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PATTERNS OF ALGAL SUCCESSION IN A PERTURBATED MARINE INTERTIDAL COMMUNITY[1]

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ABSTRACT

Patterns of algal succession for a sewage-polluted and an unpolluted habitat near Wilson Cove, San Clemente Island, California, were studied from December 1974 to June 1977. Resident populations were analyzed for 56 fully denuded and 34 undisturbed control quadrats during 11 assessment periods. The denuded quadrats in the perturbated (polluted) habitat showed recovery within 1.0 mo as determined by cover, percent similarity and species diversity comparisons with control plots. The short recovery times of the algal populations dominating the perturbated habitat indicate that these species maintain relatively constant overall abundances due to their potential for rapid recruitment and growth. Denuded quadrats in the unpolluted habitat did not show recovery even after 30.0 mo. These quadrats were dominated during the first 1.3 mo by algae characteristic of the perturbated area, including filamentous Ectocarpaceae, colonial diatoms and bluegreen algae. Petalonia fascia *(Müll.) Kuntze (1.3–3.0 mo), and* Scytosiphon lomentaria *(Lyngb.) J. Ag. and* Colpomenia sinuosa *(Roth) Derb. & Sol. (1.3–5.0 mo) were abundant shortly following plot denudation and provided thick growths that may have excluded other algae. The similarity between the species occupying the sterilized plots during the first few months and those that provide the majority of cover in the perturbated area supports the hypothesis that the dominant algae of the upper and mid-intertidal regions of this habitat consist largely of early successional or opportunistic species with high capacities for growth and reproduction. Additionally, these experiments suggest that algal populations described for other perturbated epilithic systems also represent resilient subclimax associations.*

Key index words: colonization; disturbed environments; pollution; rocky intertidal community; sewage; succession

Although numerous successional studies in rocky intertidal habitats have been done, these have rarely generated quantitative data or tested hypotheses concerned with the structuring of communities. The manipulative approach, so successfully employed for example by Dayton (1971, 1973a, b, 1975), represents an exception where communities have been studied by performing realistic perturbations and monitoring subsequent successional events. These studies have mostly involved the removal or addition of species presumed to be functionally important and have not included succession from fully denuded surfaces.

Studies of perturbated communities have generally concentrated on field descriptions of populations or laboratory analyses of physiological responses of individual organisms. The latter approach, although providing much data on the physiological ecology of marine plants and animals under stress, has generally failed to yield predictive information concerning perturbations of natural populations because of the failure to simulate field conditions or to understand fully the functional roles of the dominant organisms. Additionally, many earlier studies of perturbated systems have been of limited value due to the unavailability of data describing the pre-impact condition or comparable unpolluted systems suitable for controls.

The rocky intertidal near the Wilson Cove sewage outfall on San Clemente Island, California (Fig. 1) is ideally suited for studies of the role of environmental perturbation in the structuring of algal communities. Both disturbed and undisturbed habitats have been described previously (Littler and Murray 1975) and the environmental features of the outfall have been reported (Kenis et al. 1972). We view this study as an attempt to experimentally verify interpretations of community structure for the Wilson Cove outfall area derived from extensive published (Murray and Littler 1974, Littler and Murray 1975) and unpublished standing stock data. These include the hypothesis that the dominant algae of the upper and mid-intertidal portions of the sewage-impacted area consist largely of early successional or "opportunistic" species with high capacities for growth and reproduction. Theoretically, the abundances of these organisms result in a subclimax community for the upper shoreline near the outfall which is characterized by a physically fluctuating environ-

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ment due to the variable discharge of nutrient rich but sporadically toxic effluent.

