6 Southern California Rocky Intertidal Ecosystems: Methods, Community Structure and Variability

MARK M. LITTLER

Department of Ecology and Evolutionary Biology, University of California, Irvine, California, U.S.A.

Abstract: No comparable spectrum of rocky intertidal systems has previously been examined to the level of sampling effort and synoptic overview provided herein. The scope of this work is such that temporal and spatial variations of the macroinvertebrate and macrophyte species have been assessed in terms of tidal location, cover, frequency, density, wet weight, dry weight, ash-free dry weight, species diversity, evenness, richness and cluster analysis. These descriptive parameters were used at each of 12 representative sites during four separate quarters of 1976–1977 to characterize a spectrum of intertidal systems and to relate important aspects of distribution and abundance to possible causal (biotic and abiotic) features of the environment.

Many of the methods employed were newly developed and have not been treated in detail in the scientific literature. In particular, the undisturbed sampling method, utilizing permanently-marked sampling locations, provides a powerful tool for quantification of seasonal and yearly biological differences and this is what we have emphasized. This procedure has the advantage of being rapid and simple to use, thus enabling a greater number of samples to be taken per unit of time. When used with infrared film, the technique permits the quantification of blue-green algae, the predominant cover organisms in most rocky intertidal habitats. This system also permits a high degree of quality control because photo-samples scored by various individuals can be reviewed

---

Systematics Association Special Volume No. 17(b), "The Shore Environment, Vol. 2: Ecosystems", edited by J. H. Price, D. E. G. Irvine and W. F. Farnham, 1980, pp. 565–608, Academic Press, London and New York.

by the total research staff, including senior taxonomic personnel, to ensure standardization and accuracy in the quantification process. The infrared photographs also emphasize unhealthy thalli with reduced chlorophyll contents that are often masked by accessory pigments; these would otherwise not be visible by color photography or to the unaided eye. Another important feature of the technique is that permanent historic data sets (i.e. photo-samples) are obtained which depict the status of the biota at a given point in time; these may become useful at a future date for purposes not originally intended. Additionally, changes (e.g. due to human disturbance) can easily be documented by direct comparison of photo-samples taken of the same quadrats at different times. Seasonality can also be demonstrated by direct comparisons of photo-samples taken of the identical quadrats over different sampling periods.

The broad range of environmental variability within the Bight results in a complex intermingling of physical conditions that is reflected in the diversity and complexity of intertidal and other biological systems. The present data, and those from the 1975–1976 study (Littler, 1980), strongly suggest that local or even site-specific conditions tend to predominate most often and to obscure broad overall effects. Numerous workers (Emery, 1960; Schwartzlose, 1963; Jones, 1971) have emphasized that the Southern California Continental Borderland is a very unusual region located within the overlapping boundaries of two major biogeographic regions, which results in a complex biological regime. Throughout the Bight, there exists a mosaic of temporally and spatially changing water temperatures, substrate types and slopes, upwelling conditions, wave exposures, water transparencies, levels of natural and human-induced stresses and nutrient concentrations. Therefore, it was not surprising that the different systems showed a high degree of site-specific autonomy.

Overall, water temperature mediated by oceanic current systems accounts for much of the large-scale biogeographic pattern exhibited by rocky intertidal ecosystems in Southern California. Operating at a less coarse level are factors such as wave action and coastal upwelling, moderate levels of which lead to richer intertidal communities. A still finer (site-specific) level of organization would seem to be controlled by such parameters as stability of the substrate, sand inundation, beach slope, desiccation stress, substrate type, level of human disturbance and unpredictable disturbances (e.g. floods or storms). Within this framework, predation and competition among the biotic elements themselves have been shown (Paine, 1966; Connell, 1972; Dayton, 1971, 1975) to be important in fine-tuning of the community structure.

The highly epiphytized, compact turf morphology, characterized by algal populations having relatively great surface-to-volume ratios, large reproductive capacities, high growth rates, simple thallus forms and mechanisms for short and simple life-histories is suggested to be characteristic of communities in stressed environments. As substantiated by the community-recovery data, such populations may in fact be extremely useful in identifying intermediate seral communities maintained in subclimax by lack of environmental constancy or by some form of stress.

PREFACE

This chapter summarizes the second year (1976–1977) biological baseline studies for the rocky-intertidal portion of the Southern California Islands and mainland. The purpose of the 3.8-year (July 1975–April 1979) program was to provide the scientific and resource management communities with a description of the major biological elements present and their variation in space and time throughout the Outer Continental Shelf (OCS) region. Such research constitutes an essential first step towards understanding community dynamics and is critical to the development of future experimental studies.

Sufficient data have now been accumulated and analyzed to provide a reasonable basis for comparisons with conditions at some future date, presumably during petroleum resource development. Knowledge of other variables, such as biogeographic patterns, is being enhanced through additional (1977–1978 and ongoing) rocky-intertidal assessments, while others remain relatively intractable due to their great variability and limitations in analytical resolution. Moreover, the erratic change in weather experienced during the 1977–1978 year of study (i.e. extremely heavy rainfall) may force reassessment of some patterns and conclusions presented here. Nevertheless, we have reached a point where experimental studies designed to elucidate the fundamental processes governing major ecological phenomena have become necessary, and several are under way. The purpose of such studies is to generate predictive capabilities for environmental managers and to focus on key or indicator aspects of the rocky intertidal systems during future monitoring programs.

INTRODUCTION

The Southern California Outer Continental Shelf (Fig. 1) is defined as the triangular area bounded by Point Conception, Tanner and Cortez submarine banks (about 200 km west of San Diego) and the U.S./Mexico International Border. This region is one of the most physiographically intriguing and well-studied continental terraces of the world's oceans. Sheppard and Emery (1941) aptly labelled this area the Southern California Borderland, recognizing its similarity

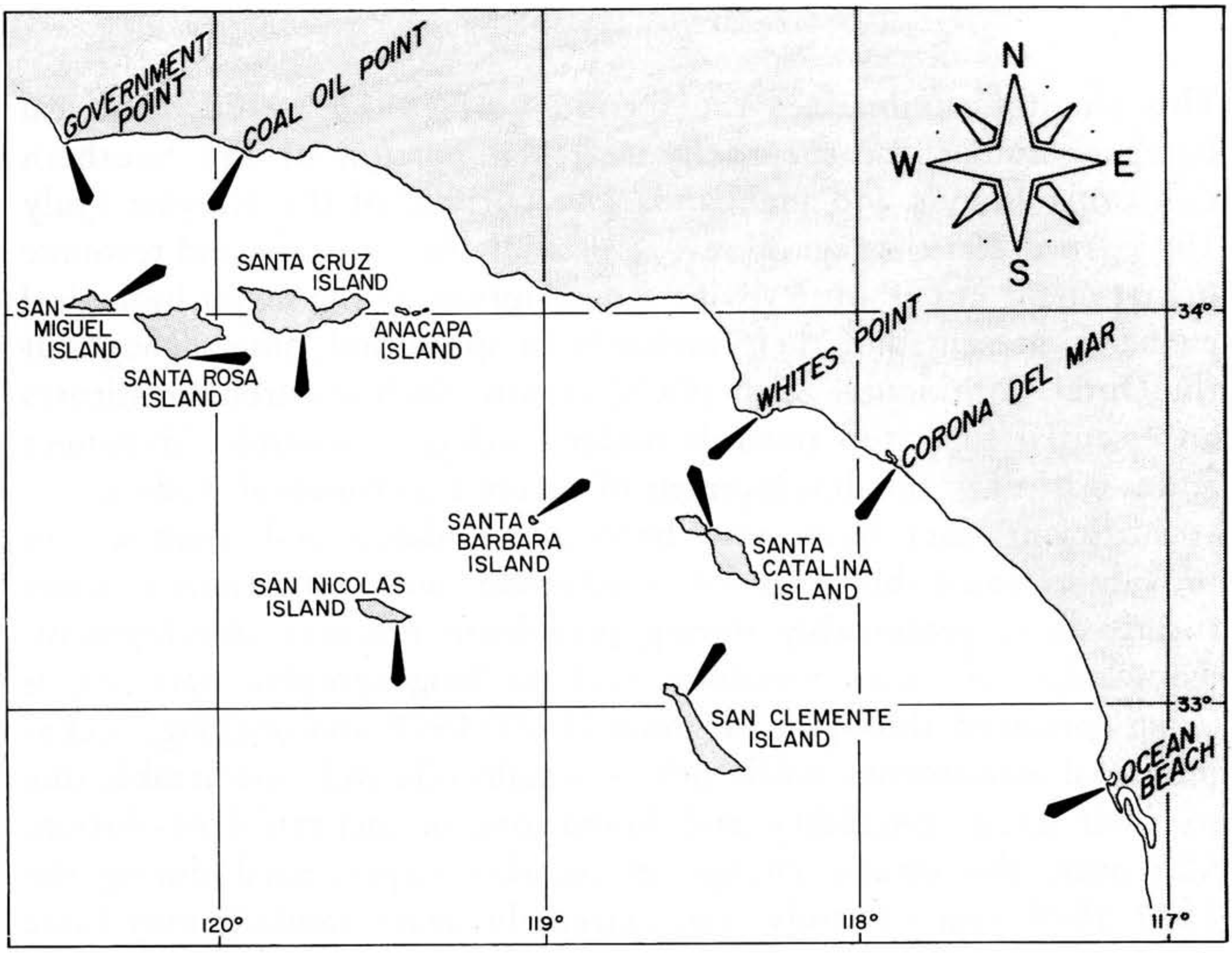

Fig. 1. Location of study sites.

to the adjoining coast. However, due to the concavity of the shoreline south of Point Conception, this region has more recently been referred to as the Southern California Bight (SCCWRP, 1973). Much is known about the climatology of this system (Kimura, 1974); however, published biological information is extremely scarce. Cockerell (1939) has emphasized that the Southern California Bight is unusual because of the effects of both cold and warm water mixing and in certain respects is comparable to such diverse regions as the Galapagos Islands. The changing climatic patterns result in a complex intermingling of physical conditions that are reflected in the broad spectrum and variability of the biological systems within the Bight.

