CHAPTER SIX

PATTERNS OF DEVELOPMENT OF INTERTIDAL MACRO-EPIBIOTA

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INTRODUCTION

The majority of studies of sewage effects on biological communities have concentrated on descriptive assessments of the component populations or have involved laboratory analyses of physiological responses of individual organisms. The latter approach, while providing a wealth of information on the physiological ecology of marine organisms under sewage stress, has often failed to yield the knowledge necessary to interpret changes in communities because of the failure to simulate natural conditions or because of an insufficient understanding of the functional roles of the organisms under study. Descriptive studies have seldom provided the quantitative data base required to define the relative abundances of species populations which therein leads to the development of predictive hypotheses designed to determine the causal factors important to community function. Most frequently, descriptive assessments have been limited in value by the inability to sample comparable unpolluted habitats. Yet, as discussed by Connell (1976), an accurate and comprehensive descriptive data base is prerequisite to the successful design of carefully controlled experiments to test hypotheses concerned with the role of organisms in community structure and function.

Connell (1972, 1974, 1975) and others have repeatedly stressed the value of field experiments in marine ecology. Dayton (1973a) has described the rocky intertidal as representing a relatively workable and understandable system. Experimental work performed in this habitat has recently provided important conceptual advances in ecological theory, particularly in elucidating the functional roles of rare, disproportionately important species in the structuring of communities (e.g., Paine, 1966, 1971, 1974; Dayton, 1971, 1973a, 1973b, 1975). As pointed out by Connell (1974), however, few marine biologists appear to test their hypotheses by true field experimentation, i.e., carefully designed experiments utilizing appropriate controls.

The rocky intertidal near the Wilson Cove sewage outfall has been described previously (see Chapter One). For the past five years we have sampled the rocky intertidal biota to determine the seasonal and annual dynamics in the distribution, abundance, and structure of the biological components of a sewage-polluted and a nearby unpolluted (control) community (see Chapter Two). This detailed descriptive data bank represents the background essential for the design of field and laboratory experiments (e.g., see Chapter Seven) to test hypotheses concerned with the organization and function of sewage-polluted marine communities. The present contribution represents an extension of earlier work (Murray and Littler, 1974, 1976; Littler and Murray, 1975) and was designed to determine the following:

- Do communities characteristic of sewage-stressed habitats show high resiliency by their ability to recover quickly after major perturbations?
- Is a primary effect of sewage stress to favor early successional populations?

A primary objective of this study was to test the hypothesis developed earlier (see Chapter Two) that the upper to mid-intertidal region of the sewage-affected area, which represents a fluctuating environment directly exposed to deleterious components of discharged sewage (e.g., pine oil disinfectant), is dominated by disclimax communities.

Murray,S.N. & Littler,M.M. (1977). Patterns of development of intertidal macro-epibiota.
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METHODS AND MATERIALS

Earlier experimental work on community development and recovery was performed in 1972 (Littler and Murray, 1975) in an attempt to document the successional patterns prevalent in the outfall versus unpolluted areas. During this preliminary work, 16 uniformly weathered rocks (30 to 40 centimeters diameter) were sterilized by burning with 95% ethanol and were placed in the outfall and unpolluted regions, whereupon the successional patterns were followed. These studies, although yielding the qualitative findings reported previously (Littler and Murray, 1975), were terminated because of the movement and loss of samples during storms and the difficulties inherent in the quantification of biota colonizing the vertical edges of experimental substrates. The present design has overcome these deficiencies by utilizing relatively flat and highly stable portions of the rocky intertidal as experimental substrates.

Four contiguous 0.15 square meter plots arranged as a 0.6 meter by 1.0 meter rectangle were established in December 1974 on comparable surfaces in both the sewage-affected and unpolluted areas at tidal heights between +0.5 and +1.5 feet. Plots were marked with bolts embedded in the substrate and the contents were photographed. Subsequently, all of the macro-epibiota were manually removed and the bared rock surfaces were scraped with wire brushes and knives to remove encrusting basal portions of algal thalli and calcareous animals. The rock surfaces were then burned for up to 1.0 hour with portable propane torches; sponges soaked in 70% ethanol were used to scrub the substrate and intensify the burning. After sterilization, plots were photographed with infra-red film which reveals living plant material by recording chlorophyll fluorescence. These photographs provided a means to determine the effectiveness of the sterilization treatment; their examination revealed all plots to be thoroughly sterilized.

