Overview of the Rocky Intertidal Systems of Southern California

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INTRODUCTION

The Southern California Bight (Fig. 1) has been defined (SCCWRP 1973) as the open embayment of the Pacific Ocean bounded on the east by the North American coastline extending from Point Conception, California, to Cabo Colnett, Baja California, Mexico, and on the west by the California Current. The climate of the Southern California Bight has been amply studied in quantitative terms and is relatively well known (for physical, air, and seawater data, see Kimura 1974). Wind conditions are extremely important in that major reversals occur predominantly throughout late fall and winter.This results in strong, hot, and dry "Santa Ana" winds from the inland desert regions at the time of low tides during the daylight hours, thereby causing extreme heating, desiccation, and insolation stress to intertidal organisms. Another important ecological factor is the protection of certain mainland shores and the mainland sides of islands from open ocean swell and storm waves. This leads to a higher wave-energy regime on the unprotected outer island shores with marked effects on their biological communities. Nearly all of the southern California mainland coastline is protected to some degree by the outlying islands (Ricketts, Calvin, and Hedgpeth 1968). The only mainland sites receiving direct westerly swell are near the cities of Los Angeles and San Diego. A number of substrate types were present among the 10 rocky intertidal habitats studied (Fig. 1), ranging from hard, irregular flow breccia to smooth sandstone or siltstone. Some sites were heavily influenced by sand which inundates and removes organisms. The presence of extensive loose boulder fields at some habitats constitutes another form of environmental instability limiting community development. The existence of such natural disturbances has important implications in interpreting changes associated with petroleum exploration and development. Cockerell (1939) was among the first to point out that the region, especially near the Northern Channel Islands, is remarkable for the impingement and mixing of both cold and warm waters, and is thus comparable in certain respects to such diverse regions as the Galapagos Islands. For example, Santa Cruz Island is periodically exposed to both cold and warm currents, San Clemente Island lies in relatively warm southern waters, while the cold California Current impinges on San Nicolas Island throughout much of the year (Neushul, Clarke, and Brown 1967). These climatic, physical, and hydrographic variations result in a complex intermingling of environmental conditions that are reflected in the diversity of marine biota in the Bight.

The rocky intertidal shoreline of southern California's mainland is subjected to exceptionally intense usage by a concentrated, recreation-oriented human population; this creates some unique conservational problems. The often excessive usage (*e.g.*, collecting, beachcombing, tidepooling, field trip outings) may stress this interface between land, sea, and air, making it particularly sensitive to additional forms of disturbance.

Previous compilations of review data on the Southern California Bight included information on intertidal macrophytes (Murray 1974) and macroinvertebrates (Bright 1974). These reviews pointed out the remarkable paucity of information regarding the ecology of southern California's rocky seashores. Of the limited data base, the most widely used information was generated during the studies of Dawson (1959, 1965) on marine macrophytes. Dawson noted

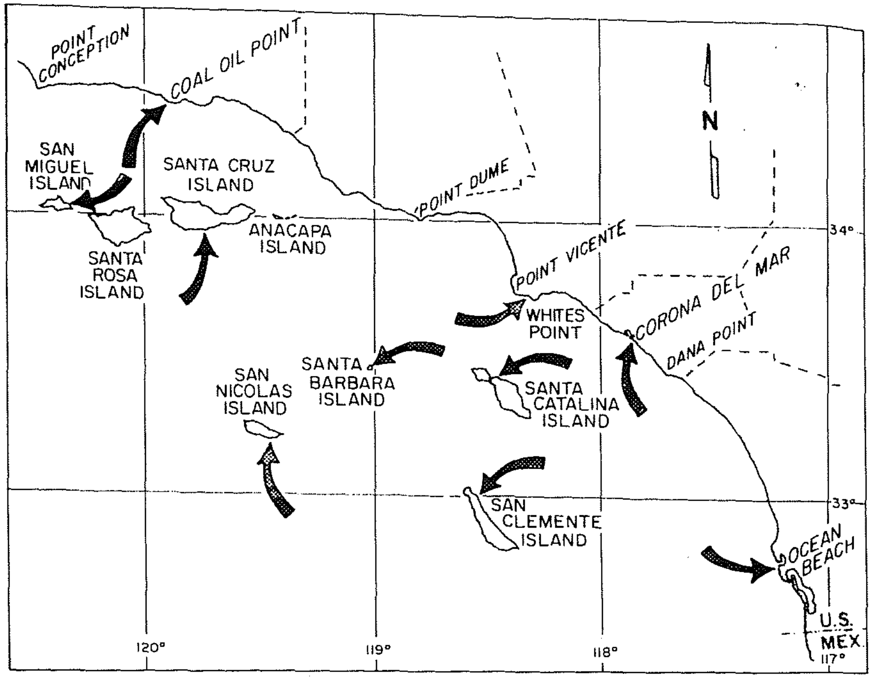

FIGURE 1. *Location of the 10 study areas (arrows) within the Southern California Bight.*

reductions in species numbers ranging from 50 to 70 per cent at sites near sewage outfalls. Others (*e.g.*, Nicholson and Cimberg 1971, Widdowson 1971, Thom 1976) have since measured further declines in macrophyte species numbers at some of the same sites studied by Dawson. They attributed such declines to human influence but presented only correlative evidence as documentation. Such declines do not seem to have been instantaneous, as pointed out by Nicholson (1972), but probably are the result of human pressures that have been increasing markedly since the turn of the century. With the further expansion of the human population in southern California, even the marine communities of some of the relatively inaccessible offshore Channel Islands (*e.g.*, Anacapa Island) are being altered by visitor trampling and collecting (Littler 1978).

The marine ecosystems of the Southern California Islands are virtually unknown to science. Although limited taxonomic lists have been published for Anacapa, Santa Catalina, Santa Cruz, and San Clemente Islands (Hewatt 1946, Dawson and Neushul 1966, Neushul, Clarke, and Brown 1967, Sims 1974, Seapy 1974, Dawson 1949, Nicholson and Cimberg 1971), quantitative data are available only for San Nicolas Island (Caplan and Boolootian 1967), Anacapa Island (Neushul, Clarke, and Brown 1967), and San Clemente Island (Littler and Murray 1974, 1975, 1978, Murray and Littler 1978, Kindig and Littler in press).

The cumulative effects of environmental degradation and a general lack of proper baseline information have posed severe problems, particularly during the last 10 years when attempts have been made to assess the immediate effects of specific pollutants on southern Californian coastal organisms. These problems were glaringly obvious (*e.g.*, Nicholson and Cimberg 1971,

Straughan 1971, Foster, Neushul, and Zingmark 1971, Cimberg, Mann, and Straughan 1973) in the attempts to evaluate effects of the Santa Barbara oil spills of 1969 on mainland intertidal populations. The research reported here was explicitly responsive to the specifications and requirements dictated by the Bureau of Land Management, U.S. Department of the Interior. The ongoing purpose of this program is to establish quantitatively reliable and reproducible baseline assessments of the distribution and abundance of rocky intertidal organisms. Both field and laboratory efforts were directed toward the determination of the kinds and levels of biological variation shown by six island and four mainland ecosystems. Within this framework, sites were selected to reflect the major ecological systems throughout the Bight.

This paper is the product of comprehensive investigations during 1975-76 into the following three aspects of study: (1) taxonomic and systematic studies of the macroepibiota, (2) determinations of the seasonal distribution and abundance patterns in macrophyte and macroinvertebrate standing stocks, and (3) temporal and spatial analysis of variation in community organization. No comparable spectrum of rocky intertidal systems has been examined with the level of sampling effort and resolution of data undertaken in this research program. The scope of this work is such that temporal and spatial variations of the macroinvertebrate and macrophyte populations have been assessed in terms of tidal location, cover, frequency, density, wet weight, dry weight, ash-free dry weight, species diversity, evenness, richness, and species assemblages. These descriptive parameters were used at each of 10 representative sites during four separate quarters of the year to characterize a range of intertidal systems and to relate important aspects of distribution and abundance to possible causal (biotic and abiotic) features of the environment.

This paper attempts to place in perspective the salient features within each study area, contrasts the 10 sites, and discusses overall patterns and trends. In the last regard, it is appreciated that habitats having markedly different substrates, environmental regimes, and levels of human stress would be expected to differ greatly; comparisons or interpretations without supportive experimental data must be viewed as preliminary.

The design of the study was such that trends and correlative insights might begin to be drawn through intensive seasonal studies of a few sites selected to be as representative as possible. Generalizations concerning the specific degree to which our study sites are characteristic of intertidal systems throughout the Bight are contingent upon a more synoptic approach to sampling. Such an approach has been taken during our 1977-78 program and it has become apparent that the 10 sites reported here are characteristic of the major intertidal systems. The mainland areas studied were exposed to relatively more human-induced stresses, but we felt that, with few exceptions, this is characteristic of the more prominent rocky mainland sites in general. A baseline has not yet been established, particularly due to the exceptionally warm and dry winter experienced during 1975-76; under wetter or colder winter conditions, we would expect different patterns of seasonality.

METHODS AND MATERIALS

The intertidal study of mainland and island rocky shores consisted of: (1) taxonomic and systematic studies of the macroepibiota, (2) determinations of the seasonal distribution and abundance patterns of macrophyte and macroinvertebrate standing stocks, and (3) temporal and spatial analyses of variation in community organization. We have also developed programs to predict the ecological effects of disturbances as well as experimental studies that include: (1) the responses of intertidal communities to natural catastrophic events (such as storms, high surf conditions, sedimentation, and floods), (2) recovery rates and patterns of various communities at different times of the year at contrasting tidal heights following artificial disturbances (harvesting), (3) manipulative assessments of the role of possible key species populations, and

(4) the synoptic surveying of all island intertidal communities during daytime low tides by means of helicopter overflights and mapping techniques. This last study gives us considerable confidence that our 10 sites are indeed representative of major intertidal systems within the Southern California Bight. Although we have extensively used all of these methods over the last several years, only those methods and the data resulting from the 1975-76 baseline analysis of standing stock will be presented in this paper because of space limitations.

Standing Stock Data

Much of our knowledge of benthic marine organisms is based upon subjective observations, although some studies have employed "quasiquantitative" methods. Among such methods used previously in the field are those in which diagrammatic sketches within sample units are made and subsequently used to obtain estimates of abundance (*e.g.*, Manton 1935, Abe 1937), those in which transect lines are used to visually estimate cover (*e.g.*, Nicholson and Cimberg 1971, Widdowson 1971), and those that utilize metal grids (*e.g.*, Caplan and Boolootian 1967) to assess visually the abundance of organisms. Such *in situ* assessments are usually time-consuming and often physically exhausting, thereby severely limiting the number of samples that can be taken within the field time available (*e.g.*, during the low-tide cycle). A significant problem with all of these visually based *in situ* techniques is that of parallax (due to movement of the observer and organisms relative to the sampling devices) which has been shown (Littler 1971) to be an unsatisfactorily large source of error when measuring the cover of organisms.

The principal method of assessing the standing stocks of intertidal organisms during this study was a photographimetric technique of undisturbed sampling (modified from Littler 1971) which yields parallax-free samples that can be used to generate precisely detailed and highly reproducible quantitative information, *i.e.*, cover, density (number of individual organisms per unit area), and frequency (percentage of sample plots in which a given species occurs). This method has the advantage of being rapid and simple to use, thus enabling a greater number of samples to be taken per unit of time. This technique, when used with infrared film, permits the quantification of blue-green algal cover, the predominant cover taxon in most rocky intertidal habitats. The system also permits a high degree of quality control because photo-samples scored by various individuals can be reviewed by the entire staff, including senior taxonomic personnel, to assure standardization and accuracy in the quantification process. The infrared photographs also emphasize unhealthy thalli (which have reduced chlorophyll contents that are often masked by accessory pigments) which would otherwise not be visible by color photography or to the unaided eye. Another important feature of the technique is that the photo-samples are permanent historic data sets which depict the status of the biota at a given point in time. Changes can easily be documented by direct comparison of photo-samples taken of the same quadrats at different times.

Quarterly sampling was accomplished at the 10 general areas shown in Figure 1. An overview of the tasks involved during each of the 40 site visits is elaborated upon in the account that follows. Two to four belt transects, 4 to 70 m apart as dictated by the steepness of the shoreline and topography, were laid perpendicular (by means of a sighting compass) to the waterline at each site from immediately above the highwater level of intertidal organisms to just below the waterline at low tide to provide locations for a minimum of 40 samples. The general location of each study site was determined by consulting aerial photographs and maps of the area. After extensive reconnaissance of each area, the precise location of the upper end of each transect was determined, by consensus of several experienced marine biologists, along a biologically representative part of the shoreline. To provide permanent sample locations, holes were drilled and eyebolts cemented into the substrate at the upper and lower ends of the transect tapes; this enabled the precise replacement of the transects during seasonal studies. A sampling optimization analysis employing the Poisson statistic (Wilson 1976) revealed that a minimum of 30 0.15-m^2 samples was required to adequately assess a typical rocky intertidal site. Consequently, no fewer than 40 rectangular quadrats, 30 cm x 50 cm (0.15 m^2), and 40 square quadrats, 1.0 m x 1.0 m (1.0 m^2), were placed along the transect tapes at 1.0 to 3.0-m intervals, depending upon the steepness of the shoreline, thereby providing permanent, stratified plots for sampling temporal and spatial distributions of organisms. To furnish statistically adequate representation, no fewer than four replicate quadrats of each size were represented in a given 0.3-m tidal interval whenever possible. This was done after the first site visit by adding quadrats to the immediate right and left sides (in some cases upper and lower sides) of quadrats known to be at tidal heights that were "under-sampled" due to the steepness of the shoreline. Tidepools were not discriminated against in positioning any of the quadrats; however, space does not permit their treatment here. The 1.0-m^2 quadrats were used to sample large macrophytes and the rarer forms of large invertebrate species. Quadrat locations were permanently marked with metal studs, epoxy putty, or eyebolts set in "hard-rock" cement.

Relative vertical tidal heights for each quadrat were measured from permanent reference points by means of a vertical leveling rod and a standard (20-power) surveyor's transit. A permanent reference point was established at each of the 10 study sites for surveying the tidal heights of the individual quadrats. The height of this reference point was determined in relation to mean lower low water (MLLW) by measuring, at six or more places along the shoreline, the midpoint between low and high wave peaks at the time of the predicted low tides (U.S. Department of Commerce 1975, 1976).

Repeatability of measurements checked on different site visits was ± 0.1 m. Throughout the program, considerable care was taken to minimize trampling and other forms of disturbance to the biotic communities under study.

Physical descriptions of each study site, including date, time, tidal stages, wave heights, air and water temperature, cloud cover, and salinity, were recorded at the time of each visit. Oceanographic literature and climatological data were used (Table 1), where available, to further characterize the respective environmental features of each study site.

Undisturbed Samples

Samples were obtained by photographing the numbered quadrats at right angles to the substrate with two cameras equipped with electronic flashes. Each quadrat contained a grey plastic label affixed to the upper left corner that was marked with a wax pencil to permanently identify each of the photo-samples. One camera contained 35-mm Kodachrome-64 slide film and the other contained Ektachrome infrared (IR) slide film.

Two miniature tape recorders and waterproof (polypropylene) data forms were used as a rapid method of taking field notes on the contents of the photo-samples. For every disturbed and undisturbed sample, a taxonomist recorded the taxa, counted the individual macroinvertebrates, and visually estimated the cover of each species in a detailed section-by-section format; each quadrat was subdivided into 20 equal subsections. It is worthwhile noting that most previous studies stopped at this level of quantification. We found that such estimates usually could not be repeated precisely (*e.g.*, within ± 25 per cent for dominant organisms) because of parallax problems and differences between observers and even between observations by the same person. Observer differences were influenced by varying degrees of field distractions and stresses, which were especially pronounced during heavy surf and nighttime low-tide conditions. Recorded *in situ* information was transcribed in the laboratory and used for density counts of small animals and to minimize taxonomic and other problems encountered while interpreting the photo-samples in the laboratory.

The method as applied here does not allow for the quantification of microalgae, small

Table 1. Physiographic attributes of the 10 rocky intertidal habitats studied.