The predominant driving force of water circulation in the Southern California Bight is the cold California Current. This system, a portion of the eastern limb of the clockwise North Pacific gyre, originates in north-west North America and flows southerly along the western coast of the United States. At Point Conception, the northern boundary of the Southern California Outer Continental Shelf (OCS), the coastline turns to the east deflecting the California Current to the south-east. Off northern Baja California, the system divides into two branches, one which curves towards the coast then north through the Channel Islands (forming the Southern California Countercurrent), while a second branch continues south along the coast of Baja California. The north-west flow of the Southern California Countercurrent is a reasonably permanent feature of the circulation pattern (Schwartzlose, 1963), being well developed in the winter but weaker during the spring. In addition to the southerly flowing California Current, the area is influenced by a deep (200 m) undercurrent, the Davidson Current, that also flows north-west along the coast. During late fall and early winter, when northerly winds are weak, the Davidson Current rises to the surface along the coast as far south as the tip of Baja California and flows north past Point Conception (Reid *et al.,* 1958). This system transports warm, highly-saline water great distances along the coast and is in evidence as far north as the state of Washington. While both the Davidson and California Currents include complex systems of eddies and gyres, each flows with moderate speeds of 12–25 cm/s at the surface (5–10 cm/s at 200 m) maintaining net water transport in the two directions.

Apparently neither current system completely dominates the other, although the effect of the Davidson Current diminishes as it submerges during part of the year. However, the deflection of the California Current as it impinges on Point Conception results in the formation of a strong counter-clockwise gyre (most pronounced during the winter months) between the mainland and the northern Channel Islands geographic group (Schwartzlose, 1963). This pattern of surface water circulation has also been substantiated by Hendricks (1977) and a satellite thermal imagery overview is presented in Fig. 2.

Another hydrographic feature is the pattern of wind-driven upwelling. In Southern California this process occurs along both mainland and island shores where strong, steady winds displace surface water in a southerly direction; this surface water is replaced by deep offshore water containing high levels of nutrients. In Southern

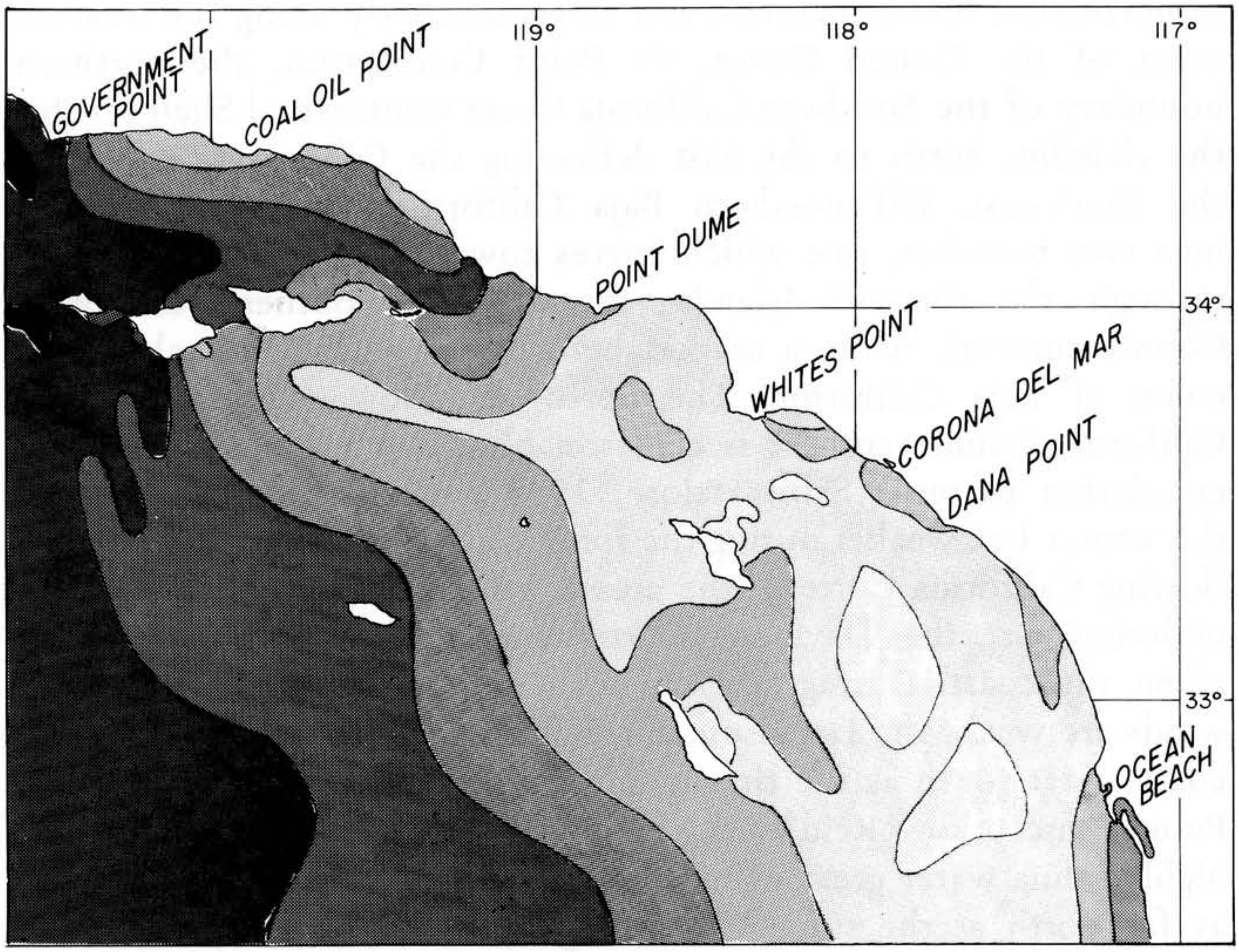

Fig. 2. Distribution of surface water temperatures within the Southern California Bight based on remote sensing (redrawn from the 23 June 1976 NOAA-3 satellite imagery in Hendricks, 1977). Darkest tones represent coldest temperatures with 1.4°C increases for each successively lighter tone.

California, upwelling is most intense in April, May and June; occasionally, wind conditions result in cases of non-seasonal upwelling (Jones, 1971). Upwelling is most intense south of capes and points (e.g. Point Conception) that extend into nearshore current streams (Reid *et al.,* 1958). Such upwelling of deep nutrient-laden water may partially account for the high productivity and richness of the Southern California Bight's biological components. Wind conditions are also important in that major reversals occur (Kimura, 1974) 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 and desiccation stress to intertidal organisms.

An important ecological factor related to water movement on the Southern California OCS 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 *et al.*, 1968). The only mainland sites receiving direct westerly swell are near the cities of Los Angeles and San Diego. The combination of prevailing currents and their associated eddies and gyres, the deflection of currents and swell by island land masses, and wind-driven coastal upwelling results in complex intermixings of distinct water masses, each with its particular hydrographic features.

Rocky shorelines occur throughout the entire coastal area of the Southern California Bight. The rocky-intertidal habitat is found interspersed at irregular intervals with sandy beaches and inlets to lagoons or estuaries. The 12 study sites sampled under this program (Fig. 1) are divided between islands (7) and mainland(5) and, less clearly between north (north-west) and south (south-east). The northern Channel Islands (San Miguel, Santa Rosa, Santa Cruz and Anacapa) form a discrete geographic group with some affinity to the northern mainland sites of Government Point and Coal Oil Point. Similarly, the southern islands (San Nicolas, Santa Barbara, Santa Catalina, San Clemente) together with the three sites to the south of Santa Monica Bay (Whites Point, Corona del Mar and Ocean Beach) may be considered a discrete unit. However, the trend of increasing water temperatures to the south is partially offset by exposure of the outermost islands (San Miguel and San Nicolas) to the eastern margin of the cold California Current system (Fig. 2), so that a division of island sites into northern and southern on the basis of geographic location related to temperature regime is not accurate.

A number of substrate types were represented among the 12 rocky intertidal habitats sampled (Table I), ranging from hard, irregular flow breccia to smooth sandstone or siltstone. Some sites (especially Coal Oil Point and San Nicolas Island) are heavily inundated on a yearly basis by sand, which scours and removes organisms and often completely buries them. Sand appears to be consistently present at these two sites in the upper intertidal, eliminating an entire zonal

Table I. Physiographic attributes of the 12 rocky-intertidal habitats studied

Study areas	Latitude & Longitude	Water temperature	Substrata	Tidal range (m)	Wave exposure	Disturbance source	Sand cover
Government Point	34°26′35″N 120°27′06″W	cold	Monterey shale/siltstone	− 0.3 to + 2.1	exposed (heavy)	oil seeps	mid-intertidal
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
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 Rosa Island	33°53′31″N 120°06′31″W	cold (moderate)	Smooth sandstone	+ 0.3 to + 3.4	exposed (moderate)	none	lower intertidal
Santa Cruz Island	33°57′43″N 119°45′16″W	intermediate	Irregular volcanic breccia	+ 0.3 to + 4.0	surge	none	none
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 Nicolas Island	33°12′54″N 119°28′22″W	cold	Sandstone	− 0.3 to + 1.5	exposed (moderate)	none	extensive
San Clemente Island	33°00′06″N 118°33′03″W	warm	Stable granitic boulders	− 0.3 to + 2.1	protected	none	none

component from the biota. The presence of extensive loose boulder fields (e.g. Whites Point and Corona del Mar) constitutes another form of environmental instability limiting community development. The existence of such natural disturbances in rocky intertidal habitats has important implications in interpreting changes associated with petroleum exploration and development.

The Southern California Bight contains a mixture of relatively low temperature and low salinity water transported from the north by the California Current system and higher temperature and salinity water brought north by the Davidson Current (Maloney and Chan, 1974). Added to this are the effects of seasonal upwelling and the concomitant input of cold nutrient-rich deep water. The mean monthly surface water temperatures on the Southern California OCS range from a low of 13°C in March and April to 20°C in August and September. Although the area over the continental shelf undergoes considerable mixing from differential currents and waves, the system becomes extensively stratified throughout the summer months with the depth of the thermocline rarely exceeding 50 m (Jones, 1971).