Briefly, the Wilson Cove effluent consists primarily of untreated human excreta, food scraps from a mess hall, disinfectants, bleach and detergents which are released at the rate of approximately 95,000 l/day onto a rocky shoreline 1.6 m above mean lower low water. Bleach and detergent concentrations are minimal; however, pine oil disinfectant is used abundantly ($\sim$182 l of 90% concentrate/yr) in the daily sanitation of lavatories and is an important but sporadic component of the effluent. The average dissolved O_2 concentration of the sea water is ca. 5.5 mg/l at the point of discharge and increases to 7.0–8.0 mg/l, a range typical for unpolluted ocean surface waters, at a distance 30 m from the outfall terminus (Kenis et al. 1972). Measurements of biochemical oxygen demand were 90–405 mg O_2/l (mean = 223), values typical of raw domestic waste waters. Wilson Cove effluent is diluted several hundred to a thousand times within 30 m of the outfall terminus where oxygen concentrations are above levels adverse for sensitive marine organisms. Coliform levels in excess of California administrative Code minimum standards (1,000/100 ml) for public water-contact areas are also restricted (Kenis et al. 1972) to within 30 m of the outfall. Mixing maintains sewage particles in suspension as evidenced by a lack of sedimentation observed intertidally or subtidally near the study region.

For the past five years we have sampled the algal-dominated rocky intertidal macro-epibiota to determine the seasonal patterns of distribution and abundance of the biological components of the sewage-polluted and the nearby unpolluted communities (Murray and Littler 1974, Littler and Murray 1975). The present contribution represents an extension of this earlier work and was designed to determine: i) if algal communities characteristic of stressed habitats show high resiliency by their ability to recover quickly after perturbations, and ii) whether a primary effect of environmental stress is to favor early successional algal populations. A primary objective was to test the hypothesis developed earlier that the upper to mid-intertidal region of the disturbed area, which represents a fluctuating environment directly exposed to deleterious components of discharged sewage (e.g., pine oil disinfectant), is dominated by subclimax algal forms.

MATERIALS AND METHODS

Four contiguous permanent 0.15 m^2 plots arranged as a 0.6 × 1.0 m rectangle were established during December 1974 on comparable surfaces in sewage-affected and unpolluted areas at tidal heights between +0.2 and +0.5 m. Plots were marked with bolts embedded into the substrate and the contents photographed. Subsequently, all of the epibiota was manually removed and the rock surfaces thoroughly scraped with wire brushes and knives. Surfaces were then burned for up to 1.0 h with portable propane torches; sponges soaked in 70% ethanol were used to scrub the substrate and intensify the burning. Following this sterilization procedure, plots were photographed with infra-red film which reveals living plant material by recording chlorophyll fluorescence; these photographs revealed all plots to be thoroughly sterilized.

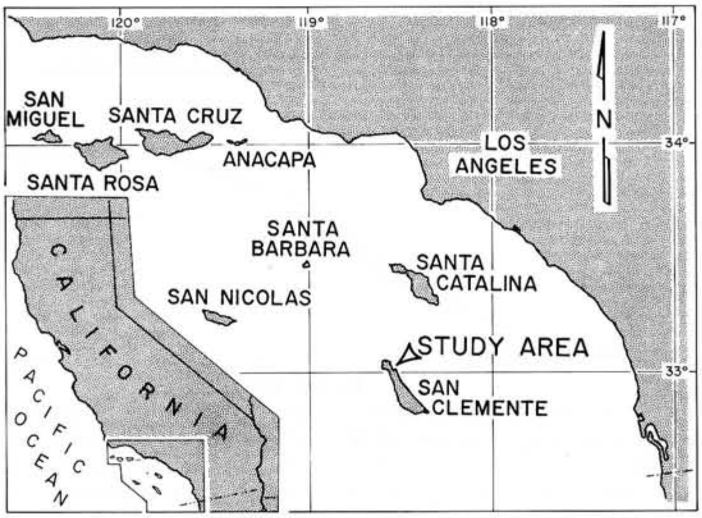

FIG. 1. Location of the San Clemente Island (California) study sites.

Assessments of the unpolluted shoreline were made for 30 mo following denudation. Sampling in the outfall habitat was terminated after 3 mo because of the inability to qualitatively detect experimental surfaces from surrounding natural communities (i.e., complete recovery had apparently occurred).