Study area	Latitude and longitude	Water temperature	Substrata	Tidal range (m)	Wave exposure	Disturbance source	Sand cover
San Miguel Island	34°02'55"N 120°20'08"W	cold	Irregular volcanic flow breccia	−0.3 to +2.7	exposed (moderate)	none	lower intertidal
Santa Cruz Island	33°57'43"N 119°45'16"W	intermediate	Irregular volcanic flow breccia	+0.3 to +4.0	surge	none	none
San Nicolas Island	33°12'54"N 119°28'22"W	cold	Sandstone	−0.3 to +1.5	exposed (moderate)	none	extensive
Santa Barbara Island	33°28'43"N 119°01'36"W	intermediate	Vesicular volcanic rock	+0.3 to +3.7	surge (heavy)	none	none
Santa Catalina Island	33°26'47"N 118°29'04"W	warm	Vesicular volcanic rock	−0.6 to +3.0	protected	none	none
San Clemente Island	33°00'06"N 118°33'03"W	warm	Stable volcanic boulders	−0.3 to +2.1	protected	none	none
Coal Oil Point	34°24'27"N 119°52'40"W	cold (moderate)	Monterey Shale/siltstone	−0.6 to +0.9	exposed (moderate)	oil seeps	extensive
Whites Point	33°43'11"N 118°19'39"W	warm to intermediate	Diatomaceous Monterey Shale and unstable boulders	−0.3 to +0.9	exposed (moderate)	domestic wastes	upper intertidal cobbles
Corona del Mar	33°35'14"N 117°51'54"W	warm to intermediate	Unstable granitic boulders on sandstone/siltstone	−0.3 to +0.9	exposed (moderate)	human usage (extensive)	upper intertidal
Ocean Beach	32°44'35"N 117°15'15"W	warm to intermediate	Poorly-consolidated friable sandstone	+0.3 to +4.0	exposed	none	none

epifauna, or infauna when they occur in low abundances. We realize that these may be metabolically very active, but including them requires special techniques and expertise which constitute separate problems in themselves. For this reason, our measurements were restricted to macroepibiota that could be discerned with the unaided eye. However, we did quantify microbiota (*e.g.*, turfs of filamentous algae) when it occurred in high abundances, and most of the residual infaunal organisms from disturbed sampling have been identified and retained for future analyses. These latter samples never exceeded 1.0 per cent of the biomass in a given quadrat.

In the laboratory, the developed pairs of transparencies (color and IR) were projected simultaneously through a panel of glass (45 x 55 cm) onto two sheets (each 21 x 28 cm) of white bristol paper taped and glued to the glass. The paper contained a grid pattern of dots at 2.0-cm intervals on the side of the transmitted light; this has been shown (Littler and Murray 1975) to be an appropriate density (*i.e.*, 1.0 per cm^2) for consistently reproducible estimates of cover. Red dots were found to contrast best with the biological detail shown by the projected color transparencies; black dots were used in conjunction with the IR transparencies. The transparencies were aligned and focused onto the paper from the side opposite the field of dots (out of view) to assure unbiased assessments. The number of dots superimposed on each species was then scored twice (*i.e.*, replicated after movement of the grid) with the per cent cover values expressed as the number of "hits" for each species divided by the total number of dots contained in the quadrats. Reproducibility was high and seldom varied more than ± 5 per cent cover for a given species. Species that were not abundant enough to be scored by the replicated grid of point intercepts were assigned a cover value of 0.1 per cent.

The IR transparency was found to be instrumental in the delineation of the various species of primary producers and in assessing the state of their health. Blue-green algae, for example, are dominant forms that can only be discerned reliably on dark, wet substrate by use of IR photography. Each species fluoresces differently in the infrared band depending on its chlorophyll content and the percentage of dead branches on an algal thallus. In cases of multilayered communities, more than one photograph per quadrat was taken to quantify each stratum after upper strata had successively been moved aside, often yielding total biotic cover values of greater than 100 per cent. The only organisms removed from the permanent undisturbed quadrats were very small samples occasionally taken for taxonomic purposes.

Disturbed Samples

Biomass measurements of the standing stock give information contributing to community description and provide an additional set of variables to be examined with time; we used the wet weight, dry weight, and ash-free weight data in the same manner as the cover, density, and frequency data from the undisturbed method. The nonpermanent disturbed quadrats were selected for their biological similarity to the photo-quadrats and the organisms within each were harvested quantitatively by means of nylon or metal scrapers and fixed in formalin for subsequent sorting in the laboratory. All portions of algae having holdfasts within a given quadrat were taken. If most of the holdfast of an alga was outside the quadrat, it was not harvested. Organisms half in and half out of a quadrat were harvested only from the left and upper sides of the quadrat. Disturbed plots (0.15 m^2 for complexes of small organisms and 1.0 m^2 for larger organisms) were photographed and harvested within the high, middle, and lower intertidal regions. Approximately 12 plots of each size were harvested per visit at each intertidal site.

In the laboratory, the harvested specimens were identified, packaged, and catalogued. After sorting to species, the samples were rinsed quickly in distilled water to remove salt deposits, shaken to remove excess water, and weighed in tared aluminum foil containers. The samples were then dried to constant weight at 50°C, wrapped and sealed in heavy-duty aluminum foil, cooled to room temperature in desiccators, and weighed to 0.001 g. For those organisms having large inorganic components (such as calcium carbonate), ash-free dry weights were determined following 24 hours of combustion at 400°C in a muffle furnace. We feel that ash-free dry weight is the best measure of biomass, but because of the time constraints of the study only representative calcifying species were combusted. All fleshy organisms (such as frondose algae) were analyzed for wet and dry weight. Consequently, the results of this study expressed as organic dry weight will include ash-free dry weights for organisms with hard parts and dry weights for noncalcareous species.

All biomass data were considered by 0.3-m tidal intervals to formulate an overall picture of the distribution of standing stocks for each study site. Mean wet and dry organic biomass were averaged for each species in each tidal interval and the wet and dry organic weights per square meter for all species were summed to yield a distributional pattern of biomass as a function of tidal height. Values over all of the various tidal heights were averaged to produce a mean standing stock number (in wet and dry organic weight) per average square meter of substrate; these values were then used to compare all 10 study sites.

Collection of Floristic and Faunistic Data

Additional representative organisms were collected in duplicate, catalogued, and archived as permanent taxonomic voucher specimens. These were listed by site for disturbed samples, undisturbed samples, and collections outside the study quadrats. Each site was sampled sufficiently to provide a comprehensive species list of all taxa identifiable by recognized taxonomic experts during the course of the study. Some taxa (*e.g.*, *Chthamalus fissus/dalli*) include more than one species that could not be accurately separated and are treated here as single species complexes. An effort was made to relate variations in the environmental and biological conditions to changes in the composition and organization of intertidal associations.

Analyses of Data

Information obtained by the photographimetric sampling method (undisturbed) and by the harvest method (disturbed) provided quantitative data on the distribution of standing stocks in relation to tidal height. Species cover, frequency, and density distributions were calculated for 0.3-m vertical intervals throughout the intertidal zone. Biomass data were computed each season for wet weight (including hard parts) and organic dry weight (minus hard parts) in grams per square meter of substrate.

Species diversity indices are of particular value in assessing community changes with time: *i.e.*, Margalef's (1968) Index D', which stresses richness; Pielou's (1975) Index J', stressing evenness; and the Shannon and Weaver (1949) Index H', incorporating both richness and evenness. Diversity indices, calculated using natural logarithms and based on cover and biomass, were used to quantify seasonal changes in compositional patterns of the biota at each site and to provide between-site comparisons of community structure. Poole (1974) has indicated that in most ecological cases natural logarithms should be used in the Shannon-Weaver Index; however, the base of the logarithms is very much open to choice. By simply multiplying our H'_e diversity values by the factor 1.443, interested readers can obtain H'_2 numbers.

To characterize objectively natural, within-site assemblages of organisms in an unbiased manner, the quarterly, undisturbed cover data for each quadrat were subjected to cluster analyses by an adaptation of the weighted pair-group method (Sokal and Sneath 1963). This produced a dendrogram of assemblages based on correlation coefficients that were then characterized by their cover dominants and used to label the quadrats along their respective transect lines to produce maps of the prevalent zonal patterns for the various sites (see Figs. 2 and 3). All of the sites combined were also examined by cluster analysis based on overall combined macrophyte and macroinvertebrate species wet weight, organic dry weight, frequency, and cover to reveal common between-site ecological patterns and similarities.

SITE-SPECIFIC FEATURES

Island Study Areas

San Miguel Island Site

The Cuyler Harbor study area on San Miguel Island (34°02′55″N, 120°20′08″W) is the westernmost of all of the rocky intertidal zones studied and is consistently bathed by the cold California Current. The highly irregular volcanic flow breccia substrate of the study area extends over a 3.0-m intertidal range (from −0.3 to +2.7 m). A 0.7-m-wide band of aged bituminous residues of unknown source was present at the high-water line. The biota was reflective of a cold-water habitat and this site appeared more closely aligned taxonomically with San Nicolas Island than with the other eight sites. Macrophytes with the greatest mean cover throughout the year were *Gigartina canaliculata* (17.2 per cent), blue-green algae (9.9 per cent), and *Pelvetia fastigiata* (8.8 per cent). Macrophytes occurred maximally in the −0.3 to +0.3-m interval, with *P. fastigiata* establishing another smaller peak at +1.5 m. Only the lower samples were affected by sand movement, which appeared to be a minor environmental influence on the rocky intertidal community at this site. *Pelvetia fastigiata* had reduced cover during the spring while *G. canaliculata* showed spring and summer maxima. *Corallina vancouveriensis* declined in close association with the increases of *G. canaliculata*. *Gigartina canaliculata* and *C. vancouveriensis* dominated the macrophyte wet biomass with the peak in their standing stocks occurring at the +0.6-m level. Along with Santa Cruz Island, this site represented one of the few island areas lacking a large standing stock of *Egregia*. Macroinvertebrates with the highest densities were *Chthamalus fissus/dalli* (1,407/m²), *Balanus glandula* (378/m²), and *Littorina planaxis* (140/m²). *Phragmatopoma californica* (9.2 per cent cover), *Dodecaceria fewkesi* (4.4 per cent), *C. fissus/dalli* (3.9 per cent), and *Mytilus californianus* (3.4 per cent) had the highest yearly mean macroinvertebrate cover. Invertebrate cover was highest at +0.9 m and showed little seasonal variability. An April peak in macroinvertebrate densities resulted from increases in *C. fissus/dalli* which recruited at that time. The greatest macrophyte wet and dry biomass constituents were *P. fastigiata* (894 g/m²) and *G. canaliculata* (862 g/m²). Macroinvertebrates with the highest wet biomass were *Tegula funebralis* (138 g/m²) and *Anthopleura elegantissima* (100 g/m²); considerable dry organic weight also was contributed by these species (15 g/m² and 21 g/m², respectively), along with a brown encrusting sponge (21 g/m²). *Anthopleura elegantissima* declined slightly in February and April, but otherwise dominated the low intertidal invertebrate wet biomass.

The total flora and fauna of 116 taxa included 61 macrophytes and 55 macroinvertebrates discernible in the quadrat samples. San Miguel Island contained many species assemblages (11) arranged in 6 seasonally constant zones (Fig. 2). In general, seasonal trends at this site were minimal and were attributable more to populations with inherent annual cycles than to major environmental events. The San Miguel biota had the highest Shannon-Weaver diversity (H' = 2.95) of all sites studied and consisted predominantly of perennial organisms characteristic of mature, constant communities (*e.g.*, *Pelvetia*, *Mytilus*, *Phyllospadix*); species normally found (see Murray and Littler 1978) in early seral stages (*e.g.*, *Porphyra*, *Scytosiphon*, *Ulva*) were uncommon.

Santa Cruz Island Site

The study area on the west side of Willows Anchorage (33°57′43″N, 119°45′16″W) is located near the central portion of the southern shore of the island and receives a consistently strong

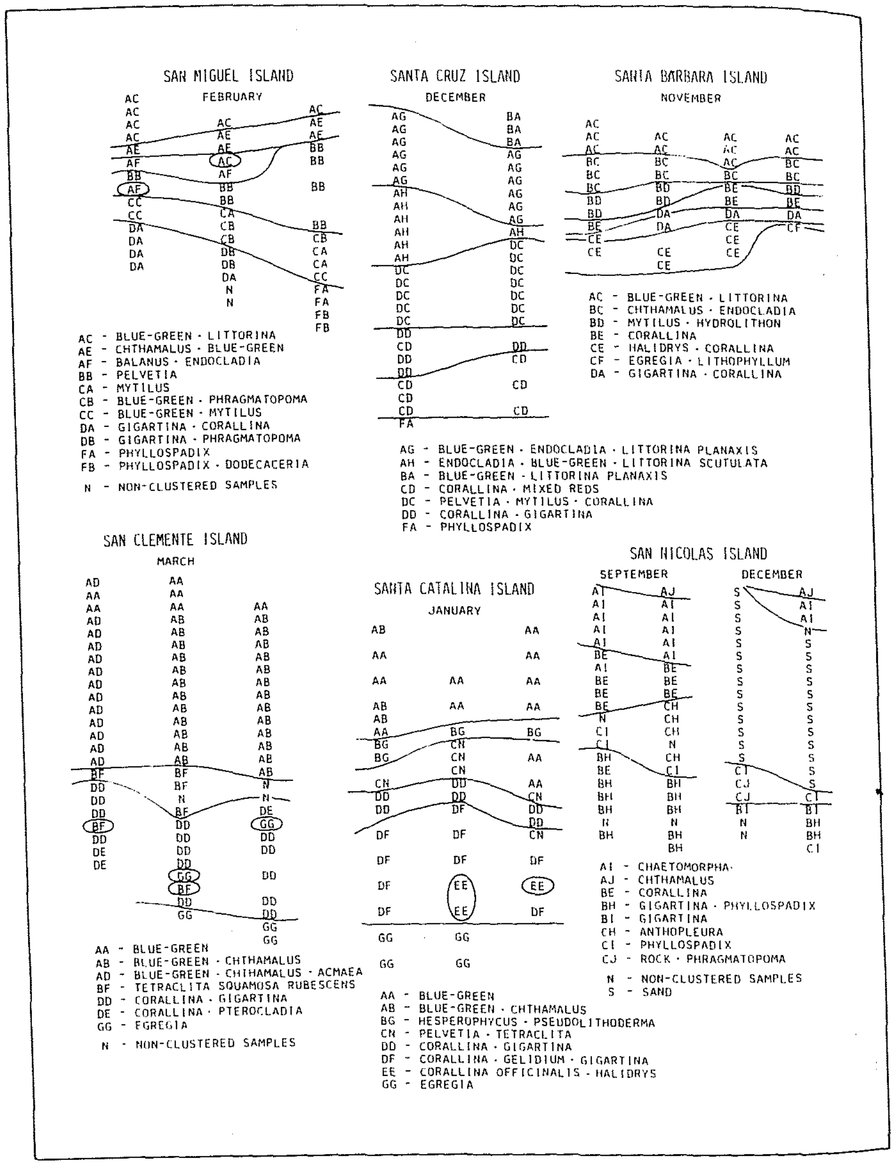

FIGURE 2. *Representative distributional patterns of dominant species assemblages (as determined by cluster analyses based on cover) in relation to positions of transects and locations of quadrats in which they occurred for each of the six island study areas. For each island, columns of letters represent line transects, with the most landward samples at the top and the most seaward at the bottom. Combinations of letters represent specific quadrats within transects, each letter combination specifying certain dominant species, according to the legends. Contour lines are drawn between transects to delineate assemblages in common.*

wave surge. The substrate consists of very rough volcanic breccia extending over a 3.7-m interval (+0.3 to +4.0 m). This site receives afternoon shade and is relatively protected from the prevailing waves and surf. Strong, dry, warm Santa Ana winds recorded during February apparently had been blowing for some time prior to that visit, judging from the desiccated state of the upper intertidal algae. With 77 macrophytes and 100 macroinvertebrates, the Santa Cruz Island site had considerably more taxa (177) in the quadrats throughout the year of study than any of the other sites. Blue-green algae contributed the most cover (29.6 per cent), followed by *Lithophyllum proboscideum* (7.6 per cent), *Corallina officinalis* var. *chilensis* (6.5 per cent), *Endocladia muricata* (4.4 per cent), *Pelvetia fastigiata* (2.6 per cent), and *Gigartina canaliculata* (2.5 per cent). There was a December peak in macrophyte cover due to increases in blue-green algae in the high intertidal region and a low in February correlated with the condition of desiccating winds. The macrophyte species reduced in February included *E. muricata*, *P. fastigiata*, *C. officinalis* var. *chilensis*, and *C. vancouveriensis*. Only four species of macroinvertebrates had an average mean cover greater than 1.0 per cent: *Anthopleura elegantissima* (2.6 per cent), *Mytilus californianus* (1.6 per cent), *Tetraclita squamosa rubescens* (1.2 per cent), and *Strongylocentrotus purpuratus* (1.2 per cent). *Littorina planaxis* had the highest average mean density (532 individuals/m^2), followed by *Chthamalus fissus*/*dalli* (386/m^2), *T. squamosa rubescens* (310/m^2), and *L. scutulata* (254/m^2). Density data showed striking increases (*i.e.*, recruitment) of *C. fissus*/*dalli* and *T. squamosa rubescens* during February and May. In terms of species composition, it is surprising that this site more closely approximated the intermediate biota of Santa Barbara Island than the colder-water communities of either San Nicolas or San Miguel Island. *Pelvetia fastigiata* (96 g/m^2) was the highest dry organic biomass contributor, followed by *Halidrys dioica* (75 g/m^2), *Egregia menziesii* (27 g/m^2), *Gelidium coulteri* (16 g/m^2), and *C. officinalis* var. *chilensis* (16 g/m^2). The macroinvertebrate contributing the highest dry organic weight was *A. elegantissima* (47 g/m^2), along with *S. purpuratus* (44.3 g/m^2) and *M. californianus* (33.8 g/m^2). This site warrants special mention as one of the few island sites lacking a large stock of *E. menziesii*. The mean yearly Shannon-Weaver diversity (H') was 2.58, richness (D') was 28.86, and evenness (J') was 0.53. None of these measures of species diversity varied appreciably over the year. Cluster analysis resolved seven biological zones and subzones with seven assemblages (Fig. 2) that did not vary throughout the year. These zones, like those at Ocean Beach and Santa Barbara Island, were shifted upward relative to most other sites, indicating consistently strong wave surge conditions. The intertidal biota generally lacked marked seasonal patterns and presented a temporally constant and relatively mature ecosystem dominated by long-lived organisms (Fucales, *Endocladia*, *Tetraclita*, acmaids). This interpretation was supported by the consistent patterns of zonation shown by the cluster analyses for each quarter.