Intertidal habitats in Southern California, although little studied, are unique in the U.S.A. owing to their large usage by an exceptionally dense, recreation-oriented, human population. This intensive usage makes the intertidal zone particularly sensitive to additional forms of environmental stresses. The effects of environmental deterioration and general lack of adequate baseline information have posed severe problems, particularly during the past 10 years when attempts have been made to assess the immediate effects of specific pollutants on Southern California coastal organisms. Problems were obvious in the attempts to evaluate the impacts of the Santa Barbara oil spills of 1969 (see Nicholson and Cimberg, 1971; Straughan, 1971; Foster, *et al.*, 1971).

Previous reviews of existing information on intertidal macrophytes (Murray, 1974) and of macroinvertebrates (Bright, 1974) in the Southern California Bight have pointed to the paucity of information on the ecology of this region. The most widely used information has been that of Dawson (1959, 1965) on marine algae. Dawson noted reductions in species numbers ranging from 50 to 70% at sites near sewage outfalls. Others (Nicholson and Cimberg, 1971; Widdowson, 1971; Thom, 1976; Thom and Widdowson, 1978) have since measured further declines in macrophyte species numbers at many of the same areas studied by Dawson. These workers attributed such declines to human influence but presented only circumstantial evidence as documentation. The declines do not seem to have been instantaneous (Nicholson, 1972), but probably are the result of human pressures that have been increasing markedly since the turn of the century. With further expansion of the human population in Southern California, even the marine communities on some of the relatively inaccessible offshore Channel Islands (e.g. Anacapa Island) are being altered (Littler, 1978).

The marine ecosystems of the Southern California Channel Islands have received relatively little scientific attention. Although limited taxonomic lists have been published for Santa Catalina Island (Dawson, 1949; Nicholson and Cimberg, 1971), Santa Cruz Island (Hewatt, 1946), Anacapa Island (Dawson and Neushul, 1966; Neushul *et al.,* 1967) and San Clemente Island (Sims, 1974; Seapy, 1974), quantitative data concerning the ecology of intertidal organisms are available only for San Nicolas Island (Caplan and Boolootian, 1967) and San Clemente Island (Littler and Murray, 1974, 1975, 1978; Murray and Littler, 1978a; Kindig and Littler, 1980).

The research reported here was responsive to the specifications and requirements determined by the Bureau of Land Management. Study sites were selected to cover a broad spectrum of habitats, with the majority located near lease tracts that might have a high probability of being affected by oil development operations. The primary objective was the quantification of biological variability as well as the relation of any variation to possible causal mechanisms. This paper is the synthesis of the first two years (1975–1976 and 1976–1977) of comprehensive investigations along the lines of the following programs: (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.

MATERIALS AND METHODS

The intertidal study of mainland and island rocky shores consisted of several approaches including: (1) determinations of the spatial and temporal variability of dominant intertidal populations at 12 sites; (2) the responses of intertidal communities to natural catastrophic events (such as storms, high surf conditions and floods); (3) recovery rates and patterns of various communities at different times of the year at contrasting tidal heights following artificial disturbance (harvesting), as well as specialized studies undertaken during 1977–1978 concerning (4) assessments of the role of possible key species populations and (5) 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 12 sites are indeed representative of major intertidal systems within the Southern California Bight. We have also developed methods for use in examining the ecological effects of anthropogenic disturbances including: (6) comparative studies of growth rates following transplantation, (7) measurements of primary productivity for dominant rocky intertidal macrophytes (Kindig and Littler, 1980) and (8) calorific investigations of dominant producer and consumer populations (Littler and Murray, 1978). The last two provide energetic data of value for analyzing community function. Although we have extensively used all of these methods over the last several years, only the methods and data resulting from the 1976–1977 baseline analysis of standing stock will be presented here because of space limitations.

1. Standing Stock Sampling and Analysis

Much of our knowledge of benthic marine organisms is based upon subjective observations, although some studies have employed "quasi-quantitative" methods. Among such methods 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), the use of transect lines to estimate cover (e.g. Nicholson and Cimberg, 1971; Widdowson, 1971) and the utilization of metal grids (e.g. Caplan and Boolootian, 1967) to assess 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 space-occupying organisms.

The principal method of sampling the intertidal biota during this study was a photogrammetric technique of undisturbed sampling (modified from Littler, 1968, 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). 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 study site from immediately above the high-water level of intertidal organisms to just below the waterline at low tide thus providing locations for a minimum of 40 samples. The general location of each study area was determined by consulting aerial photographs and maps of the region. 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 lines; this enabled the precise replacement of the transects during seasonal studies. A sampling optimization analysis by the Poisson statistic (Wilson, 1976) revealed that at least 30, 0.15 m^2, samples were required to assess adequately a typical rocky intertidal site. Therefore, approximately 40 rectangular quadrats, 30 cm × 50 cm (0.15 m^2), and 40 square quadrats, 1.0 m × 1.0 m (1.0 m^2), were placed along the transect lines at 1.0 to 3.0-m levels (depending upon the steepness of the shoreline), thereby providing permanent, stratified plots for sampling temporal and spatial distributions of organisms. To furnish statistically-adequate numbers, 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". 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, stainless steel nails, epoxy putty or eyebolts set in "hard-rock" cement. Totals of approximately 2000 0.15 m^2 and 2000 1.0 m^2 quadrats were analyzed during 1976–1977 and compared with the data set from about the same number taken in 1975–1976.

Relative vertical tidal heights for each quadrat were measured from permanent reference points by means of a stadia rod and a standard (20-power) surveyor's transit. A permanent reference point was established at each of the study sites for surveying the tidal heights on 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 on successive days, the midpoint between low and high wave peaks at the time of the predicted (U.S. Department of Commerce Tide Tables, 1976, 1977) low tides. Repeatability of measurements checked on different site visits was $< \pm 0.1$ 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, where available, to characterize further the respective environmental features of each study site (Table I).

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

In the laboratory, the developed pairs of transparencies were projected simultaneously (the IR below the color) 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 on to 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 percentage 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% 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%.

The IR transparency was found to be essential in the delineation of the various species of primary producers (e.g. blue-green algae are dominant forms that can only be discerned reliably on dark, wet substrate by use of IR photography) and in assessing the status of their health. Each species fluoresces differently in the infrared band, according to its chlorophyll content and health (the percentage of dead branches on an algal thallus can be seen more clearly in IR). In cases of multi-layered 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 of greater than 100%. The only organisms removed from the permanent undisturbed quadrats were very small samples taken occasionally for taxonomic purposes.

Two miniature tape recorders and plastic (polypropylene) coated paper 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 sections). It is worthwhile noting that most previous studies stopped at this level of quantification (by estimation *in situ*). We found that such approximations usually could not be repeated precisely (i.e. often exceeding ± 25% for dominant organisms) because of parallax problems and differences between and within observers. Observer differences were influenced by varying degrees of field distractions and stresses, which were especially pronounced during heavy surf and night-time 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 undisturbed samples (i.e. IR and colour transparencies) in the laboratory.

The method as applied here does not allow for the quantification of microalgae, small epifauna or infauna when they occur in low abundances. We realize that these may be metabolically very active, but their analysis requires special techniques and expertise, which latter comprise separate problems in themselves. For this reason, our measurements were restricted to macro-epibiota that could be discerned in the field 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% of the biomass in a given quadrat.

These undisturbed methods were used at a total of 12 different habitats over the two years of study, including re-assessments following catastrophic disturbances (e.g. flooding and storm surf) at two of these sites.

(b) Disturbed samples. Biomass measurements of the standing stock yield 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 organic dry weight values in the same manner as the cover, density and frequency data from the undisturbed method. The disturbed quadrats were selected for their biological similarity to the undisturbed photo-quadrats; 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 margins 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 levels. Approximately 12 plots of each size were taken per

visit at each intertidal site, yielding a total of ~ 1400 disturbed samples from 1975–1977.

In the laboratory, the harvested specimens were identified, packaged and catalogued for determinations of wet, dry and ash-free biomass. After sorting to species, the samples were rinsed quickly in distilled water and weighed in aluminum foil containers of known weight. 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 h 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 time constraints only representative calcifying species have been 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 included ash-free dry weights for organisms with hard parts (e.g. crabs, bivalves, coralline algae) and dry weights for non-calcareous species.

All biomass data were considered on the basis of 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 every 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 the 12 study sites.

(c) Collection of floristic and faunistic data. Additional representative organisms were collected in duplicate, curated, and archived as permanent taxonomic voucher specimens. These were listed by site for disturbed samples, undisturbed samples and collections outside the study quadrats. An effort was made to relate variations in environmental and biological conditions to changes in the composition and organization of intertidal associations. These specimens have been deposited in the Smithsonian Institution's National Natural History Museum, Washington, D.C., U.S.A.

(d) Analyses of data. Information obtained by the photogrammetric sampling method (undisturbed) and by the harvest method (disturbed) provided quantitative information on the distribution of standing stocks in relation to tidal height. These data were summed and averaged to interpret differences in intertidal populations and communities between sites and seasonally within sites. Species cover frequency and density fluctuations have been 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.

Diversity measurements have been widely used by those responsible for assessing the effects of human stresses on biotic communities. Species diversity is often measured by indices that include components of both richness and equitability. The problem with any single index is that both components of diversity are confounded. Many diversity indices also contain the underlying assumption that the ecological importance of a given species is proportional to its abundance. We attempted to avoid these problems by using the standardly-applied Shannon and Weaver (1949) index (H′) (incorporating both richness and evenness) along with separate indices for richness [counts of taxa, Margalef's (1968) D′] and evenness [Pielou's (1975) J′]. These were calculated for the cover data using natural logarithms and used as supplementary information 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, regarding the Shannon-Weaver Index, the base of the logarithms is very much open to choice; however, in most ecological cases natural logarithms should be used. By simply multiplying our H'_e diversity values by the factor 1.443, interested readers can obtain H'_2 numbers.