Concomitant with the experimental study, quantitative analyses of the distribution and abundance of algal standing stocks for the outfall and unpolluted areas were performed. These data substantiated our earlier report (Littler and Murray 1975) that seasonal and annual changes in the Wilson Cove biological communities are few. However, since one of the experimental goals was to determine when the successional plots for both areas had come into equilibrium with their surrounding natural communities, four control plots were selected for each area from among the standing stock samples. Plots were chosen on the basis of their visual and quantitative similarity to the algal communities occupying the experimental surfaces prior to clearance. This procedure presented the advantage that for each area, comparisons were made with the biota of undisturbed plots that had experienced environmental conditions identical to the experimental samples. Due to the low degree of seasonality, control sampling was not necessary at intervals less than three months.

A total of 20 samples (12 experimental, 8 control) were analyzed in the sewage-perturbated area and 70 (44 experimental, 26 control) in the undisturbed habitat during the study. Data are presented as percent cover and calculated for each species as a mean of the four replicated samples taken during each monitoring period, except in the control plots of the undisturbed habitat where on two occasions only three samples were assessed.

The photographimetric method described previously (Littler and Murray 1975) for standing stock assessments of macro-epibiota was used. During each visit, photographs (color and infra-red) and detailed field notes were taken for each quadrat to generate the numerical data employed in the analyses.

Three methods were employed to measure changes in diversity patterns; simple counts of taxa were used to indicate richness, with the Shannon (Shannon and Weaver 1949) index (H'_e) and Pielou's (1969) evenness index (J'_e) utilized to construct diversity patterns emphasizing the apportionment of cover among the taxa. The Bray and Curtis (1957) index was employed to measure the degree of recovery (% similarity) of experimental samples by comparisons with the unaltered control plots.

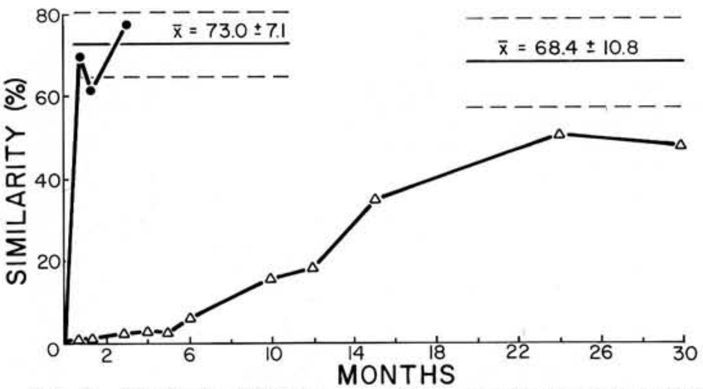

FIG. 2. Similarity (%) between experimental and control plots for perturbated (polluted) (●-●) and unpolluted (△-△) habitats based upon algal cover: mean ($\bar{x}$) similarity ± SD for control plots from perturbated area are based upon comparisons between December 1974 and April 1975 (n = 4); those for unpolluted area controls are from progressive comparisons for December 1974 through June 1976 (n = 6).

RESULTS

In both the perturbated (polluted) and unpolluted quadrats lateral encroachment by attached algae was insignificant and all recruitment appeared to result from suspended reproductive cells or vegetative fragments. Additionally, both study areas were occupied almost entirely by macroalgae; only rarely did macroinvertebrates contribute measurable cover (see Littler and Murray 1975). Hence, because of their low abundance and sporadic occurrence in samples, macroinvertebrates have been excluded from our analyses.

Perturbated area. The sterilized plots in the outfall area showed rapid recovery. Due to layering of thalli, overall biotic cover exceeded 100.0% prior to the sterilization of plots in the sewage-impacted zone and consisted of small, turf-forming organisms; dominant forms were bluegreen algae, *Ulva californica* and *Pseudolithoderma nigra.* Within 1.0 mo after sterilization, overall cover had reached 100.1% (Table 1) and cover values for bluegreen algae (49.9% vs. 45.0%) and *U. californica* (42.7% vs. 44.9%) were reasonably similar to those determined for the identical plots prior to the experimental treatment. *P. nigra* and *Gelidium pusillum,* two species characteristic of the experimental area, showed slower recovery when compared with controls, although within 3.0 mo both approached abundances determined for the experimental quadrats prior to denudation. Epiphytic growths of filamentous Ectocarpaceae and colonial diatoms grew sporadically in the outfall area during the study and reached maximum cover (21.3%) in late January (1.3 mo).