San Nicolas Island Site

The San Nicolas Island study area represents an intertidal sandstone bench (33°12′54″N, 119°28′22″W) strongly influenced by sand movements (particularly in the upper intertidal region) and has a 1.8-m tidal range from −0.3 to +1.5 m. This site is exposed to the cold California Current most of the year. Although the cold-water species composition of this site had the closest affinity with that of San Miguel Island, the patterns of distribution and abundance of dominant forms were closest to those recorded for Coal Oil Point, which also is subjected to comparable levels of sand movement. There were 120 taxa in the sample plots, of which 69 were macrophytes and 51 were macroinvertebrates. The greatest cover of both macrophytes and invertebrates occurred low in the intertidal zone and decreased upward. Macrophytes with the greatest mean cover throughout the year were *Gigartina canaliculata* (19.8 per cent), *Phyllospadix scouleri* (8.8 per cent), and *Chaetomorpha linum* (8.5 per cent). Of the prominent macroinvertebrates, *Dodecaceria fewkesi* (8.2 per cent), *Anthopleura* *elegantissima* (5.5 per cent), and *Chthamalus fissus/dalli* (5.4 per cent) had the greatest mean cover. Macroinvertebrates with the highest densities were *C. fissus/dalli* (2,183 individuals/m²), *A. elegantissima* (136/m²), *Littorina scutulata* (91/m²), and *Mytilus californianus* (62/m²). Seasonal fluctuations among the major species were apparent (cover and density were lowest in winter) with the exceptions of *M. californianus*, *D. fewkesi*, and *P. scouleri*. For example, total macrophyte cover, particularly of *G. canaliculata* and *C. linum*, declined sharply in winter. There was little seasonality in invertebrate cover except for a *C. fissus/dalli* settlement in May. The low intertidal cover peak of macroinvertebrates (mostly *Phragmatopoma californica* and *D. fewkesi*) was unique among the 10 sites studied. The wet biomass peak for macroinvertebrates occurred at +0.6 to +0.9 m, mostly due to *M. californianus*, *C. fissus/dalli*, and *Haliotis cracherodii*.

Community mean yearly biomass was very high at San Nicolas Island (4,659 g/m² wet weight, 896 g/m² organic dry weight) and was exceeded only at Santa Catalina Island. *Phyllospadix scouleri* (343 dry organic g/m², 1,173 wet g/m²) and *Halidrys dioica* (149 dry g/m², 846 wet g/m²) had the greatest biomass of the macrophytes; among the macroinvertebrates, *Mytilus californianus* (20 dry organic g/m², 218 wet g/m²) and *Anthopleura elegantissima* (47 dry g/m², 212 wet g/m²) were predominant. Sand movement during winter caused large alterations in the six species assemblages that were somewhat arranged into five indistinct zones (Fig. 2). By early spring, the macrobiota exhibited nearly complete recovery; richness, evenness, and Shannon-Weaver diversity indices were highest in spring. This recovery and the high abundance of *Anthopleura* clones and *Chaetomorpha* suggest, hypothetically, that much of the intertidal biota at the study site was comprised of environmentally-stressed communities adapted to periodic conditions of sand inundation.

It seems that raised portions of the intertidal bench serve as islands of refuge upon which mature abalone and mussel-dominated communities develop. These raised pinnacle communities are of interest in that their lower limits may be determined by the physical smothering action of sand movement rather than by the kinds of biological factors so well documented in the literature (see Paine 1966, Connell 1972).

Santa Barbara Island Site

The study site is located on the east side of the island near the mouth of Cave Canyon (33°28′43″N, 119°01′36″W). The intertidal region extends over a steep, vesicular volcanic rock shoreline which is very rough in texture and has a 3.4-m tidal range (from +0.3 to +3.7 m). Comparable biotic zones were considerably elevated relative to most of the other sites, probably due to the predominant wave surge effect and a high degree of shading during the afternoon. The macrophytes sampled numbered 88 taxa, while macroinvertebrates numbered 69; macrobiota totaled 157 taxa. The macrophytes contributing the highest per cent cover averaged over the tidal intervals sampled were blue-green algae (37.0 per cent), *Halidrys dioica* (5.7 per cent), *Corallina officinalis* var. *chilensis* (5.5 per cent), *Gigartina canaliculata* (5.0 per cent), *Egregia menziesii* (4.6 per cent), *Lithophyllum proboscideum* (4.5 per cent), *C. vancouveriensis* (2.6 per cent), and *Hydrolithon decipiens* (2.4 per cent). Macroinvertebrates contributing the highest average cover were *Chthamalus fissus/dalli* (3.0 per cent), *Mytilus californianus* (3.0 per cent), *Pseudochama exogyra* (2.8 per cent), *Petaloconchus montereyensis* (1.8 per cent), and *Tetraclita squamosa rubescens* (1.8 per cent). *Chthamalus fissus/dalli* were by far the most numerous macroinvertebrates (1,475 individuals/m²), followed by *T. squamosa rubescens* (350/m²), *Littorina planaxis* (240/m²), *M. californianus* (214/m²), *P. montereyensis* (181/m²), and *Pollicipes polymerus* (140/m²). Invertebrates showed little seasonality in cover and reached their maximum in the +0.9 to +2.1-m interval. Total macrophyte cover was highest in January due to large increases in blue-green algae above +1.8 m; frondose forms low on the shore reached their maximum in the fall. Juvenile barnacles (*T. squamosa rubescens* and *C. fissus/dalli*) were most numerous in January, then showed a steep decline in the spring.

Total mean biotic cover changed dramatically between the November visit (88 per cent) and the January visit (107 per cent), largely due to increased blue-green algae above +1.5 m. Biotic cover below +1.8 m exceeded 100 per cent with most of the biomass resulting from large algal stocks below +1.5 m. Biomass was relatively high at this site (6,775 g/m² wet weight, 876 g/m² organic dry weight) and 86 per cent consisted of macrophytes. On the basis of organic dry weight, *Egregia menziesii* was the dominant macrophyte with an average of 299 g/m², followed by *Gigartina canaliculata* (179 g/m²), and *Halidrys dioica* (174 g/m²). Only three macroinvertebrates had an average equal to or greater than 10 dry organic g/m², including *Pseudochama exogyra* (44 g/m²), *Mytilus californianus* (25 g/m²), and *Strongylocentrotus purpuratus* (10 g/m²). Seven relatively complex biotic zones (Fig. 2), as characterized by seven different assemblages, were present on the shore. There were a number of organisms usually associated with colder waters which were present at this site that were not found on nearby Santa Catalina and San Clemente Islands to the south; consequently, this site showed closer affinities with the area studied on Santa Cruz Island than with any of the other eight sites. An abundant population of the pulmonate gastropod *Siphonaria brannani*, as well as lesser numbers of the holothurian *Cucumaria pseudocurata*, were found exclusively on Santa Barbara Island during the present study.

Santa Catalina Island Site

The Santa Catalina Island site is on the north point of Fisherman Cove (33°26′47″N, 118°29′04″W) about 1.3 km northeast of Isthmus Cove and shielded from the direction of the prevailing swell. The study area extends over a 3.6-m range (−0.6 to +3.0 m) and consists of a vesicular volcanic rock substrate (middle Miocene) with many surface irregularities. A total of 169 taxa was present in the quadrats taken during the study (73 macrophytes and 96 macroinvertebrates). At this site, macrophyte abundance was highest between MLLW and +0.6 m; the macroinvertebrate maximum was localized between +0.3 and +0.6 m. Based on the yearly average, blue-green algae provided the greatest macrophyte cover (25.1 per cent), followed by *Egregia menziesii* (10.6 per cent), *Pelvetia fastigiata* f. *gracilis* (8.0 per cent), *Hesperophycus harveyanus* (6.8 per cent), *Gelidium purpurascens* (6.6 per cent), *Lithophyllum proboscideum* (6.4 per cent), and *Corallina officinalis* var. *chilensis* (5.9 per cent). Less than 5.0 per cent cover was contributed by each of 63 additional macrophytes. Total macrophyte cover was minimal during August due to large reduction in blue-green forms; however, several other macrophytes reached abundance peaks at this time. Most of the macrophyte seasonality was shown by turf species and their epiphytes, many of which can be characterized as summer annuals. For example, *Colpomenia sinuosa*, *Sargassum agardhianum*, and *Gelidium coulteri* grew rapidly from spring through summer to a fall maximum. During winter, *Gelidium pusillum* was most abundant, while the fucalean forms *P. fastigiata* f. *gracilis* and *H. harveyanus* remained directly constant over the year. The greatest macroinvertebrate cover was furnished by *Dendropoma lituella/rastrum* (3.6 per cent), *Tetraclita squamosa rubescens* (3.2 per cent), *Chthamalus fissus/dalli* (2.1 per cent), and *Serpulorbis squamigerus* (1.2 per cent). Less than 1.0 per cent cover was provided by each of 90 additional macroinvertebrates. *Chthamalus fissus/dalli*, with 802 individuals/m², was by far the most numerous macroinvertebrate, followed by *T. squamosa rubescens* (450/m²), *D. lituella/rastrum* (341/m²), *Littorina planaxis* (157/m²), *Brachidontes adamsianus* (102/m²), *Balanus tintinnabulum californicus* (97/m²), and *Littorina scutulata* (80/m²). Diversity was high at this site with the maximum occurring during August. Wet and dry organic biomass (8,078 and 1,458 g/m², respectively) were very high at this site, concentrated between −0.6 and MLLW, and from +0.6 to +1.3 m, and comprised mostly of Phaeophyta. Thirteen taxa contributed 99.3 per cent of the mean macrophyte organic dry weight. The greatest dry organic biomass was provided by *Eisenia arborea* (558 g/m^2), *P. fastigiata* f. *gracilis* (350 g/m^2), *E. menziesii* (273 g/m^2), and *H. harveyanus* (110 g/m^2). Eleven species of macroinvertebrates contributed 91.8 per cent of the mean dry organic biomass; the bulk of this was supplied by *T. squamosa rubescens* (24 g/m^2), followed by *Pseudochama exogyra* (10 g/m^2), *B. adamsianus* (6 g/m^2), a white sponge (4 g/m^2), and *C. fissus/dalli* (4 g/m^2). There were eight discrete assemblages on the shore, forming six constant major zones throughout the year (Fig. 2).

San Clemente Island Site

This site is located 450 m to the south of Wilson Cove (33°00′06″N, 118°33′03″W) on the northeast portion of the island. The study area has a 2.4-m tidal range extending from −0.3 to +2.1 m over a field of large, volcanic rocks. The Corona del Mar site also consists of a habitat mosaic of slopes, angles, and crevices from large rocks; however, the substrate on the leeward side of San Clemente Island is characteristically much more stable than at Corona del Mar and little movement of substrate occurred during the year of study. This warm-water site is the calmest of all the sites studied and receives afternoon shade during the winter. A total of 129 taxa was recorded in the quadrats (64 macrophytes and 65 macroinvertebrates). Blue-green algae provided the greatest macrophyte cover (26.8 per cent), followed by *Egregia menziesii* (13.4 per cent), *Corallina officinalis* var. *chilensis* (8.0 per cent), *Gigartina canaliculata* (7.5 per cent), and *Pterocladia capillacea* (7.3 per cent). The barnacles *Chthamalus fissus/dalli* (3.6 per cent) and *Tetraclita squamosa rubescens* (1.2 per cent) furnished nearly three-fourths of the total macroinvertebrate cover based on annual averages. Less than 1.0 per cent was contributed by each of 62 additional macroinvertebrates. *Chthamalus fissus/dalli* (1,528 individuals/m^2) provided 74 per cent of all macroinvertebrate individuals based on annual averages and was one order of magnitude more abundant than the second most abundant taxon (*Acmaea* [*Collisella*] *scabra*). Although this site showed the least seasonality of all 10 areas, there was a slight tendency for higher macrophyte cover in December and June, with a small reduction of invertebrate cover in June.

San Clemente Island's intertidal biota was very similar to that of Santa Catalina Island, but the latter showed more seasonal fluctuation. *Egregia menziesii*, which was most abundant in October, was observed to decrease in March, although many juvenile thalli were present. *Halidrys dioica* reached a cover peak in March. As was the case at most sites, blue-green algae were more abundant in December and March. *Pterocladia capillacea*, *Sargassum agardhianum*, *Colpomenia sinuosa*, *Laurencia pacifica*, and *L. snyderae* reached their peak during the warmer months of summer and fall. Biomass (mostly Phaeophyta) was greatest between MLLW and +0.3 m with invertebrate dominance above +0.8 m. Fourteen macrophytes provided 98.9 per cent of the dry organic biomass, including *E. menziesii* (181 g/m^2), *H. dioica* (62 g/m^2), *S. agardhianum* (58 g/m^2), *Phyllospadix torreyi* (47 g/m^2), and *P. capillacea* (41 g/m^2). Six macroinvertebrates contributed 96.2 per cent of the total macroinvertebrate dry biomass; the majority was provided by *Tetraclita squamosa rubescens* (6 g/m^2), *Chthamalus fissus/dalli* (5 g/m^2), and *Acmaea* (*Collisella*) *scabra* (2 g/m^2).

Invertebrates at San Clemente Island were found to contribute less to the intertidal community composition than those at the other nine sites. This site, as well as leeward San Clemente Island in general, is notable in its paucity of large mobile macroinvertebrates. Although March samples contained the most taxa (103), there was no marked seasonality in Shannon-Weaver diversity (2.55 yearly mean). Cluster analysis revealed seven assemblages of species distributed into four major intertidal zones (Fig. 2) that did not vary over the period of study.

Mainland Study Areas

Coal Oil Point Site

The Coal Oil Point study area (34°24′27″N, 119°52′40″W) is located approximately 3.0 km west of Goleta Point, which is part of the University of California, Santa Barbara campus. The rocky intertidal region consists of a sandstone substrate usually covered by sand above the +0.9-m tidal level. The habitat studied is quite flat, extends over a 1.5-m tidal range of −0.6 to +0.9 m, and has marked winter influxes of sand affecting most of the area. Sampling was restricted to the low to mid-intertidal zone, which has an important bearing on interpretations relative to most of the other study sites; that is, we would expect macrophyte and, hence, total standing stocks to be overemphasized (with macroinvertebrates underemphasized) since the high zone typically dominated by macroinvertebrates was not available for sampling. Historically, this site has received oil from nearby offshore seeps that release from 50 to 70 barrels per day into the sea.