To characterize objectively natural between-site groupings in an unbiased manner, the yearly undisturbed cover data at every site for each macrophyte and macroinvertebrate species were subjected to hierarchical cluster analyses (flexible sorting) by the Bray and Curtis (1957) percentage distance statistic (Smith, 1976). This produced a dendrogram of assemblages that were then interpreted according to their environmental affinities and used to map the prevalent biogeographical patterns for the various sites.

2. Community Recovery and Development Studies

These methods are presented in considerable detail by Murray and Littler (1978b) and only a general overview will be presented here. The biomass harvesting procedures employed during the 1975–1976 and 1976–1977 programs permitted the subsequent analysis of community recovery from the mechanically disturbed plots. Macroorganisms occupying the rock surfaces were photographed and then harvested from the substrate with the aid of knives and scraping tools; all portions of macrophytes or macroinvertebrates that were attached within the quadrats were removed. Generally, the experimental procedures were effective in producing disturbed plots devoid of macroorganisms with the exception of the encrusting forms (particularly the encrusting algae). Following the harvesting procedures, study plots were marked and reference points were established, from which compass triangulations were recorded, to aid in future sample relocation. During subsequent visits, the colonizing populations were assessed using the undisturbed sampling procedures described above.

Generally, 12 experimental (disturbed) quadrats were cleared of biota during each of the four 1975–1976 visits to each study site (see Littler, 1980). Analyses were carried out for periods approximating 3, 6, 9 and 12 months following plot harvesting for all the intertidal sites except Government Point and Santa Rosa Island, where the research program was newly begun in 1976–1977, and for Corona del Mar, where substrate instability prevented the relocation of harvested plots.

The pre-harvest and post-harvest samples for each site were grouped by 0.6 m tidal heights beginning with the -0.3 to $+0.3$ m interval and species abundance values (cover, frequency and density) were separately determined. This method facilitated comparisons of species abundances between periods before and after the mechanical removal. The Bray and Curtis (1957) index was used to measure the percentage similarity between the pre-harvest and post-harvest values.

RESULTS AND DISCUSSION

1. Species Composition

A total of 414 taxa was recorded during the year from all 12 of the study areas (Table II). The number of macrophyte taxa (197) was

Table II. Numbers of taxa by major taxonomic groups in quadrats at all 12 sites

Major groups		Numbers of taxa collected
Macrophytes		
Bacillariophyta		1
Chlorophyta		20
Cyanophyta		3
Phaeophyta		41
Rhodophyta		130
Spermatophyta		2
Total		197
Macroinvertebrates		
Annelida	– Polychaeta	8
Arthropoda	– Crustacea	24
Cnidaria	– Anthozoa	4
Cnidaria	– Hydrozoa	5
Chordata	– Ascidiacea	8
Echinodermata	– Asteroidea	6
Echinodermata	– Echinoidea	1
Echinodermata	– Holothuroidea	1
Ectoprocta (Bryozoa)		6
Mollusca	– Bivalvia	17
Mollusca	– Cephalopoda	1
Mollusca	– Gastropoda	104
Mollusca	– Polyplacophora	12
Porifera	– Calcarea	2
Porifera	– Demospongiae	18
Total		217

about equal to the number of macroinvertebrate taxa (217). Over half the number of macrophyte taxa were representative of the Rhodophyta; however, Phaeophyta (especially *Egregia menziesii*)* provided the major contribution to biomass. Of the macroinvertebrates, gastropods represented the most taxa (104), but *Mytilus californianus* Conrad was by far the biomass dominant. Taxa occurring in all 12 study sites were the same ubiquitous forms recorded during 1975–1976 (Littler,

---

*Names and authorities for benthic macroalgae follow those employed in Abbott and Hollenberg (1976).

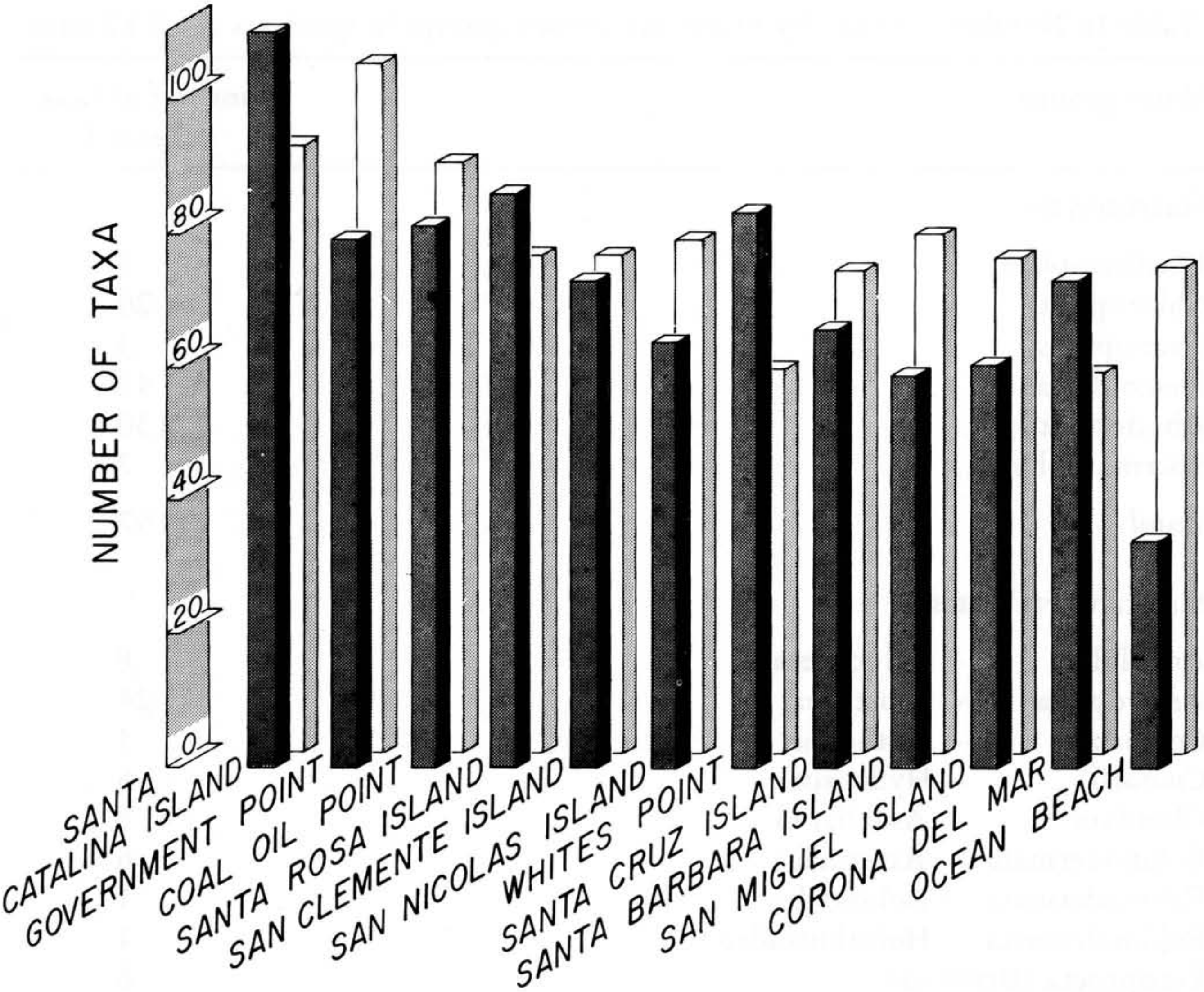

Fig. 3. Mean annual numbers of macrophyte taxa (histograms in rear) and macroinvertebrate taxa (dark histograms in front) found in quadrats.

Table III. Taxa common to all 12 sites

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

1980; Table III), except that *Pterocladia capillacea*, *Gigartina spinosa* and *Gelidium pusillum* were not as widespread in the 1975–1976 samples. The Government Point site (Fig. 3) included a unique community made up of a mixture of warm and cold water macrophytes; therefore, it is not surprising that this site contained by far the greatest number of plant taxa.

2. Abundance of Populations

Because space and light are considered (Connell, 1972) to be limiting resources in the rocky intertidal, cover is of primary ecological importance. Cover is also an aspect of structural heterogeneity; e.g. greater than 100% cover indicates vertical layering of canopy species above the understory components. Such structural complexity represents an important attribute of intertidal communities because it contributes to microhabitat diversity and is thus related to the number of species that a given site can accommodate. Major macrophytic cover throughout the 12 stations was provided by the blue-green algae (overall mean of 34% cover), the coralline algae *Corallina officinalis* var. *chilensis* and *C. vancouveriensis* (9% cover each), the red alga *Gigartina canaliculata* (6%), the tracheophytes *Phyllospadix* spp. (3%), and the phaeophyte *Egregia menziesii* (3%). This pattern is quite similar to that recorded for 1975–1976, except that blue-green and coralline algal values increased considerably. The lowest yearly mean macrophyte cover was present at Whites Point (72%), followed by Coal Oil Point (78%), San Nicolas Island (89%), and San Miguel Island (89%, Table IV). All but the last of these are under some form of environmental stress.

The dominant macroinvertebrates throughout the Bight in terms of cover were *Chthamalus fissus* Darwin/*dalli* Pilsbry (4%), *Anthopleura elegantissima* (Brandt) (3%), *Phragmatopoma californica* (Fewkes) (3%), *Mytilus californianus* (2%), *Dodecaceria fewkesi* Berkeley et Berkeley (1%) and *Tetraclita squamosa rubescens* Darwin (1%). This represents increases over the 1975–1976 values (Littler, 1980), shown by *C. fissus*/*dalli*, *P*, *californica*, *D. fewkesi* and *T. squamosa rubescens*. The habitats with the greatest macroinvertebrate cover (Table V) were those that contained large stands of either *A. elegantissima* or *M. californianus*. Minimal macroinvertebrate cover was again registered at Corona del Mar (4%), Whites Point (6%), and San Clemente Island (6%).