TABLE 1. *Cover of algae for the perturbated (polluted) area: values represent mean cover for 4 replicate 0.15 m^2 quadrats for periods following plot denudation: values for control quadrats are averages for 0.0 and 4.0 mo assessments.*

Taxa	Cover (%)			
	Control quadrats $\bar{x}$	Experimental quadrats (months)		
		0.8	1.3	3.0
Bluegreen algae	62.2	49.9	47.0	53.0
Ulva californica	21.2	42.7	52.9	38.8
Pseudolithoderma nigra	15.9	3.0	4.0	8.2
Gelidium pusillum	15.0		0.4	0.1
Ectocarpaceae/colonial diatoms	0.8	4.5	21.3	0.1
Petalonia fascia			0.1	
Overall biotic cover	115.1	100.1	125.7	100.2

TABLE 2. *Diversity of the perturbated area based upon cover (%): values for control quadrats are averages for 0.0 and 4.0 mo assessments.*

Months	No. taxa	H'_e	J'_e
Experimental quadrats			
0.8	4	0.96	0.69
1.3	6	1.17	0.65
3.0	5	0.92	0.57
Control quadrats ($\bar{x}$)	5	1.00	0.62

Within the perturbated area, similarity (%) comparisons between the experimental and control plots also indicated extremely rapid recovery of the algal community. Similarity (Bray and Curtis 1957) between the two sets of plots was calculated at 69.6% after 0.8 mo, a value similar to that established (73.0%) for inherent variability among the control replicates (see Fig. 2). Similarity decreased slightly after 1.3 mo (61.0%) due to a bloom of filamentous Ectocarpaceae, but returned to 76.7% by the third month.

Rapid recovery of the outfall biota was also indicated by community parameters. A total of five taxa were present in the experimental plots prior to sterilization (Table 2) and these were the only organisms sampled from the control plots during the study. Within 1.0 mo, four of these had appeared on the cleared substrate; only one other species was present at the conclusion of the experiment. Diversity as measured by H'_e was 1.00 for the experimental plots before clearance and averaged 1.00 for the control plots. A value of 0.96 was reached for the experimental quadrats by 0.8 mo after denudation. A similar trend occurred for the evenness measure J'_e (Table 2). Assessments performed after 1.3 mo showed slightly higher H'_e diversity for the denuded quadrats due to increased Ectocarpaceae and colonial diatom cover.

Unpolluted area. Experimental plots for the unpolluted area did not attain the characteristic layered community aspect (i.e., cover exceeding 100%; see Littler and Murray 1975) until the third month of the study (Table 3). Samples were dominated for the first 3 mo by algae structurally resembling those of the outfall area, including filamentous Ectocarpaceae, colonial diatoms and bluegreen algae (Table 3), with *Petalonia fascia* (1.3–3.0 mo), and *Colpomenia sinuosa* and *Scytosiphon lomentaria* (1.3–5.0 mo) providing the majority of algal cover. Growths of *P. fascia* and *S. lomentaria* were accompanied by in-

TABLE 3. *Patterns of development of algae colonizing cleared plots in unpolluted area: values represent mean cover (%) for 4 replicate 0.15 m^2 quadrats initiated in December 1974.*