One hundred and twenty-seven taxa, comprising 71 macrophytes and 56 macroinvertebrates, were present in the samples. Macrophytes with the greatest mean cover were *Phyllospadix torreyi* (23.0 per cent), rhodophycean turf (15.6 per cent), *Egregia menziesii* (11.1 per cent), and *Gigartina canaliculata* (8.1 per cent). The macroinvertebrate cover dominants were *Anthopleura elegantissima* (15.4 per cent) and *Mytilus californianus* (8.2 per cent). Macroinvertebrates with the highest densities were *Chthamalus fissus/dalli* (1,651 individuals/m^2), *Lacuna* spp. (1,255/m^2), and *A. elegantissima* (412/m^2). The peak in biotic cover occurred in the −0.3 to +0.3-m interval, mostly due to macrophytes. The macroinvertebrates (mostly *A. elegantissima*) reached their maximum from +0.6 to +0.9 m.

A significant portion of the macrophyte cover was a rhodophycean turf (including three species of *Polysiphonia*, *Tiffaniella snyderae*, and *Pterosiphonia dendroidea*) that was attached on substrate beneath sand. In general, macrophytes showed a winter decline, especially *Egregia menziesii* and *Gigartina canaliculata*. *Phyllospadix torreyi* (131 dry organic g/m^2) contributed the most wet biomass, which was highest in winter. *Egregia menziesii* stocks were low at this site, a trend noted for most of the northern study areas. *Anthopleura elegantissima* (169 dry organic g/m^2) dominated the macroinvertebrate biomass and apparently reproduced by asexual budding to give rise to extensive clonal populations, a form apparently (Francis 1973) adapted to environmental stresses.

Similar populations were recorded only from the site on San Nicolas Island, a habitat also influenced by sand movements. The distribution and abundance patterns at the San Nicolas site were more similar to Coal Oil Point than to any of the other eight areas studied. Probably owing to the lack of a high intertidal region, Coal Oil Point had a large number of species assemblages (nine) but a low number of discrete zones (three); these varied considerably in association with sand movement (Fig. 3). Although Coal Oil Point was the northernmost site studied, it did not contain as many cold-water organisms as did the San Miguel Island and San Nicolas Island sites.

Whites Point Site

The study site at the base of the Palos Verdes Hills (33°43′11″N, 118°19′37″W) and about 4 km northwest of Los Angeles Harbor was chosen as representative of a mainland habitat exposed to human usage and municipal wastes. Whites Point, as in the case of Coal Oil Point, also appeared to receive a certain amount of petroleum pollution; aged bituminous residues were present as a continuous band along the high tide line. This area lies just shoreward of the site of the world's largest release of sewage into the ocean (over one billion gallons per day). The substrate is both silty and diatomaceous Monterey Shale (middle Miocene). The habitats selected as representative were two tilted, bedded planes that extend shoreward from −0.3 to

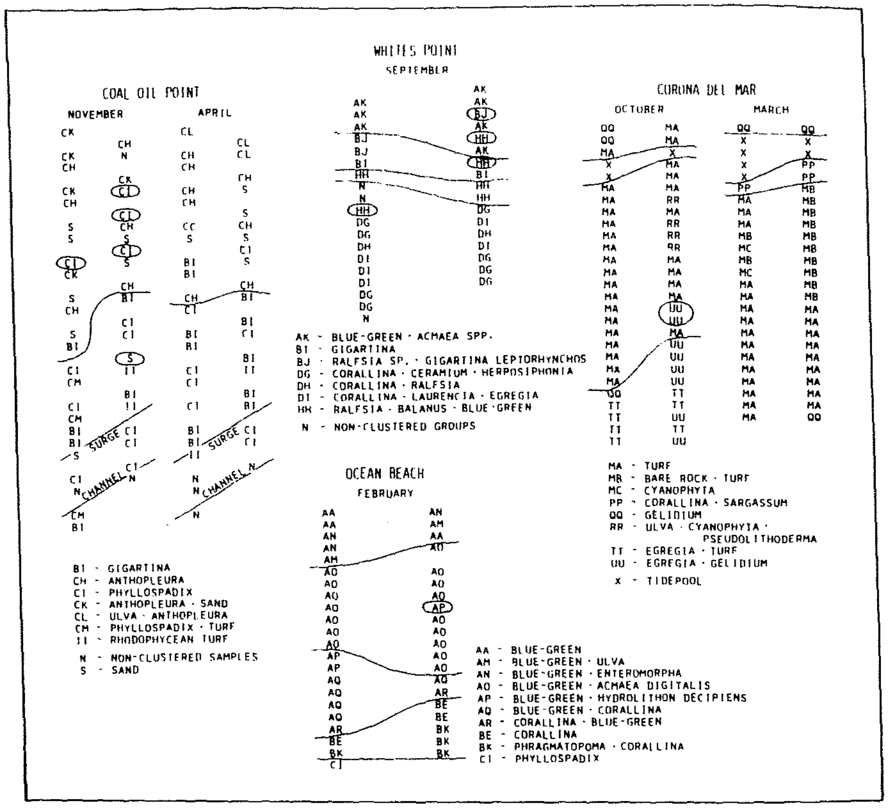

FIGURE 3. *Representative distributional patterns of dominant species assemblages (as determined by cluster analyses based on cover) in relation to positions of transects and locations of quadrats in which they occurred for each of the four mainland study areas.*

+0.9 m; above this they become covered by an unstable boulder-cobble beach. Since the middle to high zones (regions of invertebrate maxima) were not available for study, one would expect that macrophyte stocks would be overemphasized and invertebrates underemphasized relative to all of the other sites except Corona del Mar, Coal Oil Point, and San Nicolas Island.

There was a total of 125 taxa sampled by quadrats, including 36 macrophytes and 69 macroinvertebrates. Five macrophytes accounted for more than half of the annual cover. Blue-green algae provided the greatest macrophyte cover (14.8 per cent) based on annual averages, followed by *Corallina officinalis* var. *chilensis* (14.0 per cent), *Gigartina canaliculata* (7.4 per cent), *Ralfsia* sp. (7.0 per cent), and *C. vancouveriensis* (6.2 per cent). Less than 6.0 per cent cover was contributed over the year by each of 50 additional macrophytes. The following three macroinvertebrates provided almost two-thirds of the total animal cover based on annual averages: *Balanus glandula* (1.6 per cent), *Anthopleura elegantissima* (1.4 per cent), and *Strongylocentrotus purpuratus* (1.1 per cent). Less than 1.0 per cent cover was provided over the year by each of 58 additional macroinvertebrates. *Balanus glandula* (582 individuals/m²) was the most numerous macroinvertebrate, followed by *Acmaea (Collisella) conus/scabra* (336/m²), *Chthamalus fissus/dalli* (238/m²), and *A. (Collisella) strigatella* (118/m²). The maximum biotic cover (99 per cent) occurred during September but decreased in winter due to declines in algal turf species and their epiphytes. Two filamentous Rhodophyta, *Herposiphonia verticillata* and *Ceramium eatonianum*, were important epiphytes on the turf community, a relationship not pronounced at any of the other sites. *Gigartina canaliculata* formed a turf distinct from the *Corallina* turf and grew mainly on rock (unlike most of the other sites where these two usually were strongly intermingled in turfs). Kelp at Whites Point was patchy in the lower intertidal region. *Egregia menziesii* reached a peak in autumn, then declined in winter, as was the case at nearly all of the sites where it was important. Twelve macrophytes supplied 99.0 per cent of the mean macrophyte organic dry weight. The majority was contributed by *E. menziesii* (433 g/m²), which furnished 72.6 per cent of the macrophyte total, followed by *G. canaliculata* (70 g/m²), *C. vancouveriensis* (24 g/m²), *C. officinalis* var. *chilensis* (23 g/m²), and *Ralfsia* sp. (11 g/m²). Eleven species, including *Mytilus californianus* (22 g/m²), *A. elegantissima* (17 g/m²), and *S. purpuratus* (8 g/m²), comprised 95.7 per cent of the macroinvertebrate dry organic biomass; considerable contributions were also made by *Pugettia producta*, *Nuttallina fluxa*, *B. glandula*, and *Tegula funebralis*. The peak in macrophyte biomass occurred in the −0.3-m to MLLW interval and comprised mostly Phaeophyta. Most of the macroinvertebrate wet biomass was between +0.6 and +0.9 m and consisted primarily of *M. californianus*, *A. elegantissima*, and *S. purpuratus*. *Balanus glandula* recruited strongly in May.

There were seven species assemblages and four zonal communities (Fig. 3) that varied considerably during the study. Species numbers and richness (D') were maximal during May, while Shannon-Weaver diversity (H') at this site was highest in winter due to an increased macrophyte evenness associated with sand movement. Sand and gravel were important perturbatory factors at this site; a winter inundation of many of the quadrats, particularly along the north transect line, resulted in the predominance of a blue-green algal-limpet community in February.

Corona del Mar Site

The site selected for study at Corona del Mar lies near the mouth of Morning Canyon (approximately 33°35′14″N, 117°51′54″W), located 1.4 km southeast of the entrance channel to Newport Bay. The intertidal zone examined extends over a tidal range of only 1.2 m (from −0.3 to +0.9 m) and consists of loose, granitic boulders lying on a sandstone/siltstone substrate. Of the sites studied, Corona del Mar represents one of the most disturbed by both human usage (including tidepooling, rock turning, trampling, and handling of organisms) and natural disturbances (such as heavy surf which causes movement of the boulder substrate). Because of sandy beach cover above +0.9 m, sampling was restricted to only the low intertidal zone where, at comparable tidal heights in most rocky habitats, macrophytes and total standing stocks are at their greatest. Therefore, care must be taken in comparing this site with other sites sampled at high levels, *i.e.*, where barnacles and littorine populations (usually low in biomass) are typically dominant.

Quadrat samples analyzed from Corona del Mar contained 137 taxa of macroorganisms, including 66 macrophytes and 71 macroinvertebrates. The greatest overall macrophyte cover based on yearly means was contributed by *Egregia menziesii* (14.4 per cent), followed by *Corallina officinalis* var. *chilensis* (12.0 per cent), *Ulva californica* (10.4 per cent), blue-green algae (8.0 per cent), and *Pseudolithoderma nigra* (7.8 per cent). *Chthamalus fissus/dalli* and *Anthopleura elegantissima* contributed most of the macroinvertebrate cover (1.0 per cent each). *Lithophyllum proboscideum* was the most widespread species (90.4 per cent of the samples) as a result of the mosaic of crevices (its primary habitat) created by the boulder substrate. *Chthamalus fissus/dalli* was considerably more numerous (408 individuals/m²) than other significant species, which ranged from 59 individuals/m^2 to 10 individuals/m^2. Biological cover at this site averaged 91 per cent throughout the year, of which macroinvertebrates accounted for only 4 per cent. Biotic cover exceeded 95 per cent below +0.3 m due to large stands of macrophytes that were maximal (126.4 per cent) in the lowest interval sampled. *Egregia menziesii* contributed the most cover (14.4 per cent) when averaged over the year but was greatly reduced during late winter. Overall community dry organic biomass was exceptionally low at this site (361 g/m^2), with the majority (83 per cent) contributed by macrophytes. Most of the macrophyte biomass occurred at the lowest level sampled (2,822 g/m^2 wet weight and 471 g/m^2 organic dry weight). *Egregia menziesii* provided 56 per cent of the total macrophyte wet weight, while the remainder consisted mostly of turf formers. Most of the macroinvertebrate biomass was *Strongylocentrotus purpuratus* (372 g/m^2 wet weight) and *A. elegantissima* (76 g/m^2 wet weight), along with several other mobile forms.

There were no sharp zonal communities at this site and most of the quadrats showed changes in dominant assemblages during each quarter (Fig. 3). The bigger forms of invertebrates predominated, with their biomass largely attributable to *Strongylocentrotus purpuratus*, *Anthopleura elegantissima*, and *Aplysia californica*. These animals were able to move into the crevices between boulders before, during, and following substrate movement, making them less likely to be damaged by the smaller cobbles. The instability of substrate at this site was probably responsible for the predominance of early successional and eurytopic algal forms. Other abundant macrophytes were those characteristic of shaded crevices, a habitat abundantly represented throughout the study site. Nearly all of the population and community parameters recorded from the upper surfaces of boulders suggest a general subclimax system at Corona, perhaps maintained by substrate instability.

Ocean Beach Site

The study area is located on a broad section of wave-exposed coastline at Ocean Beach, San Diego (32°44′35″N, 117°15′15″W) and covers a 3.7-m intertidal range (+0.3 to +4.0 m) over a substrate of poorly consolidated, friable sandstone. This site consistently receives more wave shock than any of the other habitats. A strong seasonal pattern occurred due to the increase in winter high surf and wave splash in the upper intertidal region. This resulted in a rapid winter colonization of blue-green algae, *Ulva* sp., and *Enteromorpha* sp. on previously bare substrate.

A total of 150 taxa was present in the sample plots at this site, with 92 macrophytes and 58 macroinvertebrates. Mean cover of macrophyte species averaged over all of the tidal intervals sampled was highest for blue-green algae (38.8 per cent), *Corallina officinalis* var. *chilensis* (8.4 per cent), *Hydrolithon decipiens* (5.3 per cent), *C. vancouveriensis* (4.8 per cent), *Cryptopleura corallinara* (4.4 per cent), *Phyllospadix torreyi* (4.1 per cent), *Rhodoglossum affine* (1.9 per cent), and *Enteromorpha tubulosa* (1.6 per cent). Mean cover by macroinvertebrates was highest for the tube worm *Phragmatopoma californica* (4.8 per cent), followed by *Mytilus californianus* (2.3 per cent), *Acmaea* (*Collisella*) *digitalis* (1.6 per cent), *Chthamalus fissus*/*dalli* (1.0 per cent), *Pollicipes polymerus* (0.9 per cent), and *Nuttallina fluxa* (0.6 per cent). *Chthamalus fissus*/*dalli* was the most abundant macroinvertebrate at Ocean Beach (annual mean of 997 individuals/m^2), followed by *A.* (*Collisella*) *digitalis* (274/m^2), *P. polymerus* (274/m^2), *P. californica* (183/m^2), and *M. californianus* (134/m^2). Eleven additional macroinvertebrates were represented by average annual densities of 6 to 97 individuals/m^2 and 23 other macroinvertebrates contributed a mean of 37 individuals/m^2. Macroinvertebrates attained their maximum cover between +0.6 and +1.8 m, largely owing to extensive populations of *P. californica* and *M. californianus*. For macrophytes, the rank order using dry organic weight was *P. torreyi* first (97 g/m^2), followed by *C. corallinara* (29 g/m^2), *C. vancouveriensis* (24 g/m^2), *C. officinalis* var. *chilensis* (19 g/m^2), and *Gigartina canaliculata* (10 g/m^2). Among the macroinvertebrates, *M. californianus* had the highest dry organic weight (116 g/m^2),

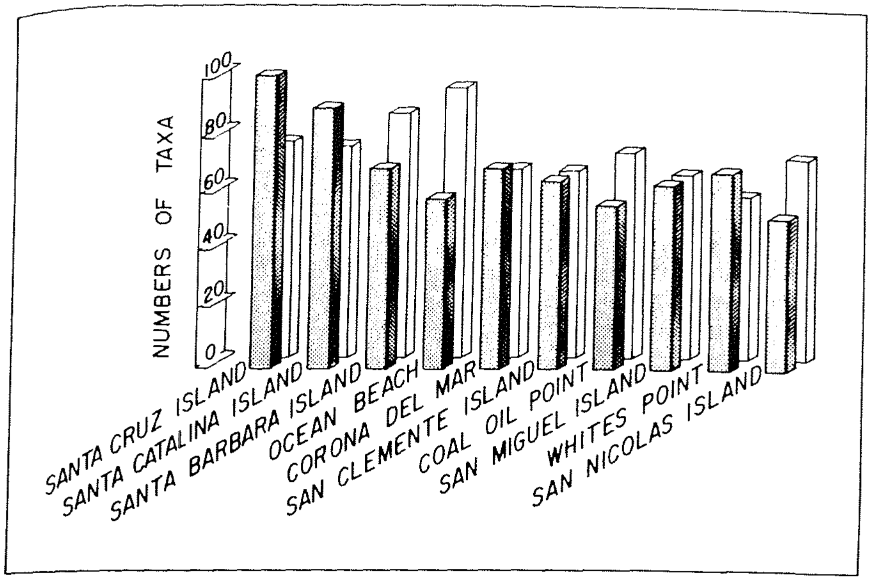

FIGURE 4. *Mean annual numbers of macrophyte taxa (histograms in rear) and macroinvertebrate taxa (dark histograms in front) found in quadrats for each study area.*

followed by *Septifer bifurcatus* (42 g/m^2), *N. fluxa* (10 g/m^2), and *Strongylocentrotus purpuratus* (9 g/m^2). Maximum biomass (mostly *Mytilus*) occurred between +0.9 and +2.1 m, with another peak, dominated by *Corallina* and *Phyllospadix*, at +0.3 to +0.9 m. The lack of large *Egregia* and *Eisenia* stocks here could be related to the friable nature of the substrate, as demonstrated by the relative ease with which these algae could be pulled loose during harvesting and collecting. Overall community biomass was low (421 g/m^2 organic dry weight) at this site. Five biotic zones made up of a large number of species assemblages (10) were present on this shore (Fig. 3) throughout the year. The flora and fauna at Ocean Beach, our most southerly site, contained no elements unique to cold-water systems, but had many forms associated with warm-water environments.