Table IV. Seasonal and mean yearly macrophyte % cover; comparisons between sites

Sites	Months MJJA	SON	DJ	FMA	Mean
Government Point	125	107	100	119	113
Ocean Beach	111	106	102	113	108
Santa Barbara Island	99	106	106	109	105
San Clemente Island	113	111	94	103	105
Corona del Mar	110	111	94	98	103
Santa Cruz Island	99	100	98	101	100
Santa Rosa Island	100	100	98	98	99
Santa Catalina Island	94	99	91	97	95
San Nicolas Island	100	94	95	66	89
San Miguel Island	94	88	84	89	89
Coal Oil Point	86	78	73	74	78
Whites Point	74	73	67	75	72
Means	100	98	92	95	96

Table V. Seasonal and mean yearly macroinvertebrate % cover; comparisons between sites

Sites	Months MJJA	SON	DJ	FMA	Mean
San Nicolas Island	33	30	29	26	30
Santa Rosa Island	31	32	30	26	30
Government Point	26	30	29	28	28
San Miguel Island	24	24	22	24	24
Santa Barbara Island	16	14	15	17	16
Coal Oil Point	18	17	19	9	16
Ocean Beach	15	12	15	12	14
Santa Cruz Island	10	11	12	11	11
Santa Catalina Island	9	10	8	8	9
Whites Point	7	6	6	6	6
San Clemente Island	6	7	6	7	6
Corona del Mar	5	2	3	5	4
Means	17	16	16	15	16

Frequency is a useful parameter for denoting the breadth of distribution of the various taxa. Of the macrophytes, blue-green algae occurred in the greatest number of samples throughout 1976–1977 (87%) followed by *Corallina officinalis* var. *chilensis* (46%), Ralfsiaceae (41%) and *Gigartina canaliculata* (40%). Widespread macroinvertebrates were *Chthamalus fissus/dalli* (44% frequency), *Anthopleura elegantissima* (41%), *Acmaea (Collisella) scabra* Gould (33%) and *Littorina planaxis* Philippi (31%).

Macroinvertebrates with the highest mean densities averaged over all 12 of the study sites were *Chthamalus fissus/dalli* with 1730 individuals/m^2 followed by *Phragmatopoma californica* (262/m^2) and *Littorina planaxis* (216/m^2).

Organic dry weight (ODW) is also an ecologically important parameter as it represents the bound food energy available to higher trophic levels. *Egregia menziesii* was by far the predominant organism with an overall mean of 119 g/m^2 ODW followed by *Phyllospadix scouleri* Hook. (86 g/m^2), *Pelvetia fastigiata* (63 g/m^2), *Gigartina canaliculata* (50 g/m^2), *Eisenia arborea* (45 g/m^2) and *Phyllospadix torreyi* S. Watson (44 g/m^2). This depicts considerable increases in *Phyllospadix* over the previous year's values, due mainly to its dominance at the two new sites (Santa Rosa Island and Government Point), and makes *Phyllospadix*, as a genus, the dominant biomass organism throughout the 12 sites. *Eisenia arborea* replaced *Halidrys dioica* as an important contributor of organic dry weight relative to 1975–1976 findings. For all 12 sites, macroinvertebrate biomass was comprised mainly of *Mytilus californianus* (49 g/m^2 ODW), *Anthopleura elegantissima* (29 g/m^2), *Pseudochama exogyra* (Conrad) (6 g/m^2) and *Tetraclita squamosa rubescens* (4 g/m^2). This represents important gains over 1975–1976 values by *M. californianus*, *P. exogyra* and *D. fewkesi*. The sites with the lowest biotic standing stocks (ODW, Fig. 4), were Corona del Mar (331 g/m^2), Santa Cruz Island (342 g/m^2), Ocean Beach (395 g/m^2), and San Clemente Island (509 g/m^2). All of these sites lack considerable standing stocks of the larger brown algal macrophytes, with the exception of San Clemente Island which was extremely depauperate in macroinvertebrate biomass. In terms of organic dry weight, the macrophytes overshadowed the macroinvertebrates at all sites. Macrophytes had their dry organic biomass maxima at Santa Catalina Island (1340 g/m^2), Government Point (1011 g/m^2), San Nicolas Island (784 g/m^2) and

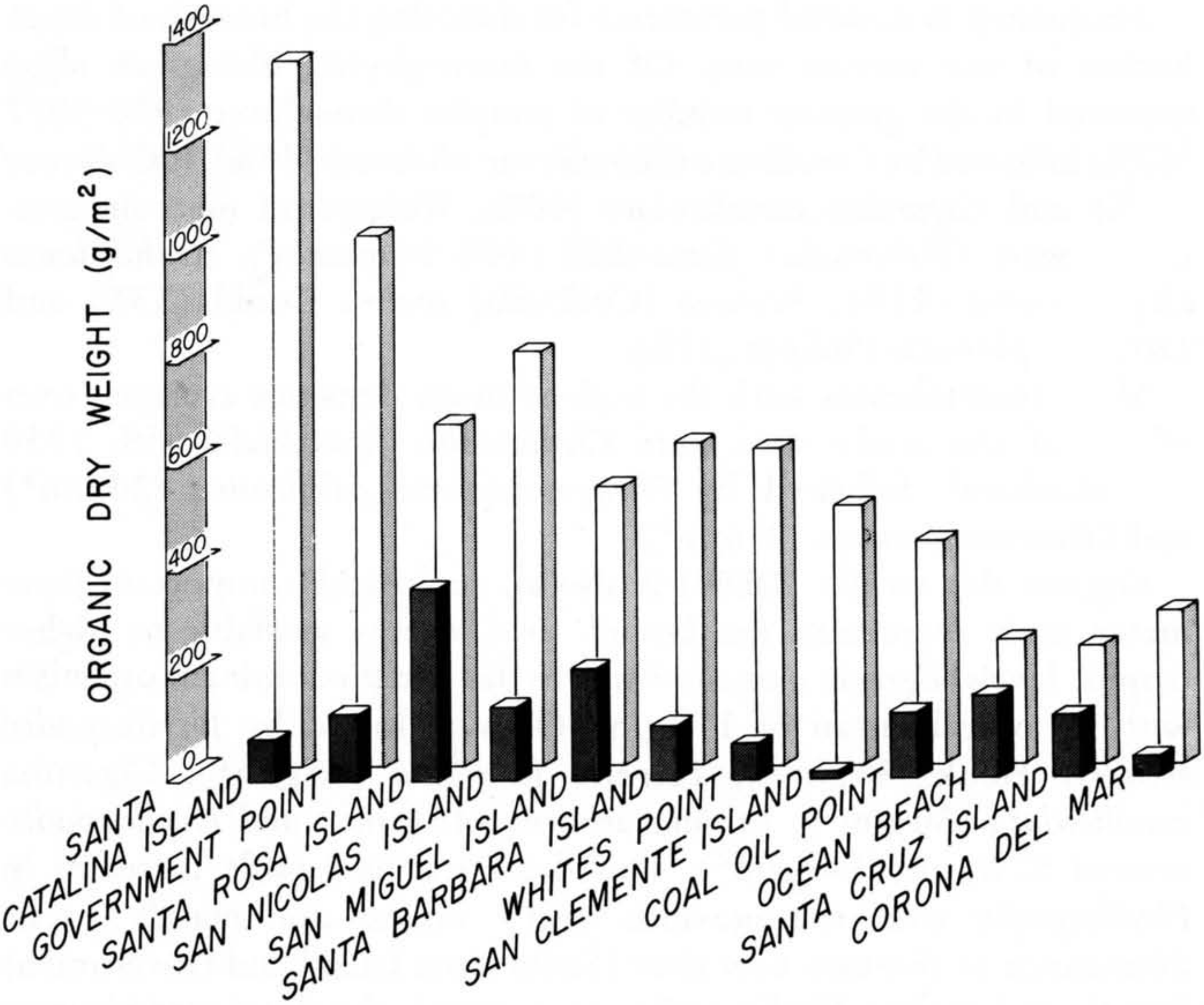

Fig. 4. Mean annual dry organic biomass of macrophytes (histograms in rear) and macroinvertebrates (dark histograms in front) for the entire intertidal zones sampled.

Santa Rosa Island ($651\,g/m^2$). The first two of these sites were dominated by larger brown algal stocks while the last two contained a large biomass of *Phyllospadix*. Santa Rosa Island ($370/m^2$) and San Miguel Island ($210\,g/m^2$) had the largest organic dry biomass of macroinvertebrates, due mainly to *M. californianus*. The lowest macroinvertebrate organic dry weights were recorded from San Clemente Island ($16\,g/m^2$), Corona del Mar ($39\,g/m^2$), and Whites Point ($69\,g/m^2$); all of these are exposed to varying degrees of disturbance, except in the case of San Clemente Island which is enigmatic in regard to its depauperate animal populations.