	Cover Months after clearance										
Taxa	0.8	1.3	3.0	4.0	5.0	6.0	10.0	12.0	15.0	24.0	30.0
Ectocarpaceae/colonial diatoms	31.5	37.8			1.0	1.3		0.1	0.1		
Bluegreen algae	16.3	<0.1	<0.1	12.4	0.1	3.8	3.0	0.1	3.9	2.7	
Pseudolithoderma nigra Hollenb.	2.9								0.1	4.1	
Ralfsia sp.	0.5		0.6	10.8	20.4	51.3	85.0	84.0	35.1	12.8	1.3
Petalonia fascia (Müll.) Kuntze		23.5	9.2	0.2				0.1	<0.1		
Colpomenia sinuosa (Roth) Derb. & Sol.		22.5	9.4	11.6	43.8	12.8	0.1	1.0	1.5	2.3	10.2
Scytosiphon lomentaria (Lyngb.) J. Ag.		5.1	82.3	43.8	31.2	1.6					
Ulva californica Wille		1.6	1.0	8.5	6.1	6.7	1.5	7.0	23.2	2.0	1.4
Egregia menziesii (Turn.) Aresch.			0.9	6.4	11.0	25.5	106.0	54.0	39.5	5.8	50.0
Gigartina canaliculata Harv.					2.0	4.3	0.1	1.5	12.6	16.9	25.7
Chaetomorpha linum (Müll.) Kütz.					0.1	0.1	0.1	1.0	0.1		
Pterocladia capillacea (Gmel.) Born. & Thur.					0.1	0.1	0.1	0.1	<0.1	3.9	5.6
Ceramium eatonianum (Farl.) DeToni and *C. sinicola* S. & G.						5.6	0.1	8.0	4.0	1.4	12.8
Peyssonneliaceae/Hildenbrandiaceae						1.2	0.1	0.1	1.2		
Corallina officinalis var. *chilensis* (Dec.) Kütz.						0.4	4.0	10.0	17.5	50.8	48.9
Lithothrix aspergillum Gray						0.2	0.1	0.1	0.1	3.2	4.5
Cladophora spp.						<0.1		2.0	2.8		
Enteromorpha sp.						<0.1					
Rhodoglossum affine (Harv.) Kyl.							7.5	19.0	15.3	0.8	43.2
Corallina vancouveriensis Yendo							0.1		0.1	8.7	9.1
Cryptopleura corallinara (Nott) Gardner							0.1		<0.1	0.3	0.3
Dictyota flabellata (Coll.) S. & G.							0.1	0.1	<0.1	0.6	
Halidrys dioica Gardner							0.1	1.0	0.8	3.9	3.3
Laurencia pacifica Kyl.							0.1	3.0	8.9	8.6	16.4
Laurencia spectabilis Post. & Rupr.							0.1	0.1	<0.1		0.1
Pterosiphonia dendroidea (Mont.) Falk.							0.1	0.1			
Sargassum agardhianum J. Ag.									0.2	4.5	11.8
Ceramium spp.									0.1		
Scytosiphon dotyi Wynne									1.4		
Gigartina spinosa (Kütz.) Harv.									<0.1		0.6
Gelidium pusillum (Stackh.) Le Jol.									<0.1		
Lithophyllum proboscideum (Fosl.) Fosl.										1.6	<0.1
Laurencia sinicola S. & G.										0.8	3.8
Polysiphohia hendryi var. *hendryi* Gardn.										1.1	2.2
Cylindrocarpus rugosus Okam.										<0.1	
Centroceras clavulatum (C. Ag.) Mont.										0.1	
Gelidium coulteri Harv.											2.3
Polysiphonia sp.											0.5
Total algal cover	51.2	90.6	103.5	93.7	115.8	115.1	208.4	192.4	169.2	137.0	254.1

creasing cover of the crustose *Ralfsia* sp. which occupied 84.0% of the primary substrate 12 mo after denudation. *Ralfsia* sp., as reported here, probably represents the alternate life-history phase for *P. fascia* and *S. lomentaria* from southern California (Wynne 1969).