COMPARISONS BETWEEN SITES

Numbers of Taxa

More taxa occurred in the communities sampled at Santa Cruz Island (177), Santa Catalina Island (169), Santa Barbara Island (157), and Ocean Beach (150) than at any of the other six sites (Fig. 4). The fewest total taxa were sampled at San Miguel Island (116), San Nicolas Island (120), and Whites Point (125); the last two of these sites exhibited stress by sand or pollutants. Inspection of the data (Fig. 4) shows that the Ocean Beach and Santa Barbara Island sites had by far the greatest number of macrophyte taxa (92 and 88, respectively); Santa Cruz Island had considerably more species (13 more) than did San Clemente Island and four more than Santa Catalina Island, both of which are somewhat protected from wave swell. As indicated elsewhere, Ocean Beach has the greatest exposure to surf, and the communities at Santa Barbara Island were displaced upward owing to the heavy surge present there. The increase in macrophyte species, therefore, may have been due to less desiccation stress because of the

Table 2. Seasonal and mean annual macrophyte cover percentage comparisons between study areas.

Study areas	MJJA	SON	DJ	FMA	Mean
	Months				
Island sites					
San Miguel Island	66	66	64	76	68
Santa Cruz Island	82	56	80	54	68
San Nicolas Island	81	84	45	66	69
Santa Barbara Island	76	71	92	74	78
Santa Catalina Island	86	104	102	108	100
San Clemente Island	94	88	104	89	94
Island Means	81	78	81	78	80
Mainland sites					
Coal Oil Point	90	58	74	91	78
Whites Point	66	94	67	63	72
Corona del Mar	87	110	81	71	87
Ocean Beach	93	67	81	79	80
Mainland means	84	82	76	76	79

greater surge allowing a greater number of normally subtidal species to inhabit higher regions. There were far more macroinvertebrate taxa in quadrats sampled at Santa Cruz Island (100) and Santa Catalina Island (96) than at the other study sites. The lowest numbers of invertebrate taxa occurred at San Nicolas Island (51) and Coal Oil Point (56), where sand movement was clearly associated with the dominance of stress-resistant clonal aggregates of *Anthopleura elegantissima* (Francis 1973), a form that our preliminary data (Taylor and Littler 1979) indicate is capable of excluding such colonial space occupiers as *Phragmatopoma californica*.

Cover

Macrophyte per cent cover (seasonal and mean annual) for all sites is presented in Table 2. The yearly mean for overall intertidal cover of macrophytes was clearly greatest at Santa Catalina Island (100 per cent), followed by San Clemente Island (94 per cent) and Corona del Mar (87 per cent). The remainder of the sites contained from 80 to 68 per cent macrophyte cover, with San Miguel and Santa Cruz Islands having the least. All 10 sites displayed seasonality in macrophyte cover, except for San Clemente Island (annual range of only 5 per cent), which is the most sheltered of all the sites. Many of the geographically southern sites (San Clemente Island, Santa Catalina Island, Santa Barbara Island, and Corona del Mar) showed high macrophyte cover from late fall to winter, mainly due to an increase in blue-green algal cover. However, the general tendency for many of the other macrophytes (particularly turf species, epiphytes on turf species, and the large brown kelp *Egregia menziesii*) was to begin an increase of cover in the spring, reach their peak in fall, and then show marked declines associated with the stressful daytime low-tide periods of late fall and winter. This trend may have been especially pronounced during the 1975-76 winter when desiccating "Santa Ana" wind conditions prevailed for at least two weeks during December and January, coinciding with early afternoon low tides. Other factors, such as preferential grazing (Vadas 1977, Lubchenco 1978), environmentally controlled alterations in life history stages (Wynne and Loiseaux 1976), or seasonal growth strategies (Hatcher *et al.* 1977), could also be important.

Table 3. Seasonal and mean annual macroinvertebrate cover percentage comparisons between study areas.

Study areas	MJJA	SON	DJ	FMA	Mean
	Months				
Island sites					
San Miguel Island	23	31	28	24	26
Santa Cruz Island	9	10	8	9	9
San Nicolas Island	21	24	26	33	26
Santa Barbara Island	17	17	15	15	16
Santa Catalina Island	13	14	12	9	12
San Clemente Island	4	7	8	7	6
Island means	16	17	16	16	16
Mainland sites					
Coal Oil Point	37	29	26	18	28
Whites Point	9	5	6	6	6
Corona del Mar	4	5	2	3	4
Ocean Beach	9	15	12	14	12
Mainland means	15	14	12	10	12

The overall intertidal macroinvertebrate cover (Table 3) was highest at Coal Oil Point (28 per cent), followed by San Miguel Island (26 per cent) and San Nicolas Island (26 per cent); these sites were all affected to varying degrees by winter sand movements. The lowest macroinvertebrate cover occurred at Corona del Mar (4 per cent), San Clemente Island (6 per cent), and Whites Point (6 per cent). At half of the 10 study areas, little macroinvertebrate seasonality was apparent; however, seasonal trends were apparent at Coal Oil Point, Ocean Beach, Whites Point, San Nicolas Island, and San Clemente Island. Seasonal periodicity appeared to be closely related to the inundation of parts of the rocky intertidal zone by onshore/offshore sand movements at three of these sites (Whites Point, Coal Oil Point, and San Nicolas Island). Many of the sites showed a late winter to early spring increase of macroinvertebrate cover associated with the decline in frondose algal cover and the recruitment of juvenile barnacles.

Macroinvertebrate Densities

Seasonal and mean yearly macroinvertebrate densities (individuals per square meter) are presented for all sites in Table 4. Coal Oil Point (3,609/m^2) had higher invertebrate densities than any other site, owing to large numbers of *Lacuna* spp. and clonal populations of *Anthopleura elegantissima*. Corona del Mar and Whites Point were by far the most depauperate sites in terms of animal numbers, with 583 and 1,494 per square meter of intertidal substrate, respectively. This is surely due, in part, to sand inundation in the upper rocky intertidal zone where invertebrate numbers usually tend to be very high, but it also may be due to disturbances such as sand and rock abrasion that are particularly stressful to barnacles and other sessile organisms. Very marked seasonality of opportunistic species such as barnacles occurred at all sites; it is felt that the density data are the most useful for depicting seasonal patterns of the

Table 4. Seasonal and mean yearly macroinvertebrate density (nos./m²) comparisons between study areas.

Study areas	Months MJJA	SON	DJ	FMA	Mean
Island sites					
San Miguel Island	3492	1609	2620	1472	2298
Santa Cruz Island	2850	1420	2050	1897	2054
San Nicolas Island	4338	2433	2566	1370	2677
Santa Barbara Island	1483	3232	4301	3574	3148
Santa Catalina Island	1792	2528	2246	2560	2282
San Clemente Island	1890	1901	2676	1816	2071
Island means	2641	2187	2743	2115	2422
Mainland sites					
Coal Oil Point	4645	5233	3536	1022	3609
Whites Point	2709	1094	1082	1092	1494
Corona del Mar	448	665	632	587	583
Ocean Beach	3259	2080	1765	2532	2409
Mainland means	2765	2268	1754	1308	2024

majority of invertebrate taxa. Most of the sites showed a late winter or spring recruitment of barnacle spat during 1975-76.

Wet Biomass

Figure 5 provides mean biomass determinations of wet weight (including hard parts) for macrophytes and macroinvertebrates at each study site. Overall wet biomass was greatest at the Santa Catalina Island site (8,078 g/m²), followed closely by Santa Barbara Island (6,775 g/m²) and Ocean Beach (5,334 g/m²). The disturbed sites, Corona del Mar (2,430 g/m²) and Coal Oil Point (2,661 g/m²), contained by far the lowest standing stocks of all areas sampled. This point is even more significant when one considers that upper intertidal samples (which usually are low in biomass) could not be taken at these two sites because of sand inundation; consequently, only regions characteristic of high standing stocks were sampled. For this reason, Whites Point and San Nicolas Island must be considered areas of only moderate biomass and not directly comparable to sites with high intertidal zones.

Macrophytes dominated the wet biomass at all sites except Santa Cruz Island and Ocean Beach, where large stands of mussels were sampled; *Egregia menziesii* stocks were also very sparse at these two sites. Macrophytes reached a wet biomass maximum at Santa Catalina Island (7,049 g/m²), followed by Whites Point (4,653 g/m²), Santa Barbara Island (4,405 g/m²), San Nicolas Island (3,703 g/m²), and San Clemente Island (3,146 g/m²); all four of these island sites are in the Southern Channel Islands geographic group. Wet macrophyte standing stock was lowest at the oil-polluted Coal Oil Point study area (1,728 g/m²) and at Santa Cruz Island (1,750 g/m²), both of which lacked well-developed brown algal stocks.

Macroinvertebrates had the greatest wet standing stocks at those sites where wave surge was highest (shown by the characteristic upward displacement of zones), namely, Ocean Beach (3,253 g/m²), Santa Barbara Island (2,370 g/m²), and Santa Cruz Island (1,942 g/m²), mostly due to *Mytilus californianus*. The lowest macroinvertebrate standing stock occurred on San Clemente Island (309 g/m²), where mussel beds were not present and wave action was minimal.

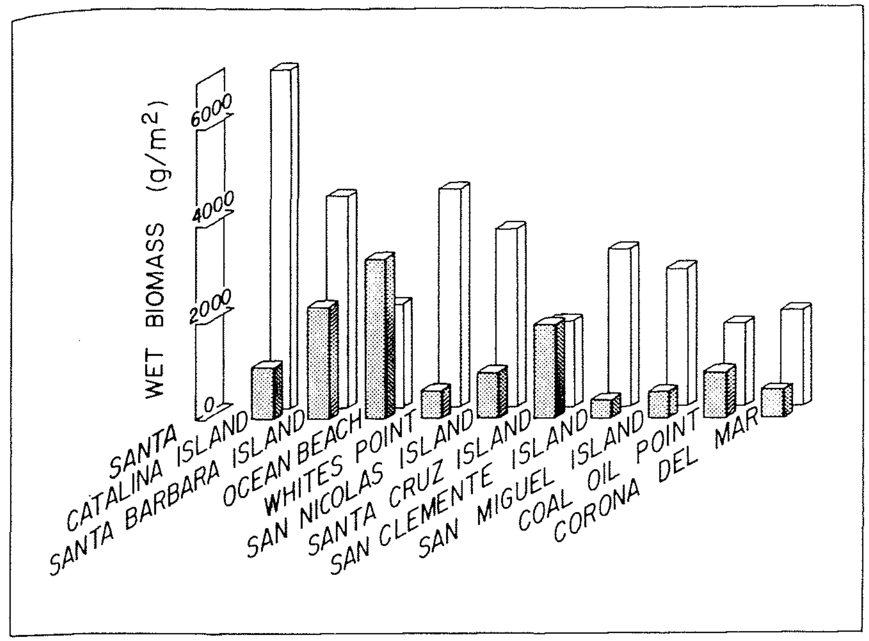

FIGURE 5. *Mean annual wet biomass of macrophytes (histograms in rear) and macroinvertebrates (dark histograms in front) for each study area.*

Dry Organic Biomass

The ash-free dry weight or organic biomass (ODW) is a much better measure of standing stock than is wet biomass (WW) because the latter includes large amounts of inorganic shell and other hard parts. Consequently, a somewhat different picture of the standing stock emerges when dry organic biomass is considered (Fig. 6). The highest dry organic standing stocks were recorded on Santa Catalina Island (1,458 g/m²), followed by San Nicolas Island (896 g/m²), Santa Barbara Island (876 g/m²), Whites Point (659 g/m²), and San Miguel Island (659 g/m²). The last site was very low in wet biomass (Fig. 5). Four sites with low stocks of *Egregia*—Corona del Mar (361 g/m²), Ocean Beach (421 g/m²), Santa Cruz Island (463 g/m²), and Coal Oil Point (466 g/m²)—had considerably lower dry organic standing stocks than any of the other study areas.

In terms of dry organic biomass, the macrophytes overshadowed the macroinvertebrates at all sites (Fig. 6). Macrophytes had their dry organic biomass maximum at Santa Catalina Island (1,396 g/m²), followed by San Nicolas Island (798 g/m²) and Santa Barbara Island (756 g/m²). The macrophyte ODW minimum occurred at Ocean Beach (225 g/m²), with similar low readings from Coal Oil Point (282 g/m²), Santa Cruz Island (288 g/m²), and Corona del Mar (300 g/m²).

Ocean Beach (196 g/m²), Coal Oil Point (184 g/m²), and Santa Cruz Island (174 g/m²) had the largest standing stocks of macroinvertebrates in terms of dry organic biomass. The smallest ODW totals were from San Clemente Island (16 g/m²), Corona del Mar (61 g/m²), Santa Catalina Island (62 g/m²), and Whites Point (63 g/m²). The site with the greatest yearly wave shock exposure (Ocean Beach; Table 1 and Ricketts, Calvin, and Hedgpeth 1968) had a

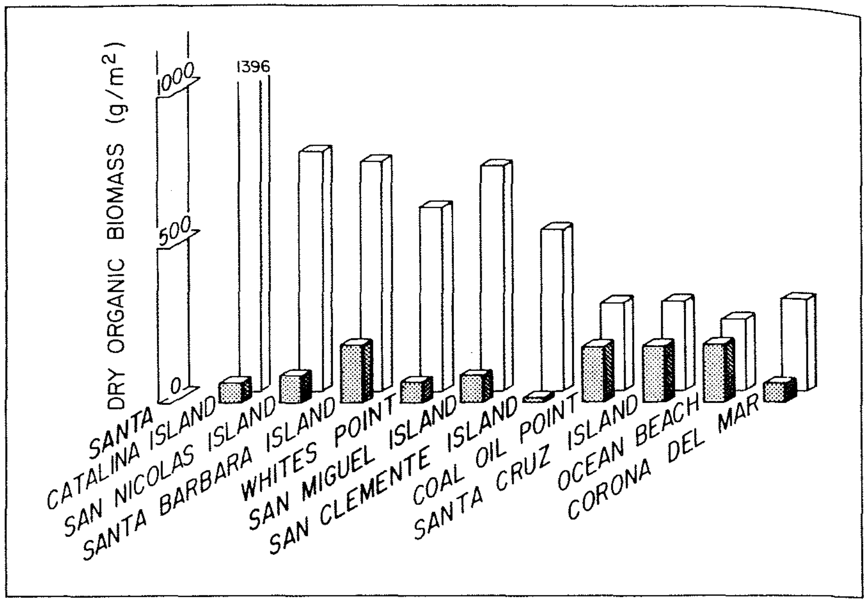

FIGURE 6. *Mean annual dry organic biomass of macrophytes (histograms in rear) and macroinvertebrates (dark histograms in front) for each study area.*

considerably lower proportion of brown algal biomass and a higher proportion of animal biomass (~46 per cent of total mean ODW) than all other sites except Santa Cruz Island (a site also high in wave surge). The two sites on protected leeward sides of islands (*i.e.*, San Clemente Island and Santa Catalina Island) had low macroinvertebrate biomass components (3 and 4 per cent of total mean ODW, respectively).