3. Biogeography

(a) Cluster analysis. All 12 sites were subjected to statistical cluster analysis based on the combined overall mean cover values for both

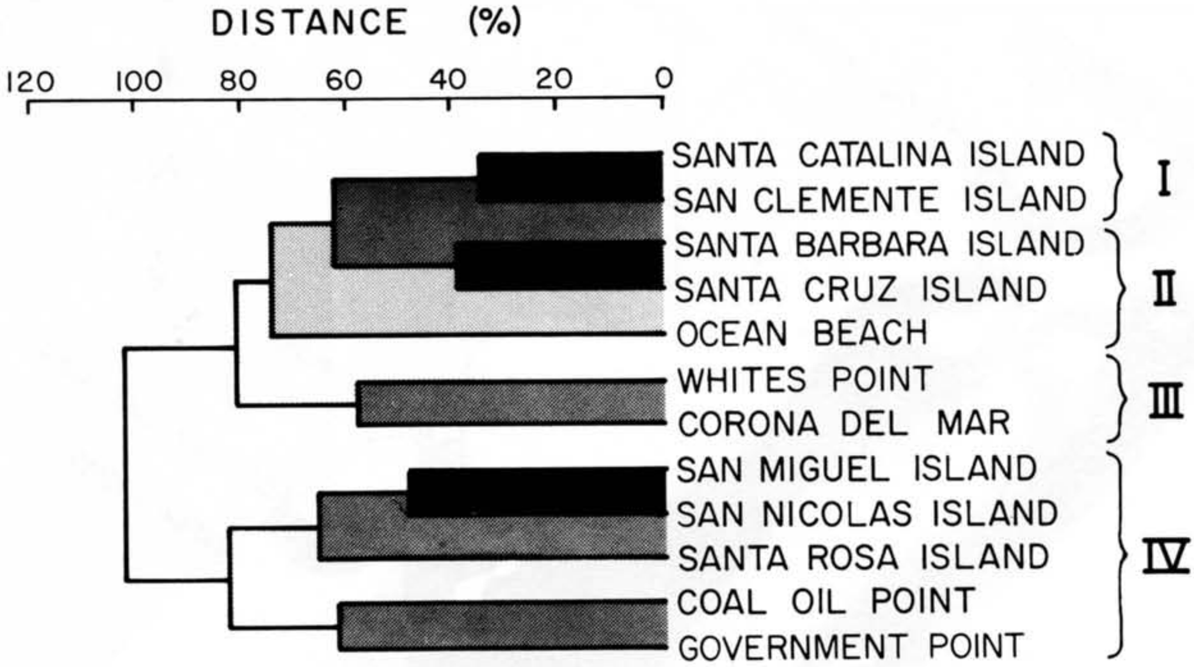

Fig. 5. Dendrogram display of differential clustering for all 12 study sites using combined macrophyte and macroinvertebrate mean cover data. Degree of shading indicates level of similarity (Bray–Curtis % distance).

macrophyte and macroinvertebrate populations (Fig. 5). These results were more clearly displayed by overlaying the cluster groupings on a map showing the 12 Southern California Bight stations (Fig. 6). Cover was chosen as the most significant and revealing biogeographic parameter because, as mentioned, intertidal organisms compete for the limiting resources of space and light using their cover and because our cover data are based on a maximum number of samples (i.e. the undisturbed quadrats). The dendrogram (Fig. 5) revealed groupings that agreed closely with our predictions (based on hydrographic information) regarding the affinities between sites. For example, the sites most strongly influenced by the cold California Current system (i.e. San Miguel Island, San Nicolas Island, Santa Rosa Island, Coal Oil Point and Government Point) formed a group broadly separated from sites exposed to predominantly warmer water systems (cf. Figs 2 and 6). Within these two broad assemblages, the island sites containing the warmest-water elements and exposed to the warmer current systems (i.e. Santa Catalina and San Clemente) were most tightly clustered. The predicted intermediate water sites, Santa Barbara and Santa Cruz Island, formed a second close grouping with the mainland Ocean Beach site, which latter was less tightly grouped. Of the warm-water sites, Whites Point and Corona del Mar

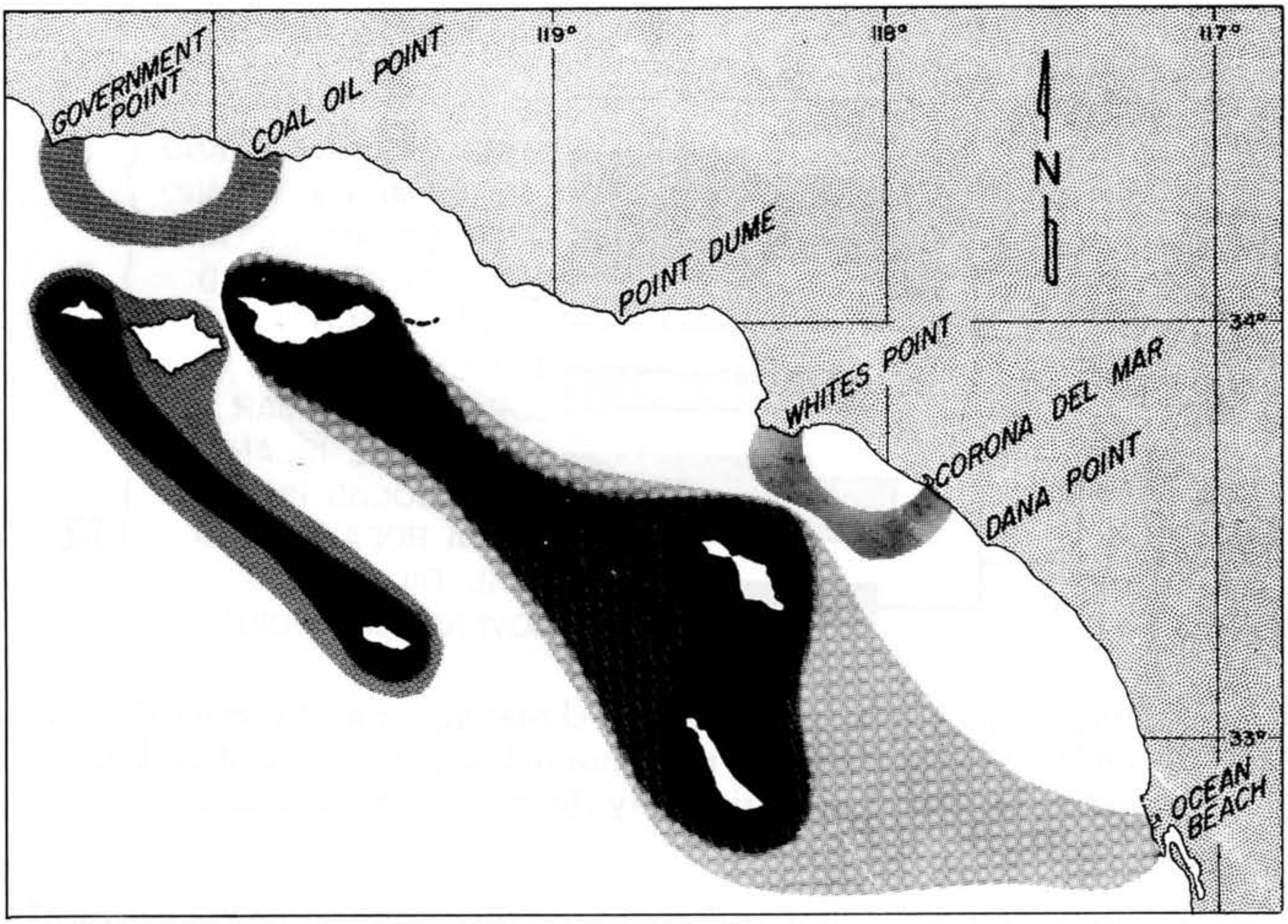

Fig. 6. Map overlay of cluster results (Fig. 5) using Bray–Curtis distance. Degree of shading indicates level of similarity.

formed a distinct pairing, no doubt related to the degree of human-induced and other disturbances to which these two habitats are exposed. They are both dominated by subclimax communities comprised of fine filamentous turfs. Both of the northernmost mainland sites (i.e. Government Point and Coal Oil Point) showed close affinities as did San Miguel and San Nicolas Islands, all of which are strongly influenced by the cold California Current system. Santa Rosa Island clustered less strongly with these last two sites. The above patterns are quite similar to those determined during 1975–1976 (Littler, 1980) from the cover data set and are also basically similar to those recently determined independently from binary (presence/absence) data for the island macrophytes (Murray, Littler and Abbott, 1980) and macroinvertebrates (Seapy and Littler, 1980).

(b) Islands vs. *mainland comparisons*

(i) Lower shore. It is instructive and quite revealing to compare island with mainland rocky intertidal habitats. First, a direct comparison