For the sewage-affected area, quadrats were monitored during 1975 on 8 January, 24 January, and 26 March. Assessments in the outfall habitat were terminated after the 26 March visit because of the inability to visually detect experimental surfaces from surrounding natural communities (i.e., complete recovery had likely occurred). For the unpolluted shoreline, assessments were continued during April, May, June, October, and December 1975, and remain on-going because of the failure of plots to blend in with the surrounding natural biota one year after clearance.

The photographimetric method described previously (Murray and Littler, 1974; Littler and Murray, 1975) for standing crop assessments (see Chapter Two) was employed to provide estimates of the abundance of colonizing organisms. During each visitation, photographs (color and infra-red) and detailed field notes were taken for each quadrat. Field notes contained a listing of species present in each plot plus estimates of their abundance, and were used in conjunction with the photographs to generate the quantitative data employed in the analyses.

Forty four successional samples were analyzed during this study, including three assessments of the foursome established in the sewage-affected area and eight assessments for the unpolluted set. Data were presented as percent cover and calculated for each species as the mean of the four replicated samples taken during each monitoring period. Three methods were employed to measure changes in diversity patterns: simple counts of taxa were used to indicate richness, while the Shannon (Shannon and Weaver, 1949) index (H_e') and Pielou's (1969) evenness index (J_e') were utilized to construct diversity patterns emphasizing the apportionment of cover among the taxa.

As stressed repeatedly by Connell (1974, 1975), careful consideration must be given during field experimentation to establishing a proper set of controls. Since one of the experimental goals was to determine when the successional plots for both the outfall and unpolluted areas had come into equilibrium with the surrounding natural communities, it was necessary to designate a set of control plots. It was previously determined (see Chapter Two) that biotic changes in the outfall area were minimal over time, and careful visual observation did not reveal differences in outfall communities during the 4.0 months of experimentation (December 1974 to March 1975). Consequently, the contents of the plots at the time of harvesting were used for comparison with subsequent patterns of development for the sewage-affected plots. However, in the unpolluted area, four control plots were chosen from the standing stock transect lines (see Chapter Two) to represent the biotic contents of neighboring natural communities. Plots were selected on the basis of their visual and quantitative similarity with the experimental surfaces at the time of clearance. This procedure has the deficiency that the four control plots are not contiguous, as is the case with the experimental quadrats, but presents the advantage that comparisons are with undisturbed communities that have experienced the identical environmental conditions over the year as experimental samples. The Bray-Curtis (1957) index ($C = 2^w/a+b$) was employed to measure the similarity (percent) between samples, where a is the sum of the measures of abundance in one data set and b is the similar sum for the second; w is the lesser value for only those species which are in common between the two stands.

RESULTS

Patterns of Species Colonization

OUTFALL AREA

Overall biotic cover was 100.0% prior to the sterilization of plots in the outfall area, indicating biota with little stratification (Table 6-1); this consisted mostly of blue-green algae, *Ulva californica,* and *Pseudolithoderma nigra.* Within one month after sterilization, overall cover had reached 100.1% (Table 6-1) and the cover of blue-green algae (49.7% vs. 45.0%) and *Ulva californica* (42.7% vs. 44.9%) was virtually identical to that determined prior to the experimental perturbation (Table 6-2). *Pseudolithoderma nigra* and *Gelidium pusillum* showed slower recovery patterns, although both species gave indications of approaching predisturbance conditions within three months. As indicated for the standing crop study (see Chapter Two), epiphytic growths of Ectocarpaceae/colonial diatoms appeared sporadically in the outfall area during the successional study. These reached a cover maximum of 21.3% in late January (1.3 months) and substantially influenced parameters used to measure community features during this assessment period.