Subsequent to the first month, *Ulva californica* provided at least 1.0% cover and reached maximum abundance (23.2%) 15 mo after the initiation of the experiment. Plots in the unpolluted area were colonized by juvenile sporophytes of *Egregia menziesii* beginning during the third month (March) and these grew into large elongate thalli which by the tenth month provided an extensive overstory canopy (106.0%). Cover of *E. menziesii* was reduced by the twelfth month (December) to 54.0% due to mortality of individuals and fluctuated during the last 18.0 mo of the experiment. *Corallina officinalis* var. *chilensis*, a turf-forming articulated coralline dominant in the area (Table 4), did not appear in samples until 6.0 mo after clearance; its cover increased through the first 24.0 mo and reached a maximum of 50.8% (Table 3). Filamentous thalli of *Ceramium eatonianum*, *C. sinicola* and the foliose, *Rhodoglossum affine*, were abundant 12 mo following clearance but their cover fluctuated during the remainder of the study. *Sargassum agardhianum*, *Gigartina canaliculata* and *Pterocladia capillacea* grew abundantly (Table 4) as coralline turf epiphytes and as saxicolous thalli on the unpolluted region of the shoreline and were dominant components of the experimental samples there prior to sterilization. Little recovery of these species was apparent after 12.0 mo; however, after 30.0 mo, cover of *G. canaliculata* increased to 25.7%, as did *S. agardhianum* (11.8%) and *P. capillacea* (5.6%).

Similarity comparisons (Bray and Curtis 1957) between the experimental and control plots for the

TABLE 4. *Mean algal cover (%) for control plots of unpolluted area.*

Taxa	Cover (%)
Gigartina canaliculata Harv.	45.4
Corallina officinalis var. *chilensis* (Dec.) Kütz.	36.0
Pterocladia capillacea (Gmel.) Born. & Thur.	19.5
Sargassum agardhianum J. Ag.	16.9
Halidrys dioica Gardn.	16.3
Egregia menziesii (Turn.) Aresch.	14.7
Corallina vancouveriensis Yendo	6.1
Lithophyllum proboscideum (Fosl.) Fosl.	3.6
Gelidium purpurascens Gardn.	2.4
Laurencia pacifica Kyl.	1.7
Hydrolithon decipiens (Fosl.) Adey	0.8
Lithothrix aspergillum Gray	0.8
Gelidium coulteri Harv.	0.6
Gelidium pusillum (Stackh.) LeJol.	0.6
Bluegreen algae	0.5
Colpomenia sinuosa (Roth) Derb. & Sol.	0.5
Rhodoglossum affine (Harv.) Kyl.	0.5
Cryptopleura corallinara (Nott) Gardn.	0.4
Ceramium eatonianum (Farl.) DeToni and *C. sinicola* S. & G.	0.1
Gigartina spinosa (Kütz.) Harv.	0.1
Haliptylon gracile (Lamour.) Johans.	0.1
Phyllospadix torreyi Wats.	0.1
Pterosiphonia dendroidea (Mont.) Falk.	0.1
Ulva californica Wille	0.1
Anisocladella pacifica Kyl.	<0.1
Bossiella orbigniana subsp. *dichotoma* (Manza) Johans.	<0.1
Ceramium spp.	<0.1
Cladophora spp.	<0.1
Codium fragile (Sur.) Har.	<0.1
Cylindrocarpus rugosus Okam.	<0.1
Dictyota flabellata (Coll.) S. & G.	<0.1
Eisenia arborea Aresch.	<0.1
Gastroclonium coulteri (Harv.) Kyl.	<0.1
Jania tenella (Kütz) Grun.	<0.1
Laurencia sinicola S. & G.	<0.1
Laurencia spectabilis Post. & Rupr.	<0.1
Nienburgia andersoniana (J. Ag.) Kyl.	<0.1
Peyssonneliaceae/Hildenbrandiaceae	<0.1
Pseudolithoderma nigra Hollenb.	<0.1
Rhodymenia californica var. *californica* Kyl.	<0.1
Schizymenia pacifica (Kyl.) Kyl.	<0.1
Tiffaniella snyderae (Farl.) Abb.	<0.1

TABLE 5. *Diversity of unpolluted area based upon cover (%): values for the control quadrats are averages for 0.0 through 30.0 mo assessments.*

Months	No. taxa	H'_e	J'_e
Experimental quadrats			
0.8	4	0.87	0.63
1.3	6	1.30	0.73
3.0	7	0.74	0.38
4.0	7	1.54	0.79
5.0	10	1.54	0.67
6.0	16	1.70	0.61
10.0	20	1.06	0.36
12.0	21	1.64	0.54
15.0	32	2.20	0.63
24.0	25	2.30	0.71
30.0	23	2.35	0.75
Control quadrats ($\bar{x}$)	18	1.83	0.64

unpolluted habitat revealed a pattern of increasing recovery during the study (Fig. 2). Similarity of the sterilized plots to the control quadrats increased almost linearly from values <6.0% during the first 6.0 mo of the experiment to 46.5% by 30.0 mo. Seasonal similarity comparisons of the control plots alone averaged 68.4% during the study indicating that even after 30.0 mo, the sterilized experimental quadrats had failed to fully recover.