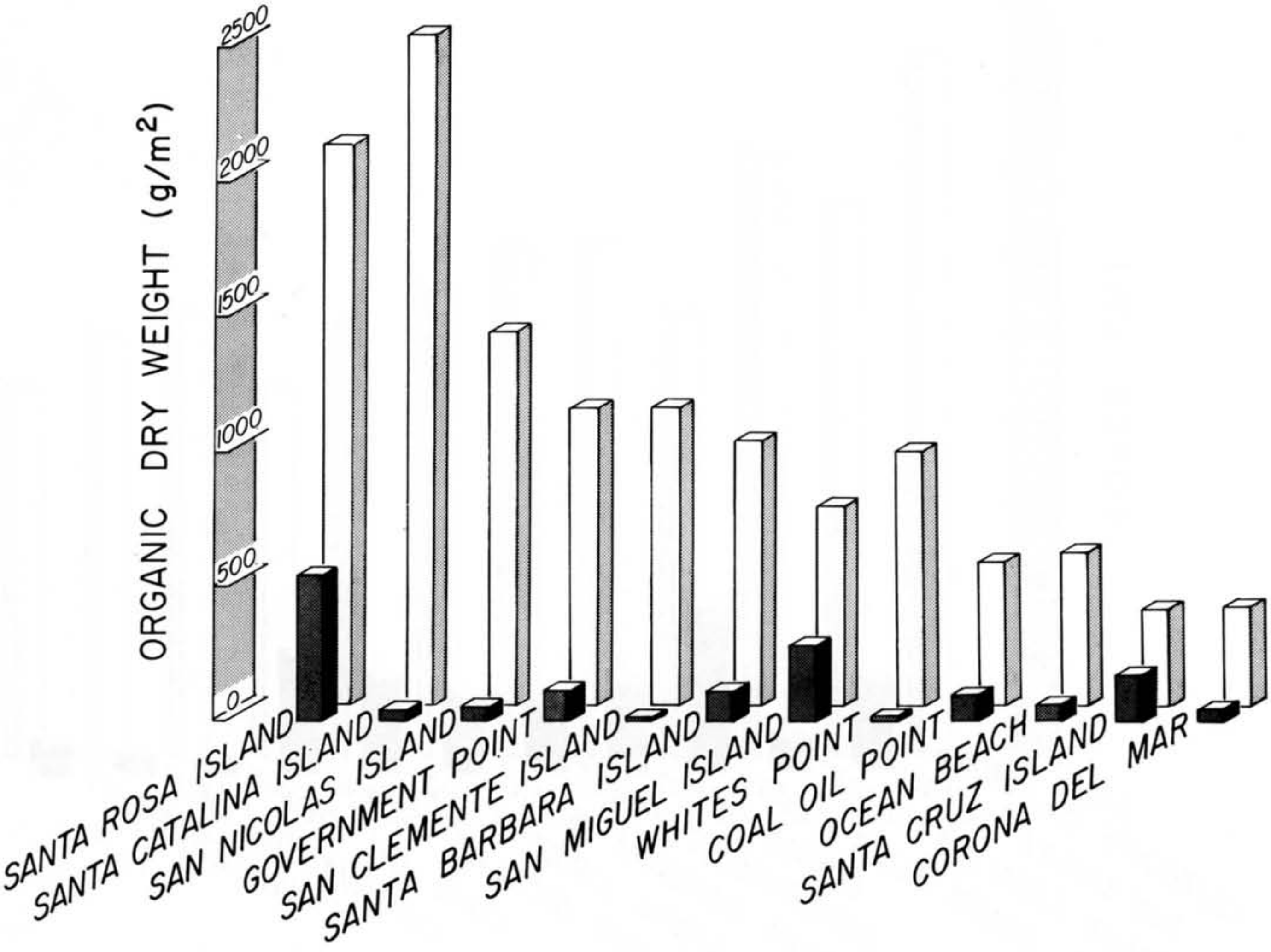

Fig. 7. Mean annual dry organic biomass of macrophytes (histograms in rear) and macroinvertebrates (dark histograms in front) for the lowest three 0.3-m intervals sampled.

was made between sites considering only the lower portions of the shoreline. This form of comparison was made so as to place all sites on an equal basis, because three of the five mainland sites do not contain an upper intertidal, whereas six of the seven island sites do. The means for the lowest three 0.3 m intervals that could be sampled throughout the year were determined for each site and are presented in Figs 7 and 8. The average lower intertidal dry organic biomass for islands (1495 g/m^2) was nearly double that for mainland sites (786 g/m^2), as had been the case for the 1975–1976 data set (Fig. 7). The bulk of this biomass was contributed by macrophytes (1313 and 712 g/m^2 for island and mainland sites, respectively) and mostly resided in the larger brown algae (e.g. *Egregia*, *Halidrys*, *Eisenia*) and surf grasses (*Phyllospadix torreyi*, *P. scouleri*). The same tendency was evident for island *vs* mainland macroinvertebrate biomass (177 *vs* 74 g/m^2 ODW).

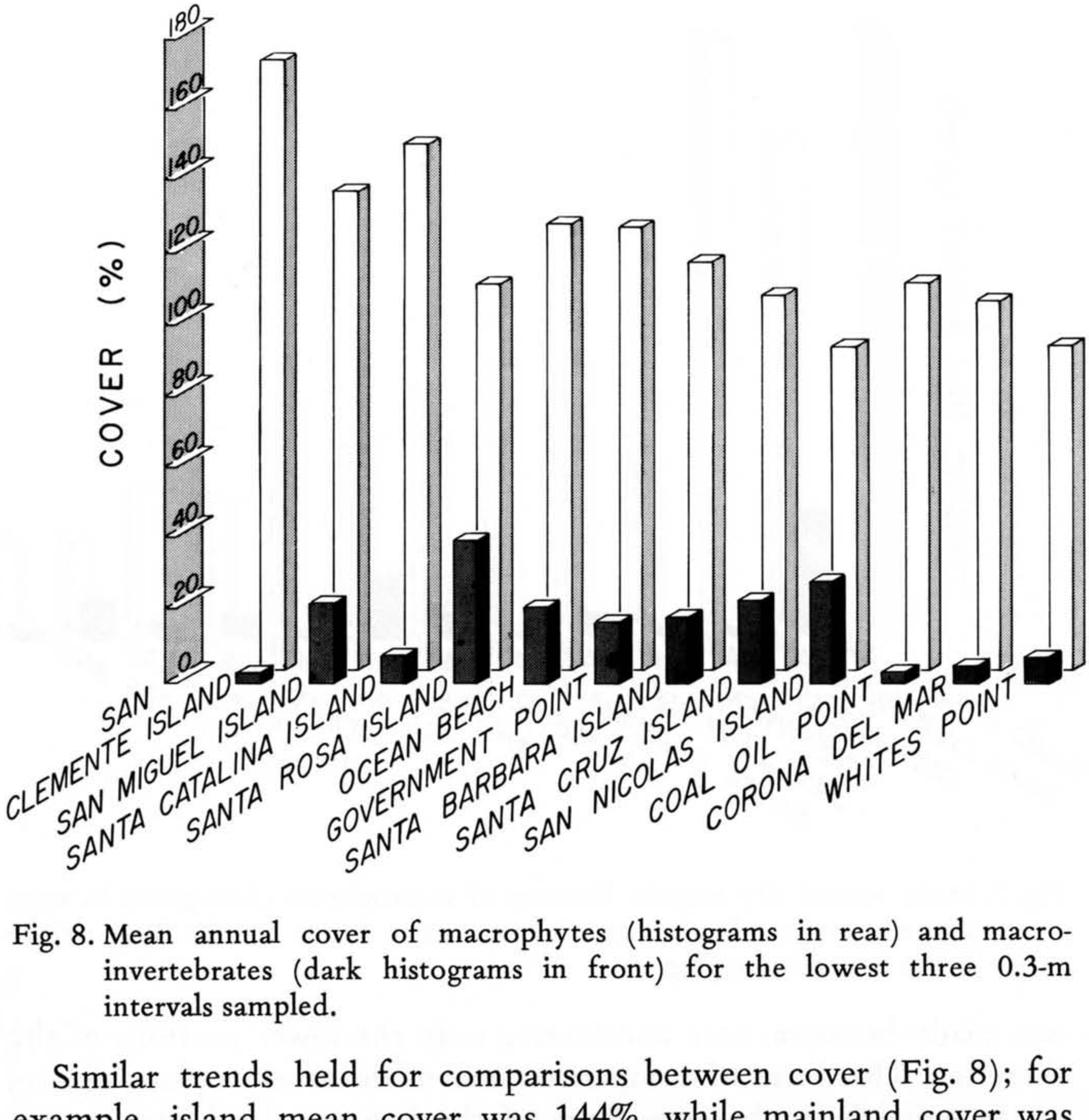

Fig. 8. Mean annual cover of macrophytes (histograms in rear) and macroinvertebrates (dark histograms in front) for the lowest three 0.3-m intervals sampled.

Similar trends held for comparisons between cover (Fig. 8); for example, island mean cover was 144%, while mainland cover was only 120%. Differences between island and mainland macrophytic cover (i.e. 124 *vs* 109%) were not pronounced. However, island mean macroinvertebrate cover was nearly double that of the mainland (20 *vs* 11%). These patterns are similar to those described for the 1975–1976 data set (Littler, 1980) and are possibly attributable to human disturbances that have occurred increasingly along the populated portions of the Southern California mainland (Widdowson, 1971; Thom and Widdowson, 1978). When one compares values at the two sites near the extreme ends of the Southern California mainland (i.e. Government Point and Ocean Beach), it becomes apparent that the biomass and cover of standing stocks at these two sites approach the levels exhibited by island sites (Fig. 4 and Tables IV and V). Although the relatively depauperate Corona del Mar and Whites Point sites are subjected to considerable natural disturbances as well, this leads one to speculate that human influence has played a major role in reducing mainland intertidal standing stocks, in terms of both biomass and cover, near heavily-populated areas.

(ii) Total intertidal. Samples could not be obtained from the upper intertidal zones at one of the island sites (i.e. San Nicolas Island) and three of the five mainland sites (i.e. Coal Oil Point, Whites Point, and Corona del Mar) because of consistent sand or boulder inundation of the upper solid substrate. On the assumption that these sites, as well as the eight others, are representative of major habitats (based on data from our ongoing 1977–1978 island survey studies, we are reasonably confident of this), we felt that comparisons of trends (e.g. between mainland and island sites) would be interesting. In other words, it was important that mainland rocky intertidal systems which often have their upper shorelines inundated by sand and gravel, and are thereby poor in upper intertidal fauna, be documented. Similarly, it was just as essential to represent major island intertidal systems, with stations having well-developed high intertidal faunal assemblages. The grand totals and means of all parameters measured were summed and averaged for the seven island sites and five mainland sites, respectively (Table VI). The islands had higher values than mainland sites in nearly every respect. One definite trend shown by the data is that mainland sites contained lower stocks than island sites. For example (Table VI), islands averaged 809 dry organic g/m^2 (663 g/m^2 macrophytes and 146 g/m^2 macroinvertebrates), while mainland sites averaged only 617 g/m^2 ODW (513 g/m^2 macrophytes and 104 g/m^2 macroinvertebrates). These comparisons of dry organic weights point to a considerable discrepancy between the sizes of the brown-algal standing stocks in the lower intertidal (i.e. *Egregia menziesii*, *Eisenia arborea* and *Halidrys dioica*) which were relatively depauperate and patchy at nearly all mainland sites near heavily populated areas (although they still dominated the biomass there). This apparent reduction of mainland brown-algal biomass is likely to be attributable to environmental stress; the data of Littler and Murray (1975) showed a comparable reduction in stocks of large brown algae, near

Table VI. Island and mainland overall yearly means for all of the parameters measured

	Means		Difference
Parameters	Islands	Mainland	(%)
Number of taxa			
Macrophytes	77	76	1.3
Macroinvertebrates	74	70	5.7
Cover (%)			
Macrophytes	97	95	2.1
Macroinvertebrates	18	14	28.6
Macroinvertebrate Density/m^2	3054	3421	−12.0
Biomass (g/m^2*)*			
Lower 3 intervals			
Wet weight			
Macrophytes	1318	712	85.1
Macroinvertebrates	177	74	139.2
Organic dry weight			
Macrophytes	124	109	13.8
Macroinvertebrates	20	11	81.8
Entire intertidal			
Wet weight			
Macrophytes	3481	3041	14.5
Macroinvertebrates	1979	1121	76.5
Organic dry weight			
Macrophytes	663	513	29.2
Macroinvertebrates	146	104	40.4
Diversity			
Richness (D')	20.02	17.01	17.7
Evenness (J')	0.56	0.59	− 5.4
Shannon–Weaver (H')	2.57	2.56	0.4

a sewage outfall on San Clemente Island, directly correlated with sewage-induced environmental stress. Thom and Widdowson (1978) arrived at similar conclusions for mainland communities, while North *et al.* (1972) and Kindig and Littler (1980) have provided relevant data on the physiological responses to domestic effluents of sewage tolerant *vs* intolerant macrophytes. This trend in biomass reduction is also emphasized when the mean total biomass values for the

Government Point and Ocean Beach sites, which are removed from the more heavily populated Los Angeles and Orange Counties, are compared. These two sites averaged $768\,\mathrm{g/m^2}$ ODW ($624\,\mathrm{g/m^2}$ macrophytes and $144\,\mathrm{g/m^2}$ macroinvertebrates), values intermediate between mainland and island sites.