UNPOLLUTED AREA

Successional plots for the unpolluted area did not provide the biotic cover exceeding 100% characteristic for this region of the shoreline until three months after the initiation of the study (Table 6-1). Samples were dominated in the early stages by Ectocarpaceae/colonial diatoms and blue-green algae (Table 6-3), with the brown algae *Petalonia fascia, Colpomenia sinuosa,* and *Scytosiphon lomentaria* providing the majority of biotic cover from 1.3 to 5.0 months. Growths of *P. fascia* and *S. lomentaria* were accompanied by increasing cover of the crustose brown alga *Ralfsia* (?) which occupied 84.0% of the primary substrate one year after the initial disturbance. *Ralfsia* (?), as reported here, likely represents the alternate crustose stage described for the life histories of *Petalonia fascia* and *Scytosiphon lomentaria* populations from southern California by Wynne (1969). *Ulva californica* provided noticeable cover throughout the period of study, with exception of the first month, and reached maximum cover four months after the initiation of the experiment. Plots were colonized by juvenile sporophytes of *Egregia menziesii* beginning in March (three months), and these grew into large elongate thalli which by October (ten months) provided a complete overstory canopy (106.0%) for the experimental plots. Cover of *E. menziesii* was reduced by December 1975 (12 months) to 54.0%, at which time increased cover of *Corallina officinalis* var. *chilensis,* the original dominant of the area, became evident. Filamentous thalli of *Ceramium eatonianum* and *Rhodoglossum affine,* a foliose red alga, were also abundant during December 1975, along with *Ralfsia* (?) crusts beneath the *E. menziesii* canopy.

TABLE 6-1

PATTERNS OF OVERALL BIOTIC COVER (IN PERCENT) FOR EXPERIMENTAL OUTFALL AND UNPOLLUTED AREA CLEARANCE PLOTS

		Cover
OUTFALL AREA	Before Clearance	100.0
	After Clearance	
	0.8 months	100.1
	1.3 months	125.7
	3.0 months	100.2
UNPOLLUTED AREA	After Clearance	
	0.8 months	51.2
	1.3 months	90.6
	3.0 months	103.5
	4.0 months	93.7
	5.0 months	117.2
	6.0 months	115.1
	10.0 months	208.7
	12.0 months	192.8
CONTROL PLOTS	12.0 months	148.4

TABLE 6-2

PATTERNS OF DEVELOPMENT OF BIOTA COLONIZING CLEARED PLOTS IN THE OUTFALL AREA

Data represent mean cover (in percent) for four replicate $0.15\ m^2$ quadrats initiated in December 1974.

	COVER			
	Before	Months After Clearance		
TAXA	Clearance	0.8	1.3	3
Blue-green algae	45.0	49.9	47.0	53.0
Ulva californica	44.9	42.7	52.9	38.8
Pseudolithoderma nigra	8.8	3.0	4.0	8.2
Gelidium pusillum	0.8		0.4	0.1
Ectocarpaceae/colonial diatoms	0.5	4.5	21.3	0.1
Petalonia fascia			0.1	

TABLE 6-3

PATTERNS OF DEVELOPMENT OF BIOTA COLONIZING CLEARED PLOTS IN UNPOLLUTED AREA

Data represent mean cover (in percent) for four replicate 0.15 m² quadrats initiated in December 1974

Taxa	Cover							
	Months After Clearance							
	0.8	1.3	3	4	5	6	10	12
MACROPHYTES								
Ectocarpaceae/colonial diatoms	31.5	37.8			1.0	1.3		0.1
Blue-green algae	16.3	<0.1	<0.1	12.4	0.1	3.8	3.0	0.1
Pseudolithoderma nigra	2.9							
Ralfsia sp.	0.5		0.6	10.8	20.4	51.3	85.0	84.0
Petalonia fascia		23.5	9.2	0.2				0.1
Colpomenia sinuosa		22.5	9.4	11.6	43.8	12.8	0.1	1.0
Scytosiphon lomentaria		5.1	82.3	43.8	31.2	1.6		
Ulva californica		1.6	1.0	8.5	6.1	6.7	1.5	7.0
Egregia menziesii			0.9	6.4	11.0	25.5	106.0	54.0
Gigartina canaliculata					2.0	4.3	0.1	1.5
Sargassum agardhianum					1.9			
Chaetomorpha linum					0.1	0.1	0.1	1.0
Pterocladia capillacea					0.1	0.1	0.1	0.1
Ceramium eatonianum						5.6	0.1	8.0
Peyssonneliaceae/Hildenbrandiaceae						1.2	0.1	0.1
Corallina officinalis var. *chilensis*						0.4	4.0	10.0
Lithothrix aspergillum						0.2	0.1	0.1
Cladophora sp.						<0.1		2.0
Enteromorpha sp.						<0.1		
Rhodoglossum affine							7.5	19.0
Corallina vancouveriensis							0.1	
Cryptopleura crispa							0.1	
Dictyota flabellata							0.1	0.1
Halidrys dioica							0.1	1.0
Laurencia pacifica							0.1	3.0
Laurencia spectabilis							0.1	0.1
Pterosiphonia dendroidea							0.1	0.1
MACRO-INVERTEBRATES								
Acmaea (Collisella) conus							0.1	
Acmaea (Collisella) scabra							0.1	0.1
Acmaea (Collisella) strigatella							0.1	0.1
Fissurella volcano								0.1
Nuttalina fluxa								0.1