In comparing the experimental quadrats with those of the controls after 1 yr, it became apparent that greater cover of crustose (*Ralfsia* sp.) and early successional algae (*Ulva californica, Ceramium eatonianum, C. sinicola, Cladophora* spp.) were prevalent in the former whereas articulated coralline algae (*Corallina officinalis* var. *chilensis, C. vancouveriensis*) and foliose red algae (*Gigartina canaliculata, Pterocladia capillacea*) were generally more abundant in the latter (Table 4). After 30.0 mo an increase in the cover of the seaweeds that typically dominate this region of the shoreline—*C. officinalis* var. *chilensis, G. canaliculata, P. capillacea, Sargassum agardhianum*—occurred producing closer similarity (46.9%) between the unpolluted experimental and control plots (Tables 3, 4; Fig. 2).

Species diversity also increased during the study. A total of four taxa were sampled in the unpolluted area 0.8 mo after initiation of the experiments with a progressive increase to 32 taxa after 15.0 mo (Table 5). Slight declines in the number of taxa were noted 24.0 mo (25) and 30.0 mo (23) following sterilization. On the other hand, the nearby control plots averaged 18 taxa for the study. Diversity, as measured by H'_e, generally increased with time (from 0.87 after ca. 1.0 mo, to a maximum of 2.35 thirty mo after plot clearance) and reached parity with the average value (1.83) for the control plots after only 6.0 mo. The exceptions to this trend of increasing diversity (Table 5) occurred during the cover maxima of *Scytosiphon lomentaria* (3.0 mo) and *Egregia menziesii* (10.0 mo) and reflected the large percentage of space occupied by these species. Evenness showed a similar depression (Table 5) at 3.0 mo and 10.0 mo and ranged from a maximum of 0.79 to a minimum of 0.36.

DISCUSSION

Bluegreen algae, filamentous Ectocarpaceae and colonial diatoms, all of which have previously been reported to commonly occur in aquatic environments under sewage stress (Borowitzka 1972, Golubic 1970, Munda 1974, Murray and Littler 1974, Littler and Murray 1975), were abundant components of the early successional stages for both the sewage-perturbated and undisturbed areas (Tables 1, 3). *Ulva californica,* which provided considerable cover in the sewage-affected region of Wilson Cove, was also an abundant component of early stages of colonization in the outfall area. However, despite the fact that *U. californica* was among the earliest organisms to appear on the moveable rocks employed in a preliminary experiment (Littler and Murray 1975) for the identical outfall and undisturbed areas, abundant growths did not occur on the unpolluted successional surfaces until 15 mo after clearance. This was not expected in view of the preliminary experiment and our extensive field observations of naturally disturbed substrata on the unpolluted shoreline where abundant patches of *U. californica* frequently could be found. We hypothesize that the failure of *U. californica* to provide greater cover during the first few months of the experiment, may have been due in part to its exclusion by the thick, extensive growths of *Scytosiphon lomentaria, Petalonia fascia* and *Colpomenia sinuosa. Ulva* spp., along with the closely related *Enteromorpha* spp., have commonly been reported to be among the first colonizers of cleared rocky intertidal surfaces (e.g., Bokenham and Stephenson 1938, Northcraft 1948, Fahey 1953, Emerson and Zedler 1978). Our results for bluegreen algae, Ectocarpaceae and colonial diatoms support the hypothesis that the predominant algal constituents of the upper shoreline in the sewage-impacted area are early successional organisms also encountered on recently disturbed substrata in nearby unpolluted Wilson Cove and other Southern California intertidal communities (Wilson 1925, Emerson and Zedler 1978). Further, the previously discussed literature as well as our own field observations on unstable sections of the unpolluted Wilson Cove shoreline and preliminary experiments for the same habitat (Littler and Murray 1975) makes tenable a similar position for *U. californica,* despite the failure of the present experiment to fully support this viewpoint.