Richness (D')

Richness indices (D') using combined macroinvertebrate and macrophyte data gave information that closely paralleled the counts of total taxa (Fig. 7). Santa Cruz Island, which appeared to be a stable climax community dominated by long-lived perennials, was considerably richer (D' = 28.86) than the other sites. Richness at Coal Oil Point (D' = 15.42), a community stressed by both oil and sand inundation, was very much lower than at the other sites. Seasonal trends in richness were less at San Miguel Island, Santa Cruz Island, and Ocean Beach than at the other sites.

Evenness (J')

The evenness index (J') combining macrophyte and macroinvertebrate cover data was a most revealing parameter (Fig. 7). Sites high in richness and numbers of taxa were often low in evenness (*e.g.*, Ocean Beach and Santa Cruz Island). San Miguel Island (J' = 0.66), San Nicolas Island (J' = 0.62), Whites Point (J' = 0.63), and Santa Catalina Island (J' = 0.62) had the most equitably distributed biota. Ocean Beach, although it had many taxa and a high richness index, had the lowest evenness index (J' = 0.52). Seasonality in evenness was apparent at Corona del Mar, Santa Catalina Island, Coal Oil Point (peaks in summer), Santa Cruz Island, Ocean Beach (peaks in fall), and Whites Point (peak in winter). The aforemen-

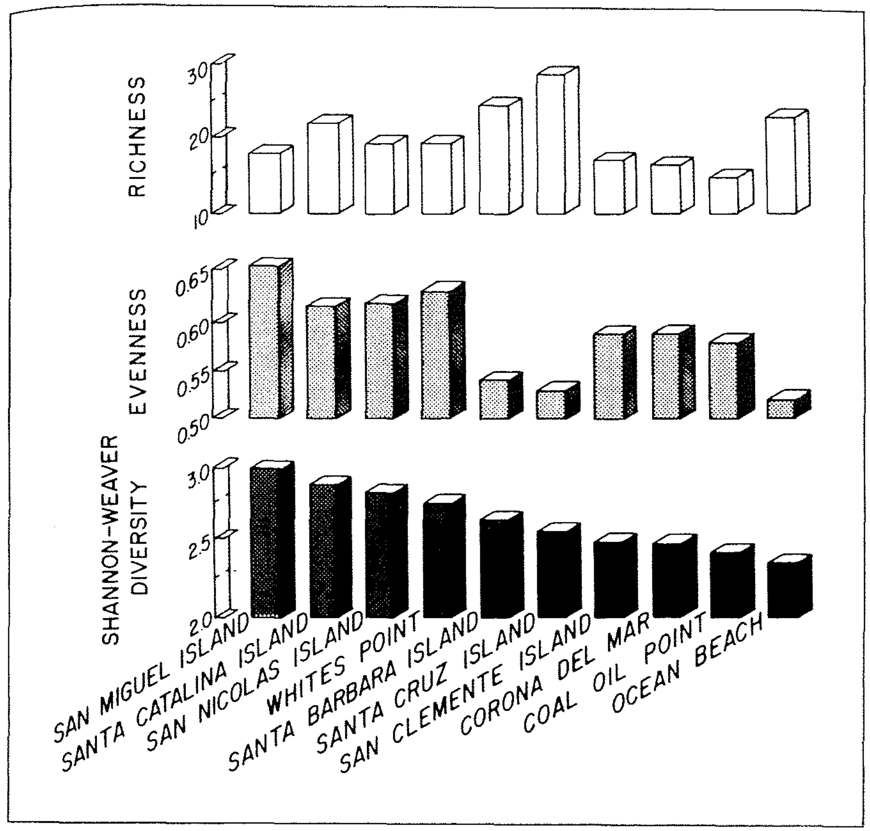

FIGURE 7. *Mean annual richness* (D'_c), *evenness* (J'_c), *and Shannon-Weaver diversity* (H'_c) *for each study area using combined macrophyte and macroinvertebrate cover data.*

tioned sites represent a mixture of pristine, stable sites and sites perturbed by pollution and sand movement. Evenness indices, at least in terms of the levels recorded, do not appear to be particularly indicative of environmental disturbance (to which the populations sampled in this study may have become somewhat adapted).

Shannon-Weaver Diversity (H')

The mean Shannon-Weaver cover diversity (H') for all seasons was greatest at San Miguel Island (H' = 2.95) and Santa Catalina Island (H' = 2.87), both quite stable systems with many taxa showing high cover values (Fig. 7). Low diversities were found at Ocean Beach (H' = 2.43) and the heavily perturbed Coal Oil Point (H' = 2.45), where relatively few taxa dominated most of the substrate. For example, rhodophycean turf, *Phyllospadix*, and *Anthopleura* constituted the bulk of the cover at Coal Oil Point, while blue-green algae, *Corallina*, and *Mytilus* were dominant at Ocean Beach. Seasonal shifts in diversity were apparent at Coal Oil Point (high in summer), Santa Cruz Island (high in fall), Ocean Beach (high in fall), and Whites Point (high in winter). The H' index incorporates both richness and evenness compo-

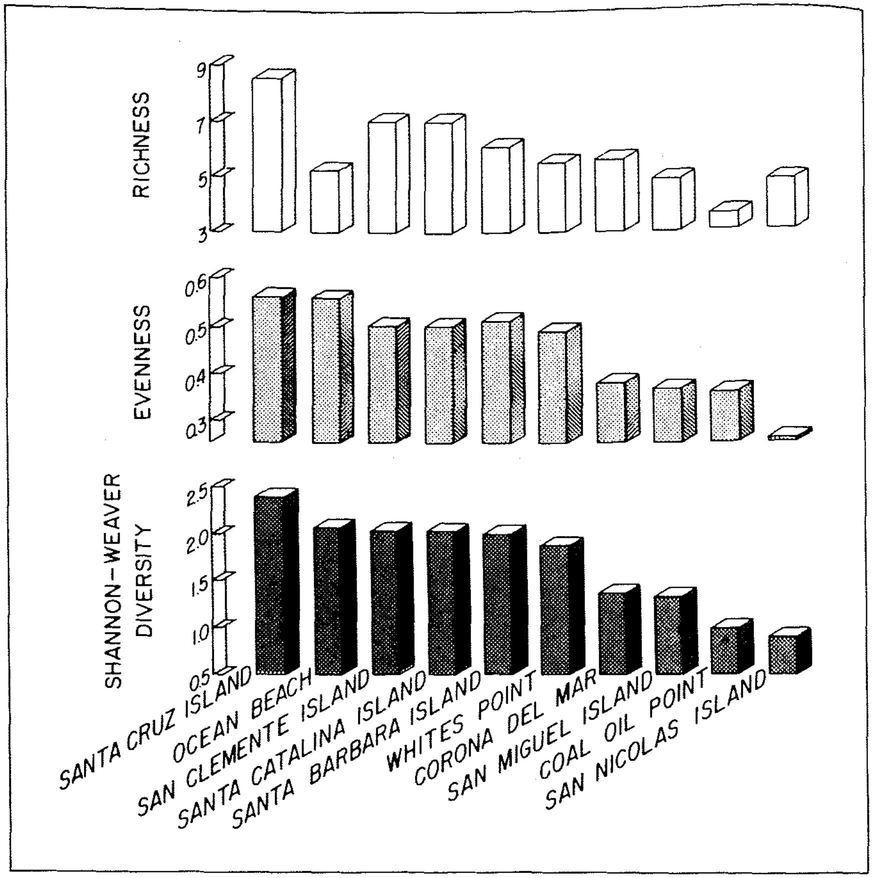

FIGURE 8. *Mean annual richness* (D'_{e})*, evenness* (J'_{e})*, and Shannon-Weaver diversity* (H'_{e}) *for each study area using macroinvertebrate density data.*

nents but stresses evenness. Consequently, as mentioned above for J', our data do not show a clear-cut relationship between the levels of environmental disturbance we observed and Shannon-Weaver diversity, as has been shown by Littler and Murray (1975) for a pristine *versus* disturbed community on San Clemente Island. However, the sand and rock movement forms of disturbance are more localized and intertidal systems may show increased diversity (Levin and Paine 1974) as a result of patches containing successional seres.

Shannon-Weaver indices employing macroinvertebrate density as the evenness component (Fig. 8) revealed that Santa Cruz Island ($H' = 2.34$) far exceeded other sites in animal diversity; this finding agrees with simple counts of taxa. The two seasonally sand-inundated sites (Coal Oil Point and San Nicolas Island) had considerably lower macroinvertebrate diversities than the other sites ($H' = 1.08$ and 0.91, respectively), reflecting the predominance of sea anemones and *Lacuna* spp. at the former and sea anemones and littorines at the latter.

Cluster Analysis

Sites having the greatest number of seasonally constant species assemblages or subassemblages (revealed by the cluster analyses) were San Miguel Island with 11, Ocean Beach with 10, and Santa Catalina Island with 8 (Figs. 2 and 3). Corona del Mar and San Nicolas Island had only six assemblages and these changed in close association with environmental features at each site. The greatest zonational complexity was observed at Santa Cruz Island (seven zones), Santa Barbara Island (seven zones), San Miguel Island (six zones), and Santa Catalina Island (six zones). Greater zonational complexity occurred over relatively even flows of very rough-textured volcanic rock. The least zonation was evident at Corona del Mar (two zones), Coal Oil Point (three zones), Whites Point (four zones), and San Clemente Island (four zones). Reductions in zonal patterns appear to be related to lack of a high intertidal zone, mosaic habitat patterns, instability of boulder substrates, and environmental stresses such as sand inundation.

All 10 sites were subjected to cluster analysis based on the combined overall mean abundances of both macrophyte and macroinvertebrate populations. The wet weight dendrogram (Fig. 9) indicated a close grouping between the two mainland sites, Whites Point and Corona del Mar, both of which are subjected to high levels of stress from substrate instability and human disturbance. The next most closely correlated sites, Santa Barbara Island, Santa Cruz Island, and Santa Catalina Island, all have uniformly sloping volcanic rock substrates. San Miguel Island and San Nicolas Island, both of which are relatively cold-water sites, were also grouped together.

The dendrogram based on organic dry weight (Fig. 9) showed groupings similar to the aforementioned. It is somewhat enigmatic that, based on both wet weight and organic dry weight, the most northern site (Coal Oil Point) and the most southern site (Ocean Beach) are more similar to one another than either is to any other cluster. This was mostly due to the large biomass contributions by mussels and *Phyllospadix*, large species found abundantly in both warm and cold water, at these otherwise dissimilar sites. The San Clemente Island site was not closely correlated with the other nine sites because of its substantially lower macroinvertebrate biomass.

Cluster dendrograms using frequency and cover (Fig. 10) are more revealing and statistically more reliable because they are based on a greater number of samples (*i.e.*, the photo-samples). Frequency distributions showed groupings between the two warm-water biotas (Santa Catalina and San Clemente Islands), the two biologically intermediate islands (Santa Barbara and Santa Cruz), and the two sites most heavily affected by sand inundation (San Nicolas Island and Coal Oil Point).

Because space and light have been shown (see Connell 1972) to be limiting resources in the rocky intertidal zone, cover is ecologically the most meaningful parameter for comparison between sites. The cover dendrogram (Fig. 10) produced groupings that agreed closely with our opinions (based on subjective observation) regarding the similarities and dissimilarities between sites. For example, the island sites having mixtures of cold-water and warm-water biotas (Santa Barbara and Santa Cruz) clustered together with the Ocean Beach habitat, which also had large amounts of macroinvertebrate cover. The two leeward warm-water sites (Santa Catalina and San Clemente Islands) were next most similar to these two, while the two disturbed mainland sites (Whites Point and Corona del Mar) were correlated with the aforementioned to a lesser extent. The two cold-water sites (San Miguel and San Nicolas Islands) formed a second cluster group, while the oil-polluted site (Coal Oil Point) was not closely correlated with any of the other sites. The above patterns are basically similar to those determined independently from binary (presence/absence) data for the island macrophytes (Murray, Littler, and Abbott 1980) and macroinvertebrates (Seapy and Littler 1980).

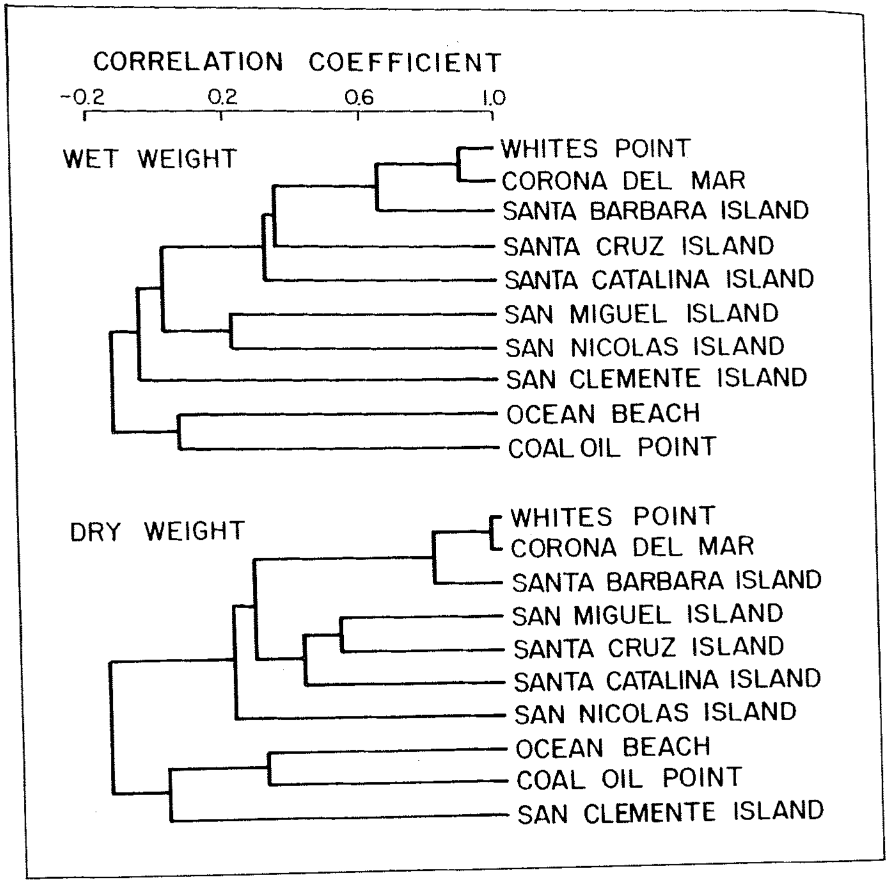

FIGURE 9. *Dendrogram displays of differential clustering for all 10 study areas using combined macrophyte and macroinvertebrate wet biomass and dry organic biomass data.*

OVERALL PATTERNS

Overall, it would appear that water temperature determined by oceanic currents accounts for much of the broad-scale, biogeographic pattern (Fig. 10, Seapy and Littler 1980, Murray, Littler, and Abbott 1980). Operating at a less coarse level are factors such as wave action and coastal upwelling, which usually lead to richer intertidal communities in moderate quantities. As indicated below, a still finer (site-specific) level of organization would seem to be related to factors such as substrate stability, sand inundation, substrate hardness and heterogeneity, desiccation stress, human-induced disturbances, and natural disturbances such as storm waves, floods, and sedimentation. Within this framework, biological interactions (*i.e.*, predation, competition, diseases) have been shown (Paine 1966, Connell 1972, Dayton 1971, 1975, Lubchenco 1978) to play an important role in determining local patchiness. It is well known that limpets and littorine snails significantly reduce algal cover in the upper intertidal zone (Castenholz 1961, Haven 1973, Lubchenco 1978), that urchins devastate algal stocks in pools (Paine and Vadas 1969) and shallow subtidal habitats, and that *Pisaster* plays a key role in maintaining community diversity by reducing the competitively dominant mussel beds (Paine 1966). These same biological interactions were clearly present throughout the Southern California Bight, but, in addition, we observed many others which will be analyzed in subsequent papers. For example, we currently have manipulative studies under way (Taylor and Littler 1979) which are beginning to show that large populations of *Haliotis cracherodii*, still abundant on some islands (San Nicolas, San Miguel, Santa Rosa, San Clemente), are able to cross the barnacle-dominated zone at night during high tides and severely reduce the conspicuous *Gigartina* and *Endocladia* stocks in the upper intertidal region. Also, at sand-inundated sites (San Nicolas Island, Coal Oil Point) where clonal colonies of *Anthopleura elegantissima* predominate, presumably because of their ability to "stretch" through shallow sand layers to avoid burial, they are able to prevent the settlement and development of *Phragmatopoma californica* colonies (Taylor and Littler 1979). An extremely important organism in the lower intertidal zone at most sites would seem to be the angiosperm *Phyllospadix*. This macrophyte was