OUTFALL AREA

A total of five taxa were present in the outfall plots prior to the initiation of the experiment (Table 6-4), and within one month four of these had recolonized the cleared substrate; these were joined by two additional taxa by the end of the experiment. Diversity, as measured by H_e', was 1.00 before clearance and 0.96 within only one month after clearance. A similar trend was exhibited for the evenness measure J_e' (0.62 vs. 0.69). The Bray-Curtis index of similarity was calculated at 95.7% in comparing predisturbance samples with those 0.8 month after sterilization, indicating a rapid rate of recovery. Assessments performed during late January (1.3 months) showed higher H_e' diversity and less similarity (C = 84.0%) with predisturbance data than at any other time due to the increased Ectocarpaceae/colonial diatom cover recorded for that period.

TABLE 6-4

PATTERNS OF SPECIES DIVERSITY FOR EXPERIMENTAL OUTFALL AND UNPOLLUTED AREA CLEARANCE PLOTS BASED UPON PERCENT COVER ABUNDANCE DATA

		No. Species	H'e	J'e
OUTFALL AREA	Before Clearance	5	1.00	0.62
	After Clearance			
	0.8 months	4	0.96	0.69
	1.3 months	6	1.17	0.65
	3.0 months	5	0.92	0.57
UNPOLLUTED AREA	After Clearance			
	0.8 months	4	0.87	0.63
	1.3 months	6	1.30	0.73
	3.0 months	7	0.74	0.38
	4.0 months	7	1.54	0.79
	5.0 months	11	1.58	0.66
	6.0 months	16	1.70	0.61
	10.0 months	20	1.06	0.36
	12.0 months	21	1.64	0.54
CONTROL PLOTS	12.0 months	23	1.89	0.60

UNPOLLUTED AREA

A total of four taxa were sampled in the unpolluted area plots 0.8 month after initiation of the experiments, with a progressive increase to 21 taxa one year later (Table 6-4). This compared to a total of 23 taxa recorded for the control plots for the unpolluted habitat for December 1975 (Tables 6-4 and 6-5). Diversity, as measured by H_e', generally increased with time from 0.87 at approximately 1.0 month to 1.64 months, twelve months after plot clearance. The exceptions to this trend occurred during the periods of maximal *Scytosiphon lomentaria* (three months) and *Egregia menziesii* (ten months) cover and reflected the dominance of these species. Evenness showed similar depression at the three month and ten month periods and ranged from 0.79 (four months) to 0.36 (ten months). H_e' diversity (1.64 vs. 1.89) and evenness (0.54 vs. 0.60) were less for experimental quadrats than for control plots at the

TABLE 6-5

MACROPHYTE AND MACRO-INVERTEBRATE COVER (IN PERCENT) FOR CONTROL PLOTS FOR CLEARANCE EXPERIMENT PERFORMED IN UNPOLLUTED AREA

Data represent mean values for four 0.15 m² plots for December 1975

	Cover
MACROPHYTES	
Gigartina canaliculata	60.5
Egregia menziesii	17.1
Corallina officinalis var. *chilensis*	15.8
Corallina vancouveriensis	13.1
Pterocladia capillacea	12.5
Halidrys dioica	11.5
Sargassum agardhianum	9.1
Lithophyllum proboscideum	6.4
Bossiella orbigniana ssp. *dichotoma*	0.1
Gelidium purpurascens	0.1
Colpomenia sinuosa	<0.1
Dictyota flabellata	<0.1
Gelidium coulteri	<0.1
Gelidium pusillum	<0.1
Laurencia pacifica	<0.1
Lithothrix aspergillum	<0.1
Pseudolithoderma nigra	<0.1
Rhodoglossum affine	<0.1
Ulva californica	<0.1
MACRO-INVERTEBRATES	
Serpulorbis squamigerus	0.8
Spirobranchus spinosus	0.3
Orange sponge	0.1
Phragmatopoma californica	<0.1
COMBINED MACROPHYTES AND MACRO-INVERTEBRATES	148.4