The outfall study plots showed rapid recovery following the experimental disturbance. Because all experimental surfaces were thoroughly sterilized and had little or no encroachment from established surrounding organisms, the quick recovery of bluegreen algae, *Ulva californica, Gelidium pusillum, Pseudolithoderma nigra,* Ectocarpaceae and colonial diatoms must have resulted from vegetative, sexual or asexual reproduction mediated through suspended cells. These algae clearly have the capacity for rapid recruitment even under the influence of sewage effluent. The short recovery times shown by the algae dominating the disturbed shoreline support our earlier interpretation of standing stock data (Littler and Murray 1975) that patches of these species appear to show considerable mortality due to exposure to sewage toxicants, yet maintain relatively constant populations due to their potential for rapid recruitment. Further, we suggest that the abundances of bluegreen algae (Golubic 1970, Munda 1974), diatoms (Golubic 1970, Borowitzka 1972), filamentous Ectocarpaceae (Munda 1974), and *Ulva* and *Enteromorpha* (Cotton 1911, Burrows 1971, Borowitzka 1972, Munda 1974) in other sewage-impacted epilithic systems probably represent resilient subclimax associations characterized by the potential for rapid recovery after periodic stressful disturbances.

The algal communities that developed on the experimental plots in the unpolluted area had not fully recovered after 30.0 mo. This was to be expected because recovery times for mature rocky intertidal communities are typically greater than 2 yr (e.g., Guiler 1954, Dayton 1971). The commonly reported trends (Odum 1969) of increasing diversity and spatial heterogeneity with time were also apparent for the unpolluted area successional plots, although diversity patterns quickly reached parity with, and exceeded those of the unaltered controls. This trend was slightly modified at 3.0 mo by the abundant growths of large thalli of *Scytosiphon lomentaria* that occurred in all of the unpolluted-area quadrats. *S. lomentaria* and its typical associate *Petalonia fascia* colonized experimental substrates in quantities vastly greater than their abundances in surrounding undisturbed communities. Comparable findings were reported by Wilson (1925) who described colonial diatoms, *Ectocarpus, Scytosiphon* and *Endarachne* (as *Euderachne* but probably *Petalonia fascia*) as dominant components of his pre-kelp successional group which colonized submerged wooden blocks as well as cleared intertidal rock surfaces at La Jolla, California. Also, Emerson and Zedler (1978) reported *S. lomentaria* during all seasons and *Colpomenia sinuosa, Ectocarpus parvus* and *Ceramium eatonianum* during certain seasons to be favored by disturbance in their recolonization studies performed near San Diego, California. During the present study, the abundant growths of *S. lomentaria, P. fascia* and *C. sinuosa* grew quickly and presumably to reproductive maturity, then disappeared leaving a community comprised of low-growing algal crusts in addition to juvenile thalli of longer-lived algal forms.

Juvenile *Egregia menziesii* sporophytes recruited and dominated the unpolluted-area successional plots during the spring and early summer and large thalli which provided considerable overstory were evident by fall (10.0 mo after denudation) of the first year. These findings suggest fast growth similar to reports by Northcraft (1948), Widdowson (1972) and Black (1974) where extremely rapid monthly growth rates of *E. menziesii,* e.g., 78 cm in length per axis (Widdowson 1972), were recorded during the spring and summer. Young *E. menziesii* sporophytes also were frequently observed to colonize naturally disturbed substrata among surrounding communities at Wilson Cove. These observations combined with our successional results indicate that although *E. menziesii* is generally thought to be a structurally-complex dominant of mature intertidal algal communities (Littler and Murray 1975), young sporophytes are able to recruit effectively during the early stages of community development.

In conclusion, our results support the theoretical successional model developed by Connell (1975). This model predicts that patches vacated within rel-