members of the coarsely branched group exhibited a recurrent pattern of seasonality, reaching greatest cover each Sep-

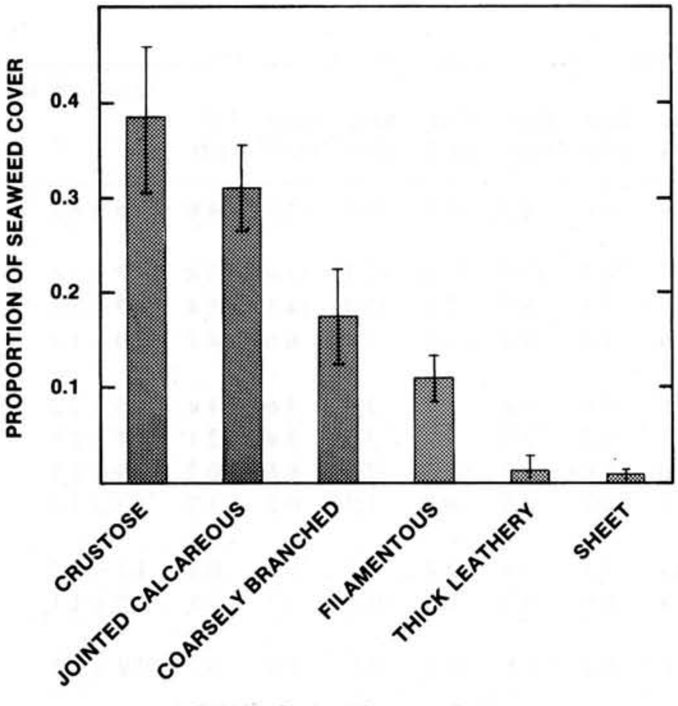

Fig. 3. Seaweed standing stocks near Whites Point based on functional-form groups. Data represent the proportion of cover provided by each functional-form group based on the 2.5-yr mean cover values of the more abundant populations. Vertical bars represent ±95% confidence intervals.

tember and least cover during either February or May. Consequently, the cover-dominance of seaweed standing stocks by species with crustose and jointed calcareous thalli is a persistent feature of the Whites Point macroalgal communities.

Discussion

Seaweed cover at Whites Point revealed a slight recurrent pattern owing to increases in standing stock each year from spring to late summer followed by declines in winter. This pattern is consistent with previous descriptions of seasonality in the southern California intertidal macroalgal flora (Murray & Littler 1977a; Gunnill 1980; Littler 1980c; Seapy & Littler 1982; Littler *et al.* 1983), whereby a summer-fall peak in seaweed standing stocks has been reported to undergo reduction in late fall-winter corresponding with the change-over from early morning to afternoon periods of low-tide emergence, and at certain sites (Littler *et al.* 1983), increased inundation by sand. Similar seasonal fluctuations in standing stocks to those observed near Whites Point also have been documented for central California seaweed populations by Horn *et al.* (1983).

It has been proposed (e.g., Sanders 1969; Connell 1975) that there is a decrease in species numbers beyond an optimal level of disturbance, as emphasized by Fox (1979). Historically, investigators (Dawson 1959, 1965; Widdowson 1971; Thom & Widdowson 1978; Harris 1980) have attempted to describe the status of intertidal seaweed communities near Whites Point in terms of the numbers of species composing the algal flora. Dawson (1959, 1965) first emphasized the disturbed nature of the Whites Point rocky intertidal zone when he reported that a reduction of more than 50% had occurred in the species of conspicuous seaweeds in the ~60-yr period after the 1895–1912 collections of W. A. Setchell and N. L. Gardner. Dawson (1959, 1965) attributed this decline in floral richness to sewage pollution. Subsequent research produced evidence that, in the 15 yr period following Dawson's 1956–1959 surveys, the number of species composing the Whites Point seaweed flora remained constant (Widdowson 1971) or increased slightly (Thom & Widdowson 1978); Haris (1980), however, has indicated a substantial increase in floral richness at Whites Point since 1974.

Unfortunately, it is extremely difficult to compare aspects of floral richness generated from our data, with the results of previous studies. Our sampling procedures were not designed to 'find' species, but rather to determine quantitatively the distributions and abundances of seaweed populations. As pointed out by Littler (1980b), Dawson (1959, 1965) misused transect sampling procedures (techniques appropriate for quantitative determinations of species abundances) for the purposes of reporting floral composition (and to give only gross qualitative estimates of species abundances). Other than our studies, all related work at Whites Point (Widdowson 1971; Thom & Widdowson 1978; Harris 1980) has been modelled after Dawson's studies, and thus has perpetuated the problems inherent in Dawson's original sampling design. Additionally, as Dawson (1959, 1965) assessed only the "conspicuous" members of the seaweed flora, it has been difficult for subsequent researchers to make direct comparisons of richness (see Harris 1980). The numbers of taxa obtained in quadrats during our sampling program suggest that the Whites Point flora has experienced an increase since Dawson's

(1959, 1965) surveys, but the magnitude of this increase is extremely difficult to determine. However, in a broad regional context, the Whites Point seaweed flora must still be regarded as low in species richness; e.g., Littler (1980b, 1980c) reported this site to rank last among 10–12 other southern California intertidal habitats in numbers of macrophyte taxa.