end of one year. The Bray-Curtis index of similarity was measured at 30.3% between the one-year-old experimental quadrats and the controls, indicating that recovery had not yet occurred. In comparing the biotic contents of the one-year-old experimental quadrats (Table 6-3) with those of the controls (Table 6-5), it became apparent that greater cover of crustose [*Ralfsia* (?)] and early successional algae (*Ulva californica, Ceramium eatonianum, Cladophora* sp.) were prevalent in the former, while articulated coralline algae (*Corallina officinalis* var. *chilensis, C. vancouveriensis*) and foliose red algae (*Gigartina canaliculata, Pterocladia capillacea*) were generally more abundant in the latter.

Although numerous studies of successional events in marine rocky intertidal communities have been performed, these have rarely been designed to generate quantitative data or to test hypotheses concerned with the parameters and events structuring biological communities. The manipulative approach, so successfully employed, for example, by Dayton (1971, 1973a, 1973b, 1975), represents an exception to this pattern where the functional components of communities have been studied by performing realistic perturbations and monitoring subsequent successional events. These studies have mostly involved the removal or addition of hypothetically functionally important species and have not included studies of succession from fully bared primary substrate.

Research on the patterns of development exhibited by natural epibiotic communities under the influence of sewage has been neglected to date. Yet, a complete understanding of the existent ecological communities of a rocky intertidal habitat must include a consideration of the patterns and stages of community development. We view this study as an attempt to experimentally verify interpretations of community structure for the Wilson Cove outfall area derived from extensive quantitative standing stock data (Murray and Littler, 1974; Littler and Murray, 1975; Chapter Two). These included the hypothesis that the dominant organisms of the upper and mid-intertidal of the sewage-impacted area consisted largely of early successional or "opportunistic" species with high capacities for growth and reproduction. Theoretically, the abundances of these organisms result in a disclimax community for the upper shoreline near the outfall which is characterized by a physically fluctuating environment due to the variable discharge of nutrient rich, but sporadically toxic, effluent (Littler and Murray, 1975).

Blue-green algae, filamentous Ectocarpaceae, and colonial diatoms, all of which have previously been reported to commonly occur in aquatic environments under sewage stress (see Chapter Two), were abundant components of the early successional stages described for both the outfall and unpolluted (control) areas. *Ulva californica,* a species occurring abundantly in the sewage-impacted intertidal at Wilson Cove, was also an abundant component of the early stages of colonization in the outfall area. Despite the fact that *U. californica* was among the earliest organisms to appear on the moveable rocks employed in preliminary experimentation (Littler and Murray, 1975) for both the outfall and control areas, abundant growths of *U. californica* did not occur on the freshly-bared unpolluted surfaces monitored during this study. The failure of *U. californica* to provide more than 8.5% cover on control area surfaces during the study period was not expected in light of the aforementioned preliminary experimental results and field observations of naturally disturbed substrate in the intertidal of the unpolluted shoreline, where extensive growths of *U. californica* could frequently be found. We hypothesize that this may in part have been due to the thick, extensive growths of *Scytosiphon lomentaria, Petalonia fascia,* and *Colpomenia sinuosa* recorded during the first four months of experimentation, which may have resulted in the partial exclusion of *U. californica* during this period. *Ulva* spp., along with the closely related *Enteromorpha* spp., have commonly been reported (e.g., Bokenham, 1938; Northcraft, 1948; Fahey, 1953) to be among the first colonizers of cleared rocky intertidal surfaces where successional work has been performed. We interpret our results for blue-green algae, Ectocarpaceae, and colonial diatoms to support the hypothesis that these abundant constituents of the upper shoreline in the sewage-impacted area are early successional organisms characteristic also of unpolluted Wilson Cove intertidal communities. Further, a consideration of the literature as well as our own *in situ* personal observations on disturbed sections of the Wilson Cove shoreline, and preliminary experiments for the same habitat (Littler and Murray, 1975), makes tenable a similar position for *Ulva californica* despite the failure of our experimental results to fully support this viewpoint.