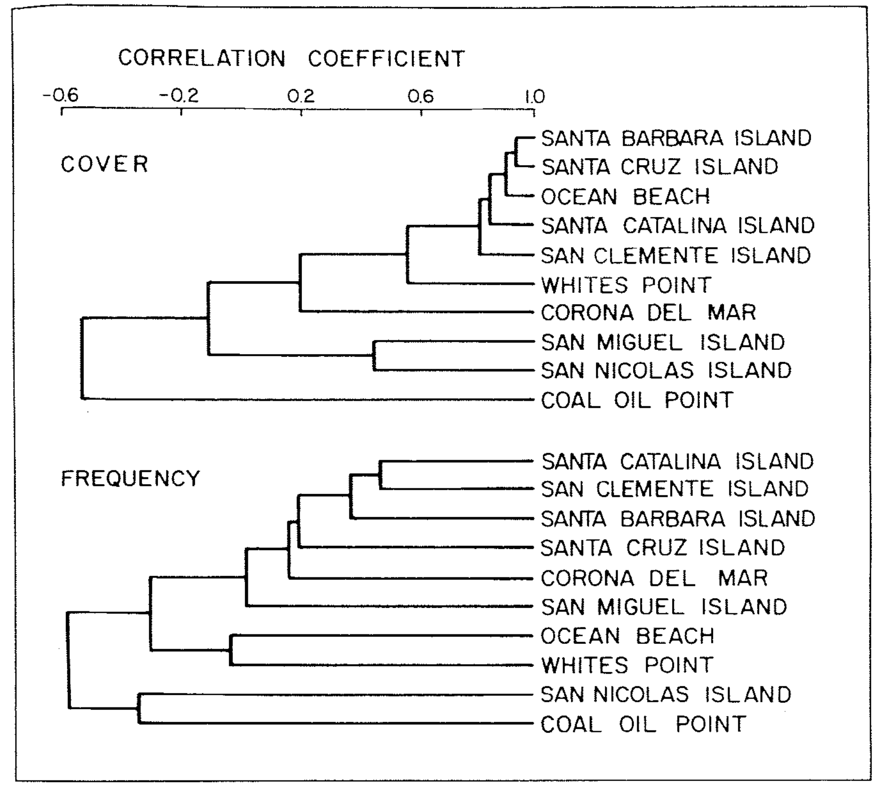

FIGURE 10. *Dendrogram displays of differential clustering for all 10 study areas using combined macrophyte and macroinvertebrate per cent frequency and cover data.*

Table 5. Number of taxa by major taxonomic groups collected at all 10 study areas during 1975-76.

Major groups	Number of taxa collected	Major groups	Number of taxa collected
Macrophytes		Macroinvertebrates	
Bacillariophyta	1	Annelida - Polychaeta	12
Chlorophyta	27	Arthropoda - Crustacea	27
Cyanophyta	4	Cnidaria - Anthozoa	6
Phaeophyta	34	Cnidaria - Hydrozoa	10
Rhodophyta	152	Chordata - Ascidiacea	4
Spermatophyta	2	Echinodermata - Asteroidea	8
Total	220	Echinodermata - Echinoidea	2
		Echinodermata - Holothuroidea	2
		Ectoprocta (Bryozoa)	8
		Mollusca - Bivalvia	15
		Mollusca - Cephalopoda	1
		Mollusca - Gastropoda	97
		Mollusca - Polyplacophora	12
		Platyhelminthes - Turbellaria	3
		Porifera - Calcarea	2
		Porifera - Demospongiae	18
		Total	227

observed over the course of the study to overgrow *Strongylocentrotus purpuratus* populations, which appear unable to graze it, and to smother the bigger algal forms by its invasive root and rhizome system which traps and binds sand, producing anaerobic conditions that are lethal to algal holdfast systems. The competitive dominance of *Phyllospadix* seems to be prevented in the intertidal zone by its relatively great susceptibility to periods of desiccation during daytime low-tide periods.

A total of 447 taxa was recorded during 1975-76 (Table 5). The number of macrophyte taxa (220) was about equal to the number of macroinvertebrate taxa (227). Over half of the macrophytes recorded were Rhodophyta, but Phaeophyta (especially *Egregia menziesii*) was the major contributor of biomass. Of the macroinvertebrates, gastropods contained by far the most taxa (97), while bivalves dominated the biomass.

As mentioned, biological cover in the rocky intertidal zone is of considerable interest because space and light are often limiting resources. Major macrophytic cover throughout the 10 sites was contributed predominantly by blue-green algae (overall mean of 20 per cent), *Corallina* spp. (9 per cent), *Gigartina canaliculata* (8 per cent), *Egregia menziesii* (6 per cent), and *Phyllospadix* spp. (4 per cent). Most of these were important at many of the sites, except for *Phyllospadix* spp. which was abundant only at Coal Oil Point and San Nicolas Island (the two sites most affected by sand), while blue-green algae were important at all other sites. In terms of cover, the dominant macroinvertebrates were the anemone *Anthopleura elegantissima* (3 per cent overall cover), the mussel *Mytilus californianus* (2 per cent), and the barnacles *Chthamalus fissus*/*dalli* (2 per cent). These four were present at most sites; however, *A. elegantissima* was predominant only at Coal Oil Point and San Nicolas Island.

Organic dry weight is also an ecologically significant parameter because it represents the standing stock of organically bound energy potentially available to higher trophic levels. In regard to biomass, *Egregia menziesii* was by far the predominant organism, with an overall mean of 155 g/m^2, followed by *Pelvetia fastigiata* (70 g/m^2), *Phyllospadix* spp. (70 g/m^2), *Eisenia arborea* (57 g/m^2), *Gigartina canaliculata* (56 g/m^2), *Halidrys dioica* (48 g/m^2), and *Corallina* spp. (29 g/m^2). All of these exhibited widespread importance except *Phyllospadix* spp. (abundant at four sites), *Pelvetia fastigiata* (predominant only at three sites), and *Eisenia arborea* (dominant only at Santa Catalina Island). Macroinvertebrate biomass throughout the 10 sites resided mainly in *Anthopleura elegantissima* (33 g organic dry weight/m^2), *Mytilus californianus* (22 g/m^2), the purple urchin *Strongylocentrotus purpuratus* (9 g/m^2), and the barnacles *Tetraclita squamosa rubescens* (4 g/m^2) and *Chthamalus fissus*/*dalli* (2 g/m^2). All of these exhibited widespread abundance except *T. squamosa rubescens* which was an important contributor of biomass at only four of the sites; most of the *A. elegantissima* biomass occurred at Coal Oil Point, while Santa Cruz Island and Corona del Mar contained most of the *S. purpuratus* biomass.

Table 6. Seasonal and mean annual population and community attributes averaged for all 10 study areas.

Parameters	Months MJJA	SON	DJ	FMA	Mean
Macrophyte cover (%)	82	80	79	77	80
Macroinvertebrate cover (%)	15	16	14	14	15
Macroinvertebrate density (nos./m^2)	2691	2220	2347	1719	2244
Richness (D'_e)	18.96	19.78	21.14	22.47	20.59
Evenness (J'_e)	0.59	0.60	0.58	0.57	0.58
Combined Shannon-Weaver diversity (cover)	2.62	2.71	2.69	2.62	2.66
Macroinvertebrate Shannon-Weaver diversity (density)	1.77	1.58	1.77	1.64	1.69

Three nearly ubiquitous intertidal zones have been broadly defined by Stephenson and Stephenson (1972) based on their extensive worldwide studies: (1) an upper littorine-blue-green algal zone, (2) a middle barnacle zone, and (3) a wetter, lower zone covered by coralline algae with abundant Phaeophyta at the lowest margin. These same generalized zones are clearly recognizable at all of the sites we investigated that have a continuous rocky slope. As indicated earlier, we were able to further differentiate from three to seven subzones and six to eleven subassemblages (depending on the particular site) within these three generalized zones by means of cluster analysis (Figs. 2 and 3).

When the seasonal means are averaged for all 10 sites and compared (Table 6), the general lack of any widespread or consistent patterns, except for a very slight lowering of most parameters following the winter months, strongly suggests that local or even site-specific conditions tended to predominate most often and obscure any broad climatic effects. This agrees with other descriptive studies (Stephenson and Stephenson 1972) of rocky intertidal systems that have also demonstrated a high degree of autonomy. Climatic conditions appeared to influence the subtler but more widespread populational declines in late fall and winter manifested by such macrophytes as *Egregia menziesii*, *Phyllospadix torreyi*, *Laurencia pacifica*, *Sargassum agardhianum*, and *Gigartina canaliculata*; this tendency may have been particularly noticeable because 1975-76 was characterized by pronounced drought conditions

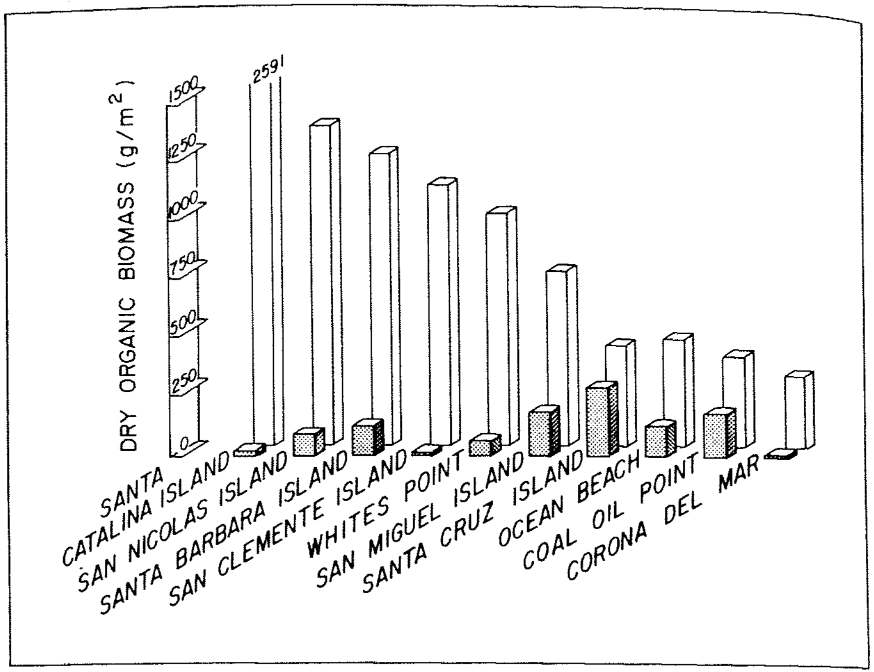

FIGURE 11. *Mean annual dry organic biomass of macrophytes (histograms in rear) and macroinvertebrates (dark histograms in front) for the lowest three 0.3-m intervals sampled at each study area.*

when winter desiccating ("Santa Ana") winds prevailed, coinciding with early afternoon low tides. Additionally, such catastrophic mortalities also have been observed for populations of upper intertidal limpets (Sutherland 1970) due to heat and desiccation when low tides occur during midday. Macrophytes and most macroinvertebrates recruited strongly during the winter-spring period, while the sea hare *Aplysia californica* was observed producing abundant egg masses in late July at Corona del Mar. Numerous workers (*e.g.*, Emery 1960, Jones 1971) have pointed out that the Southern California Bight is a very unusual system located within the overlapping boundaries of two major biogeographic regions containing a complex oceanographic and climatological regime. Throughout the Southern California Bight there exists a mosaic of frequently changing water temperatures, substrates, upwelling conditions, wave exposures, water transparencies, levels of natural and human-induced disturbances, and nutrient concentrations. It is not very surprising, therefore, that "representative" intertidal systems should show a high degree of site-specific individuality.

The data appear to suggest a trend in regard to substrate type. For example, those sites (San Miguel, Santa Cruz, Santa Barbara, and Santa Catalina Islands) having relatively even slopes created by flows of the very rough-textured volcanic rock (which holds small pockets of moisture) had considerably more macroinvertebrate taxa (mean of 80) than the other six sites (mean of 62); San Miguel Island was an exception with only 55. Corona del Mar (71), Whites Point (69), and San Clemente Island (65) were reasonably high in macroinvertebrate taxa, possibly due to the relatively structured nature of the substrate at these sites (*i.e.*, nearby

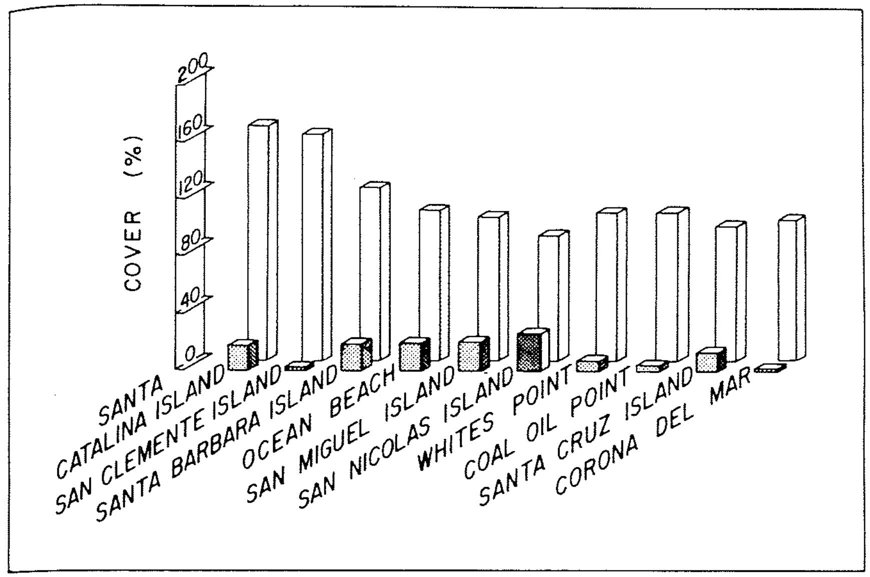

FIGURE 12. *Mean annual cover of macrophytes (histograms in rear) and macroinvertebrates (dark histograms in front) for the lowest three 0.3-m intervals sampled at each study area.*

boulder habitats having a broad spectrum of sizes and stabilities). The three remaining sites, which were entirely smooth sandstone or siltstone, contained a mean of only 55 macroinvertebrate taxa. Also, the greatest zonal complexity and constancy was observed for the same four volcanic island sites (mean of 6.5 zones), followed by siltstone/sandstone habitats (Coal Oil Point, San Nicolas Island, Whites Point, and Ocean Beach), which have an average of 4.2 zones, and boulder habitats (Corona del Mar and San Clemente Island), with the mean number of zones being only 3.0. Sites shown to be periodically inundated by sand (Coal Oil Point, San Nicolas Island, and Whites Point) had an average of 4.0 zones that were altered seasonally; areas lacking a high intertidal zone (Coal Oil Point, San Nicolas Island, Whites Point, and Corona del Mar) had a mean of 3.5 zones. Reductions in zonal pattern were most closely related to a reduction in vertical extent of the rocky shoreline, to the mosaic-like habitat distribution in the case of boulder beaches (noted also by Seapy and Littler 1978), to instability of boulder substrates, and to environmental perturbations such as sand inundations. These last two factors were shown to have especially dramatic effects, a point not very well documented in the existing literature on intertidal ecology (see Cimberg, Mann, and Straughan 1973, Daly and Mathieson 1977).