The kinds of algae composing the Whites Point intertidal flora have been of concern since Dawson (1959, 1965) described a decline in leafy red algae and increased growths of articulated coralline algae near southern California sites of sewage discharge. Subsequent researchers (Widdowson 1971; Thom & Widdowson 1978) have evaluated changes in the composition of the southern California intertidal algal flora, including that at Whites Point, in terms of the gross morphology of the taxa. The groupings used by these authors, however, bear only casual similarity with the functional-form categorization proposed by Littler & Littler (1980), and outlined by Littler & Arnold (1982) to describe seaweed productivity relationships. We describe the Whites Point macroalgal flora as consisting of relatively high standing stocks of species assigned to the crustose and jointed calcareous groups and as being distinguished by the notable paucity of thick leathery seaweeds. These findings are in agreement with earlier observations (Widdowson 1971; Thom & Widdowson 1978) that there has been a shift from massive species towards turf and crustose species in southern California since Dawson's (1959, 1965) surveys. Additionally, Thom & Widdowson (1978) report that these changes have been most pronounced in habitats exposed to greatest disturbance, i.e., locales near heavily populated metropolitan areas or in public parks subject to heavy recreational use. Sousa *et al.* (1981) described the reduction in standing stocks of long-lived, large brown algae relative to eastern North Pacific low intertidal habitats to be attributable to grazing by sea urchins and preemption of space by turfy red algae where urchins are less abundant; however, much of their southern California data were obtained from physically disturbed intertidal systems.

An inspection of the profiles of seaweed productivity outlined by Littler & Arnold (1982) leads us to characterize the Whites Point algal flora as one of low productivity. Our data indicate that the flora is dominated by low-producing seaweeds, such as the articulated coralline and crustose algae, species reported (Littler 1980a, 1981; Littler & Arnold 1982) to have the lowest photosynthetic rates among the macroalgae. Further, seaweeds known to be among the highest producers, members of Littler & Arnold's (1982) sheet group, were never found in high abundances during our sampling program. Even the moderately abundant, delicately branched, filamentous algae occurred largely as turf-like mats, a habit known (Dawes *et al.* 1978; Littler & Arnold 1982) to reduce their characteristically high photosynthetic rates significantly.

Grime (1977) has proposed a three-strategy model of adaptive specialization for terrestrial plants. More recently this model, as developed by Vermeij (1978), has been applied to rocky intertidal populations by Seapy & Littler (1982) and Littler *et al.* (1983). It is useful to analyze the Whites Point seaweed populations in this framework. According to this model, sensu Vermeij (1978), species can be categorized as: (a) opportunistic; these show high reproductive output, short life spans, high dispersibility, reduced long-term competitive abilities, and occupy ephemeral or disturbed habitats; (b) stress-tolerants; these can tolerate chronic physiological stress, exhibit low rates of recolonization, tend to be long-lived with slow growth rates and, consequently, are generally poor competitors; (c) biotically competent; these generally live in physiologically favorable environments, have long life spans, are good competitors, and have evolved mechanisms to reduce predation.

Previously, a shift from biotically competent seaweeds in favor of stress-tolerant and opportunistic strategists has been reported for rocky intertidal communities subjected to heating and desiccation stress (Seapy & Littler 1982), and to sand scouring and burial (Littler *et al.* 1983). Similar results can also be interpreted for sewage-polluted rocky intertidal communities from our previously published data (Littler & Murray 1975; Murray & Littler 1977a). The seaweed communities near Whites Point provide several features in common with these earlier findings, including depauperate populations of the relatively large, biotically competent seaweeds (e.g., *Egregia menziesii*), and moderately abundant populations of delicately branched opportunists (e.g., *Ceramium* spp., *Polysiphonia* spp.). However, seaweed standing stocks near Whites Point are dominated by species of turf-forming articulated coralline and crustose algae. These forms have been described as low-producers (Littler 1980a, 1981; Littler & Arnold 1982) that possess antiherbivore adaptations such as tough thalli (Larkum *et al.* 1967; Paine & Vadas 1969; Lubchenco 1978; Lubchenco & Cubit 1980; Littler & Littler 1980; Lubchenco & Gaines 1981; Sousa *et al.* 1981). Additionally, encrusting algae such as *Ralfsia*, and most articulated coralline algae (e.g., *Corallina*) are widely regarded (see Garbary 1976) to be relatively long-lived or perennial seaweeds, also attributes of biotically competent species.

Successional data for Whites Point seaweeds (Murray & Littler 1979b), however, reveal that articulated coralline and crustose algae are able to recover rapidly their former abundances on mechanically-disturbed intertidal surfaces. Tough thalli and rapid resilience following mechanical disturbance equip these algal forms for life in habitats subject to physical disturbances such as sand scouring or to intense grazing pressure. Consequently, the Whites Point algal flora largely consists of opportunists (delicately branched algae) and articulated coralline and crustose algal forms that have a number of attributes of biotically competent species, but at the same time are well suited for survival in physically or biologically (heavily grazed) disturbed environments.

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