The outfall area showed rapid recovery following the experimental disturbance. Since surfaces were thoroughly sterilized and we observed little or no encroachment from established surrounding organisms, recovery of blue-green 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 organisms clearly have the capability for rapid recruitment even under the influence of sewage effluent. The rapid recovery of the organisms dominating the outfall shoreline substantiates our earlier interpretation of standing stock data (see Chapter Two) that these species appear to show considerable mortality due to exposure to sewage toxicants, yet maintain a relatively constant standing stock due to their potential for rapid recruitment. Further, we suggest that the abundances of blue-green algae (Golubic, 1970; Munda, 1974), diatoms (Golubic, 1970; Borowitzka, 1972), filamentous Ectocarpaceae (Munda, 1974), *Ulva,* and *Enteromorpha* (Cotton, 1911; Burrows, 1971; Borowitzka, 1972; Munda, 1974) in other sewage-impacted epilithic systems probably represent resilient disclimax communities characterized by the potential for rapid recovery after stressful disturbance.

The biological communities that developed on the experimental plots in the unpolluted area clearly had not fully recovered after one year, as evidenced by comparisons of species abundance patterns between succession and control plots (Tables 6-3 and 6-5) and the Bray-Curtis (1957) index of similarity (30.3%). This was expected because recovery times for mature rocky intertidal communities are typically greater than two years (e.g., Guiler, 1954; Dayton, 1971). The commonly reported trends (see Odum, 1971) of increasing diversity and spatial heterogeneity with time were also apparent for the unpolluted area succession plots. This trend was slightly modified at three months by the abundant growths of large thalli of *Scytosiphon lomentaria* that occurred in all quadrats. *Scytosiphon lomentaria* and its typical associate, *Petalonia fascia,* colonized experimental substrates in numbers vastly greater than their abundance in surrounding undisturbed communities. Comparable findings were reported by Smith (1925) who described *Scytosiphon* and *Endarachne* (as *Eudarachne* 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. The abundant growths of *S. lomentaria, P. fascia,* and *Colpomenia sinuosa* grew quickly and, presumably, to reproductive maturity during our study, then disappeared, leaving a community characterized by low-growing algal crusts and juvenile thalli.

Recruitment of juvenile *Egregia menziesii* sporophytes dominated the control area succession plots during the spring and early summer, and large thalli, which provided considerable overstory, were evident by fall. These findings substantiate the earlier works of Northcraft (1948), Widdowson (1972), and Black (1975) where extremely rapid monthly growth rates [e.g., 78 centimeters in length per axis (Widdowson, 1974)] were reported during the spring and summer. Young *Egregia* sporophytes, during spring periods of recruitment (see Chapter Two), were frequently observed to colonize disturbed substrates among natural surrounding communities. These observations, combined with our succession results, indicate that, despite the fact that *E. menziesii* is generally thought of as a K-selected algal dominant of mature intertidal communities, young sporophytes are able to recruit during early successional stages in community development.

In conclusion, our interpretation of our experimental results agrees well with the predictive successional model described by Connell (1975). This model assumes that vacant patches created within relatively mature biotic communities are rapidly colonized by species with long breeding seasons and numerous motile spores or larvae. We would extend the characteristics of this species group, referred to by Connell (1972, 1975) as "opportunistic," to include algae with rapid growth rates, high productivity, and large surface to volume ratios. Additionally, previous successional research (e.g., Smith, 1925; Bokenham, 1938; Northcraft, 1948; Fahey, 1953) in the rocky intertidal has resulted in the classification of groups of early colonizers with attributes similar to those presented above. Further, Connell (1975) indicates that patterns of community development proceed along different routes under benign and harsh conditions, with the latter environments continually being colonized and vacated by opportunistic species. We have described the sewage-impacted Wilson Cove shoreline (Littler and Murray, 1975; Chapter Two) as a harsh environment due to the fluctuating inputs of sporadically toxic sewage; in contrast, the unpolluted area represents an environment exposed to considerably more benign physical conditions. The rate of recovery of the outfall community dominants on the bared experimental substrate and their characterization as early successional forms resultant from this research readily fits the Connell (1975) model for harsh environments. For the unpolluted area, more complex patterns of development were evident with greater community complexity achieved with time. This predictable trend for the less harsh unpolluted environment has been marked by large-scale variations in the abundance patterns of certain temporally dominant species [e.g., *Scytosiphon lomentaria, Egregia menziesii, Ralfsia* (?)]. We interpret these patterns as indirect evidence of the increased biological interactions suggested by Connell (1975) to characterize community development under intermediate and benign physical conditions.