It is interesting and quite revealing to compare island with mainland rocky intertidal habitats. First, a direct comparison was made between sites, taking into consideration only the lower portions of the shoreline. The means for the lowest three 0.3-m intervals that could be sampled intertidally throughout the year were determined for each of the 10 sites and are presented in Figures 11 and 12. The average lower zone dry organic biomass (Fig. 11) for the island habitats studied (1,355 g/m²) was more than double that for mainland sites (620 g/m²). The bulk of this biomass was contributed by macrophytes (1,238 and 527 g/m² for island and mainland sites,

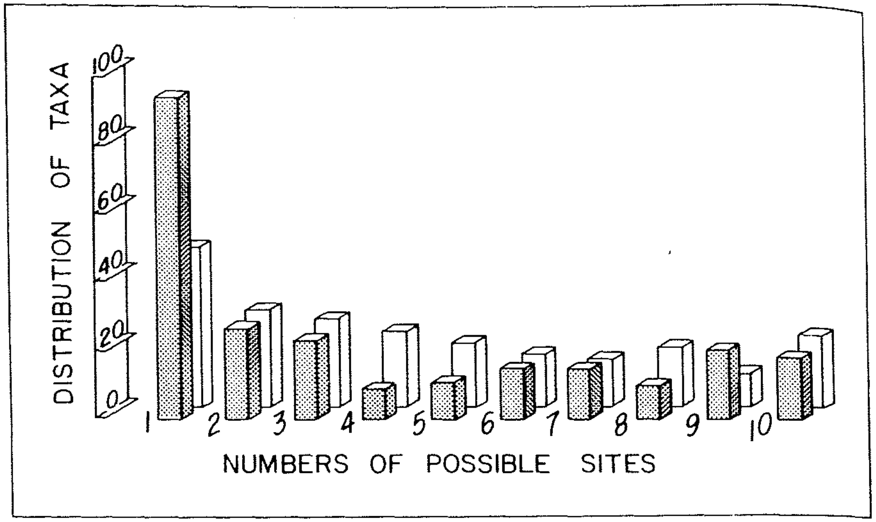

FIGURE 13. *Numbers of macrophyte (histograms in rear) and macroinvertebrate (dark histograms in front) taxa as a function of the number of sites at which they were collected.*

respectively) and mostly resided in the larger brown algae (*e.g., Egregia, Halidrys, Eisenia*) and surf grasses (*Phyllospadix* spp.). The same trend held for comparisons between lower intertidal macrophytic cover (118 per cent island *vs.* 102 per cent mainland) but the differences were not as pronounced as in the case of biomass (Fig. 12). Lower intertidal island dry organic biomass (116 g/m^2) exceeded mainland values (92 g/m^2) for macroinvertebrates and the same was true for the cover data (17 per cent island macroinvertebrate *vs.* 9 per cent mainland).

Even considering that there were more island sites sampled (six *vs.* four), the higher numbers of taxa, particularly of macroinvertebrates, that occurred only on islands are striking. Of the macrophytes taken in the quadrat samples, 117 were common to both island and mainland sites, 25 were from mainland sites only, and 39 were found uniquely in island samples. For macroinvertebrate taxa, 86 were common to both islands and mainland, 33 were only in mainland samples, and 86 were sampled only from islands.

Relatively more taxa (45 to 140) were sampled at three or less sites (Fig. 13), while many fewer (15 to 28) were found at more than five sites; this relationship applied to both macrophytes and macroinvertebrates. There were 15 macrophytes and 13 macroinvertebrates that occurred in samples at all 10 of the study areas (Table 7) and another somewhat smaller group (6 macrophytes and 12 macroinvertebrates) was sampled at 9 of the 10 sites. It is quite revealing that the site where most (66 per cent) of these otherwise ubiquitous macrophytes did not occur was Whites Point. There were two other sites where certain widespread macroinvertebrates also were not sampled: Coal Oil Point, where one-half of these were not present, and San Clemente Island, where one-third were absent.

Coal Oil Point samples, on the other hand, contained the largest number of macrophyte taxa (nine) found only at one site, while Corona del Mar and San Nicolas Island had the fewest (two). Santa Cruz Island had far more site-specific macroinvertebrates (27) and San Nicolas Island had the least (three), followed by Coal Oil Point and San Miguel Island (four). This leads

Table 7. Taxa common to all 10 sites.

Macrophytes	Macroinvertebrates
Benthic diatoms	*Acmaea (Collisella) conus*
Blue-green algae	*Acmaea (Collisella) digitalis*
Bossiella orbigniana ssp. *dichotoma*	*Acmaea (Collisella) limatula*
Ceramium eatonianum	*Acmaea (Collisella) pelta*
Corallina officinalis var. *chilensis*	*Acmaea (Collisella) scabra*
Corallina vancouveriensis	*Acmaea (Collisella) strigatella*
Egregia menziesii	*Anthopleura elegantissima*
Gelidium coulteri	*Chthamalus fissus*
Gelidium pusillum	*Chthamalus dalli*
Gigartina canaliculata	*Cyanoplax hartwegii*
Gigartina spinosa	*Littorina planaxis*
Lithophyllum proboscideum	*Mytilus californianus*
Petrospongium rugosum	*Pachygrapsus crassipes*
Pterocladia capillacea	*Pugettia producta*
Pterosiphonia dendroidea	*Tetraclita squamosa rubescens*

us to hypothesize that the presence of oil may act at Coal Oil Point to eliminate certain widespread species while providing a unique habitat for other more uncommon forms.

Samples could not be obtained from the upper vertical zones because of sand inundation at San Nicolas Island and at Coal Oil Point, Whites Point, and Corona del Mar on the mainland. On the assumption that these sites, as well as the six others, are reasonably representative of their respective habitats (island shorelines are much less subject to sand and gravel inundation than mainland shorelines), we felt that cautious comparisons of tendencies between all of the mainland and island zones sampled would be instructive. In other words, it was essential to document mainland rocky intertidal systems, which often had their upper shorelines inundated by sand and gravel and were thereby poor in upper intertidal fauna. Similarly, it was just as essential to represent the island intertidal systems with stations having well-developed high intertidal faunal assemblages. Also, it should be re-emphasized that two of the mainland sites selected as representative (Whites Point and Corona del Mar) have had considerable histories of human disturbance.

The mean grand totals of all parameters measured for the six island sites and four mainland sites showed the island sites to have higher values than the mainland sites in nearly every respect. One general trend shown by the data is that the southeastern Southern California Islands geographical group (Fig. 1) contains larger macrophyte stocks than the northwestern Southern California Islands geographical group, and mainland sites contain lower stocks than island sites (Fig. 6). For example, islands averaged 813 dry organic g/m^2 (719 dry organic g/m^2 macrophytes and 94 dry organic g/m^2 macroinvertebrates) while mainland sites averaged only 477 dry organic g/m^2 (351 dry organic g/m^2 macrophytes and 126 dry organic g/m^2 macroinvertebrates). A considerable discrepancy existed between the sizes of the island and mainland lower intertidal brown algal standing stocks (*i.e., Egregia menziesii, Eisenia arborea,* and *Halidrys dioica*); these were relatively depauperate and patchy at nearly all mainland sites (although they still dominated the biomass). The apparent reduction of mainland brown algal biomass is likely to be attributable to environmental stress; the data of Littler and Murray (1975) showed a similar considerable reduction in stocks of large brown algae near a sewage outfall on San Clemente Island directly correlated with sewage-induced environmental stress. The greater macrophyte stocks found on the southeastern Southern California Islands geographical group are due primarily to the biomass of *E. menziesii* and *E. arborea* on the warm-water islands (Santa Catalina and San Clemente).

Also, while extensive algal turf communities were prevalent in the middle to low intertidal zones at nearly all sites, the island turfs were composed of larger and more robust populations (mostly coralline algae) with epiphytes primarily of medium-sized frondose algae (*e.g.*, *Gigartina canaliculata, Laurencia pacifica, Colpomenia sinuosa*). However, mainland turf communities (corallines with *Gelidium pusillum, G. coulteri*, or filamentous Rhodophyta) tended to be lower-growing, more compact, and often heavily coated with a predominance of fine, filamentous epiphytes such as: blue-green algae, ectocarpoids, diatoms, and *Ceramium eatonianum* at Corona del Mar; *Herposiphonia verticillata* and *C. eatonianum* at Whites Point; and *Polysiphonia* spp., *Tiffaniella snyderae*, and *Pterosiphonia dendroidea* at Coal Oil Point. The exception on the mainland was Ocean Beach (with a robust coralline turf containing foliose algal epiphytes), a site that apparently has shown few effects of environmental degradation over the last three decades; the biota there closely approximates that found (Stephenson and Stephenson 1972) at a rocky platform north of Scripps pier and nearby Bird Rock during 1947. The only island site with a community of fine, filamentous forms (*C. eatonianum* and *Centroceras clavulatum*) epiphytic on *Corallina* turf (*C. officinalis* var. *chilensis* and *C. vancouveriensis*) was San Nicolas Island, which received considerable perturbation by sand inundation. It is suggested, therefore, that the highly epiphytized compact turf morphology—represented by algal populations having relatively great surface area-to-volume ratios, high reproductive capacities, high growth rates, simple thallus forms, and mechanisms for short and simple life histories (*e.g.*, continuous and rapid output of spores and gametes, perennation, vegetative fragmentation)—may be characteristic of communities in stressed environments. Such populations, particularly at the lower intertidal levels, may in fact make up intermediate seral communities maintained in subclimax by lack of environmental constancy and/or pollution stress.

Other parameters (Figs. 4 and 7) for which island sites exceeded mainland sites were the following: number of taxa (islands 145, mainland 134), richness (islands $D' = 21.90$, mainland $D' = 18.62$), evenness (islands $J' = 0.60$, mainland $J' = 0.58$), and Shannon-Weaver Diversity (islands $H' = 2.74$, mainland $H' = 2.54$).

One important consideration (Table 2) involves the lack of any difference between overall macrophyte cover on islands (80 per cent) compared with mainland sites (79 per cent). Average macroinvertebrate cover (Table 3) on islands was not much greater than on mainland sites (16 *vs.* 12 per cent), but average macroinvertebrate density (Table 4) was considerably lower at mainland sites (2,024 individuals/m^2) than on islands (2,422/m^2).

Several workers (*i.e.*, Dawson 1959, 1965, Nicholson and Cimberg 1971, Widdowson 1971, Thom 1976, Thom and Widdowson 1978) have documented large reductions in the number of macrophytic species over time through human influences (*e.g.*, pollution) on the southern California mainland. We found (Fig. 4), contrastingly, that the average number of macrophyte species occurring in our sample plots at the six relatively unpolluted island sites (72) was nearly equal to the average number at our four mainland sites (71). If it can be assumed that the islands have remained relatively unpolluted and that they historically contained roughly at least as many species as the mainland (both highly likely), then this similarity of species numbers (72 *vs.* 71) could lead to the interpretation that many, if not most, of the species recorded by the above authors as "lost" due to pollution on the mainland must have been rare or uncommon

forms that would not be likely to be found even by extensive quadrat sampling. Another more probable interpretation is that the transect sampling procedures used first by Dawson (1959) on the mainland (*i.e.*, techniques that are appropriate for the measure of abundance [cover or frequency] but which were used instead to report presence and absence of taxa) were such that only very abundant species could be recorded. This would seem to be the case because our methods, which also were not designed to "find" species but to measure distributional patterns, were considerably more effective in recording greater numbers of macrophyte taxa present at Corona del Mar, Coal Oil Point, and Whites Point than were those of either Dawson (1959, 1965) or Nicholson and Cimberg (1971). Thus, if human effects caused declines but not disappearances, as our data contrasting island with mainland biomass indicate, subsequent use of the Dawson method would record fewer species, although the original number could still be present in the area. It is likely that both declines in abundance and actual loss of rare forms explain the results recorded by workers who repeated Dawson's (1959) original sampling methods.

Some of the differences we found between island and mainland community parameters—such as total species numbers, richness, evenness, and Shannon-Weaver diversity—can be attributed to the absence of samples from the sand-inundated high intertidal habitat, usually dominated by animals, at three of the four mainland sites. On the other hand, the absence of a high intertidal zone makes the lower values of overall mean macrophyte dry organic biomass and macrophyte cover for mainland sites even more striking because only the low to middle zones, which normally contain the bulk of the macrophyte stocks, were sampled. The observation that overall mean macroinvertebrate biomass was higher for the mainland sites is not surprising because the lower zones contain macroinvertebrates with relatively high biomass.

SUMMARY

The data presented are the product of intensive research during 1975 and 1976 into the taxonomy, distribution, and abundance patterns shown by rocky intertidal macrophytes and macroinvertebrates at 10 representative study sites within the Southern California Bight. Temporal and spatial variations of the biota were analyzed in terms of tidal location, cover, frequency, density, wet weight, dry weight, ash-free dry weight, species diversity, evenness, richness, and species assemblages to characterize a spectrum of intertidal ecosystems and to relate salient aspects of changes in standing stocks to possible causal factors. The attempt has been made to describe the important features within each study area, to compare the 10 sites, and to emphasize overall patterns and general trends. The methodology used has been explained in considerable detail since some of it is new or has not appeared elsewhere.

A total of 447 taxa was recorded. The number of macrophyte taxa (220) was about equal to the number of macroinvertebrate taxa (227). Major macrophytic cover throughout the 10 stations was contributed predominantly by blue-green algae (overall mean of 20 per cent), *Corallina* spp. (9 per cent), *Gigartina canaliculata* (8 per cent), *Egregia menziesii* (6 per cent), and *Phyllospadix* spp. (4 per cent). In terms of cover, the dominant macroinvertebrates were the anemone *Anthopleura elegantissima* (3 per cent overall cover), the mussel *Mytilus californianus* (2 per cent), and the barnacles *Chthamalus fissus/dalli* (2 per cent). In regard to biomass, *Egregia menziesii* was by far the most predominant organism, with an overall mean of 155 dry organic g/m^2, followed by *Pelvetia fastigiata* (70 g/m^2), *Phyllospadix* spp. (70 g/m^2), *Eisenia arborea* (57 g/m^2), *Gigartina canaliculata* (56 g/m^2), *Halidrys dioica* (48 g/m^2), and *Corallina* spp. (29 g/m^2). Macroinvertebrate biomass throughout the 10 sites resided mainly in *Anthopleura elegantissima* (33 g organic dry weight/m^2), *Mytilus californianus* (22 g/m^2), the purple urchin *Strongylocentrotus purpuratus* (9 g/m^2), and the barnacles *Tetraclita squamosa rubes-*

cens (4 g/m²) and *Chthamalus fissus/dalli* (2 g/m²). In regard to abundance patterns, site-specific conditions tended to predominate most often and obscure any broad climatic effects. Climatic conditions appeared to influence the subtler but more widespread population changes manifested by such macrophytes as *Egregia menziesii, Laurencia pacifica, Sargassum agardhianum,* and *Gigartina canaliculata*. Macrophytes and most macroinvertebrates recruited strongly during the winter-spring period. Those sites (San Miguel, Santa Cruz, Santa Barbara, and Santa Catalina Islands) having relatively even slopes created by flows of the very rough-textured volcanic rock (which holds small pockets of moisture) had considerably more macroinvertebrate taxa (mean of 80) than the other six sites (mean of 62); San Miguel Island was an exception with only 55. Corona del Mar (71), Whites Point (69), and San Clemente Island (65) were reasonably high in macroinvertebrate taxa, possibly related to the relatively structured nature of the substrate at these sites (*i.e.*, nearby boulder habitats having a broad spectrum of sizes and stabilities). Reductions in zonal pattern were most closely related to a decreased vertical extent of the rocky shoreline, mosaic-like habitat distribution in the case of boulder beaches, instability of boulder substrates, and environmental disturbances such as sand inundation. The mean grand totals of all parameters measured for the six island sites and four mainland sites showed the island sites to have higher values than the mainland sites in nearly every respect. Considerable variation existed in the size of the lower intertidal brown algal standing stocks (*i.e.*, *Egregia menziesii, Eisenia arborea,* and *Halidrys dioica*), which were relatively depauperate and patchy at nearly all mainland sites (although they still dominated the biomass). Also, while extensive algal turf communities were prevalent in the middle to low intertidal zones at nearly all sites, the island turfs comprised larger and more robust populations (mostly coralline algae) with epiphytes primarily of medium-sized frondose algae. Mainland turf communities (corallines with *Gelidium pusillum, G. coulteri,* or filamentous Rhodophyta) tended to be lower-growing, more compact, and often heavily coated with a predominance of fine, filamentous epiphytes. Other parameters for which island sites exceeded mainland sites were the following: number of taxa (islands 145, mainland 134), richness (islands $D' = 21.90$, mainland 18.62), evenness (islands $J' = 0.60$, mainland 0.58), and Shannon-Weaver Diversity (islands $H' = 2.74$, mainland 2.54). It is likely that both declines in abundance of many species and the actual loss of uncommon forms due to disturbances have occurred at mainland habitats near large human population centers.

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