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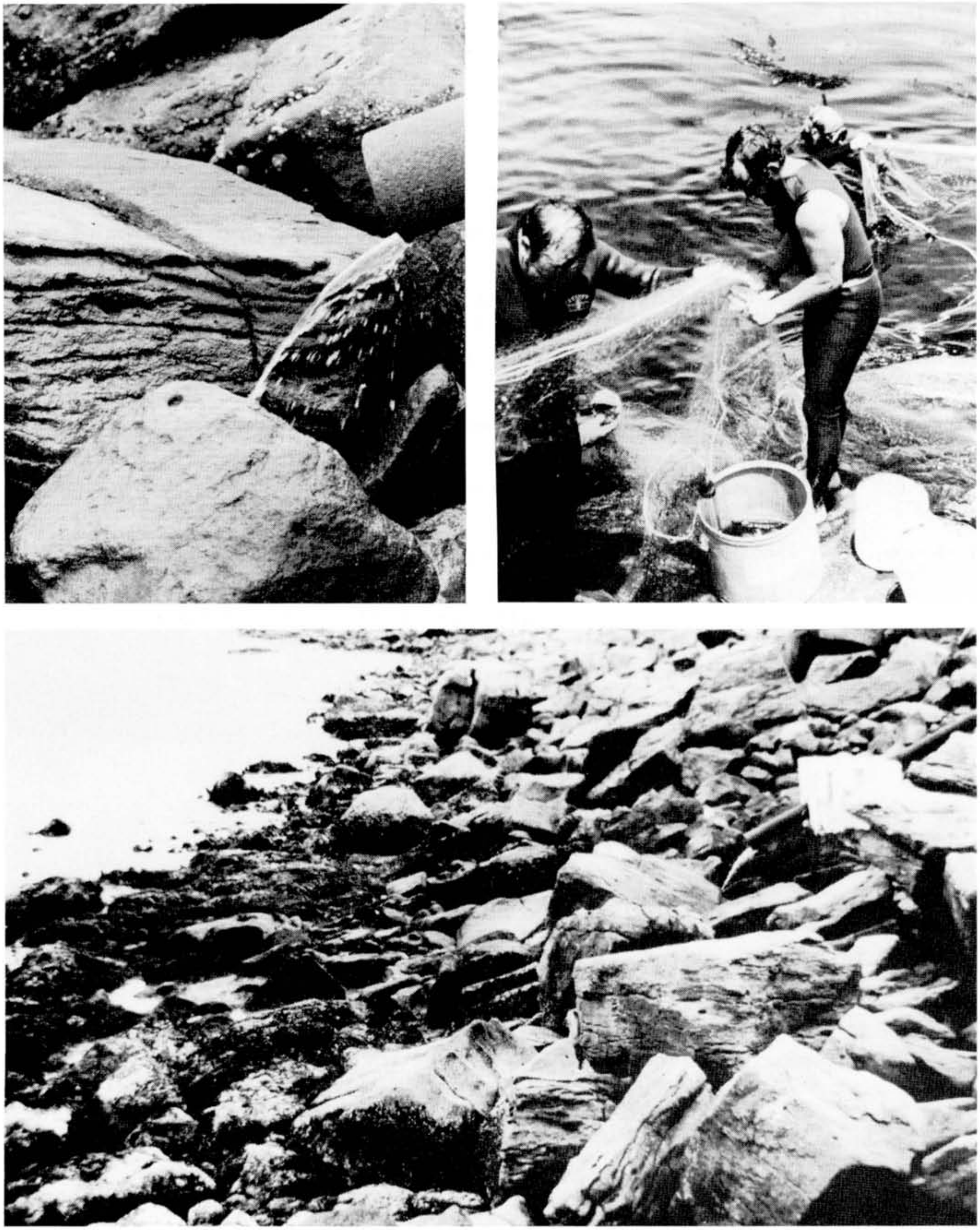

View of outfall terminus (upper left), collection of fish from outfall community at high tide by gill-netting (upper right), view of outfall community at low tide (lower).

INFLUENCE OF DOMESTIC WASTES ON THE STRUCTURE AND ENERGETICS OF INTERTIDAL COMMUNITIES NEAR WILSON COVE, SAN CLEMENTE ISLAND

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