Similar trends are also indicated by the cover data extracted from Tables IV and V. For example (Table VI), biological cover on islands was 115 *vs* 109% for mainland (97 *vs* 95% for macrophytes, 18 *vs* 14% for macroinvertebrates). This difference is slightly more pronounced than that reported during 1975–1976. Again, while extensive algal turf communities were prevalent in the middle to low intertidal zones at nearly all sites, the island turfs were comprised of larger, more robust populations with epiphytes primarily of medium-sized frondose algae. However, mainland turf communities near populated areas again were characterized by smaller and simpler forms, had more compact structures, and often were heavily coated with a predominance of fine, filamentous epiphytes similar to those documented (Littler and Murray, 1975; Murray and Littler, 1978a) from a sewage-perturbated community on San Clemente Island. The two mainland sites removed from human population centers (Government Point and Ocean Beach) had algal turf communities which more nearly approximated those of the island systems.

4. *Physical Factors*

(a) Substrate disturbance. Island sites tended to be dominated by the larger perennial species characteristic of mature communities. The sand-influenced San Nicolas Island site was unusual in that subclimax and mature communities co-occurred throughout the study area. In places where sand scouring was frequent, opportunistic organisms associated with pioneer stages of community development occurred; by contrast, slightly raised areas not inundated by sand were occupied by relatively mature assemblages. Santa Rosa Island also contained a highly variable zone, below + 0.9 m, which appeared to be affected by sand deposition. The three mainland sites that were subjected to a high degree of disturbance (Corona del Mar, Whites Point and Coal Oil Point) were distinguished by opportunistic species assemblages.

(b) Wave shock. Contrary to the previous year, there tended to be fewer macroinvertebrate taxa in samples from sites having heavy wave exposure (Fig. 3) while the highest number of macroinvertebrates was encountered on Santa Catalina Island, a relatively sheltered habitat. As in 1975–1976, macrophyte species showed increased numbers at sites with prominent surge or swell, possibly due to less desiccation stress above MLLW (Fig. 3), allowing a greater number of normally subtidal species to inhabit higher regions. The Ocean Beach community seemed to be relatively constant (Table IV) but lacked the large brown seaweeds usually found in other mature communities. The absence of these species is probably related to the high degree of wave shock that this site receives and to the friable nature of the sandstone substrate; furthermore, it was observed that the large seaweeds and barnacles were easily torn loose during periods of high wave activity.

5. Species Diversity

As was the case during the previous year, richness indices gave information that closely paralleled the counts of total taxa (cf. Figs 3 and 9). Santa Catalina Island ($D' = 25.69$), one of the more environmentally benign sites, was considerably richer than the other sites.

The sites high in evenness (Fig. 9) were generally low in richness (e.g. San Miguel Island and Government Point). Conversely, Ocean Beach and Coal Oil Point were among the lowest in terms of richness but showed only moderate evenness values. Santa Cruz Island and Santa Rosa Island were moderately rich but disproportionately low in evenness. As was pointed out during 1975–1976 (Littler, 1980), evenness indices do not appear to be particularly indicative of environmental disturbance.

The three sites lowest in H' (Fig. 9) were heavily dominated by mussels and because of their low evenness values showed lower diversity than any of the other 12 sites. As mentioned for evenness (J'), the data do not show a clear relationship between the levels of environmental disturbance observed and Shannon–Weaver diversity.

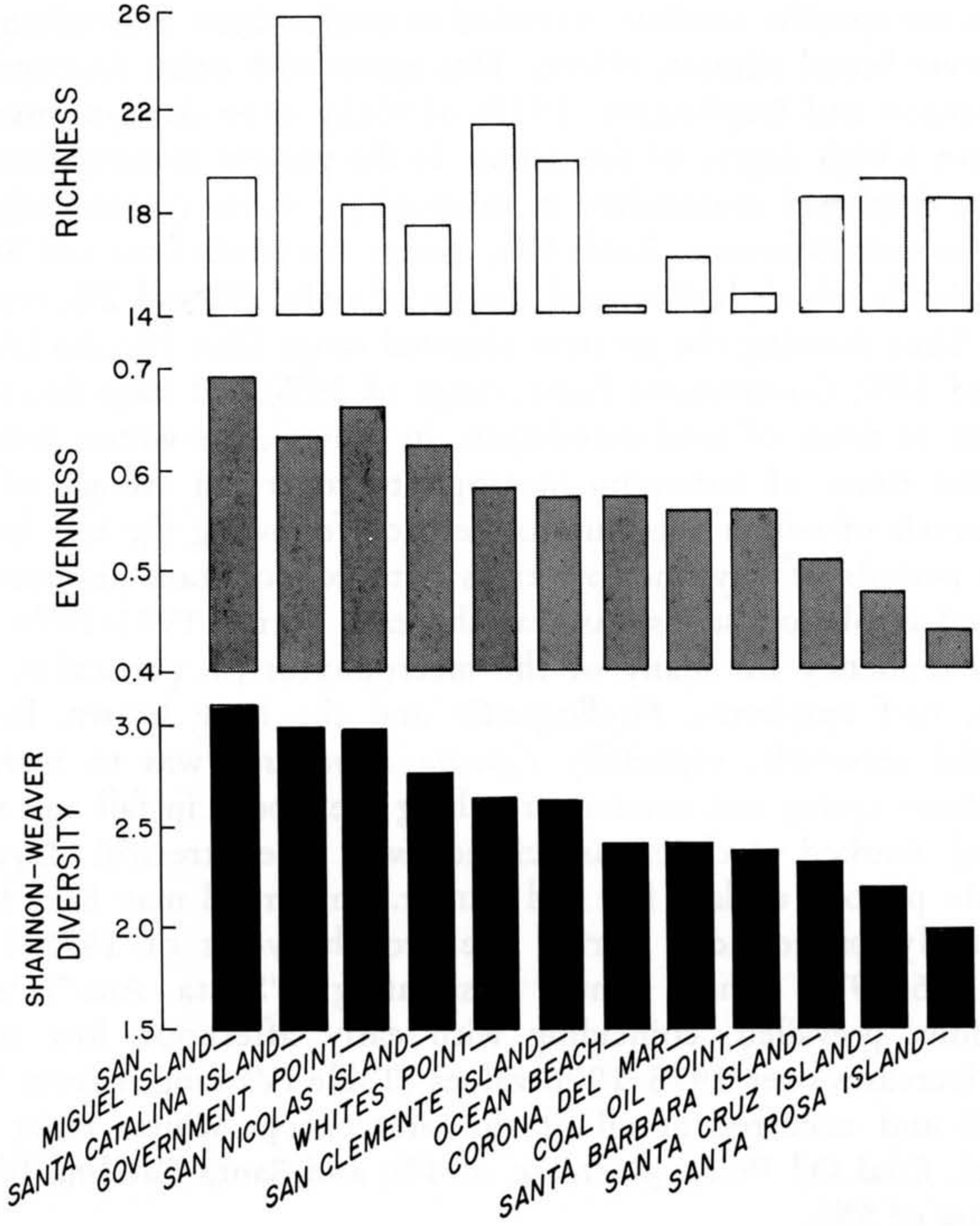

Fig. 9. Mean annual richness (D'_e), evenness (J'_e), and Shannon–Weaver diversity (H'_e), using macrophyte and macroinvertebrate mean cover.

6. *Temporal Variation*

The 1975–1976 study was characterized by a general lack of widespread or consistent temporal patterns except for (i) a slight lowering of most parameters at all sites following the winter months and (ii) recruitment of barnacles and several other macroinvertebrates at several sites during the winter through spring period. The overall lack of consistent seasonal tendencies strongly suggested that local or even site-specific conditions tended to predominate most often and to obscure broad climatic effects. This agrees with other descriptions (Stephenson and Stephenson, 1972) of rocky intertidal systems that also have a high degree of autonomy. In the present investigation, all 12 sites displayed seasonality in macrophyte cover (mean range of 14% seasonal difference, Table IV), except for Santa Cruz and Santa Rosa Islands which had annual ranges of only 3% and 2%, respectively. Sites showing the greatest seasonal range (San Nicolas Island, range of 34%; Government Point, range of 25%) had large decreases in cover at times of sand-inundation. In general, the winter months were the times of minimum macrophyte cover (an average of 8% less), much of which was due to die-back following the late fall to winter periods of daytime low tides with concomitant desiccation, heat and insolation stress. As was the case during 1975–1976, the general tendency for many of the macrophytes (in particular, turf species, turf epiphytes, *Phyllospadix* and the large brown, lower-intertidal seaweeds, especially *Egregia menziesii*) was to increase throughout spring and summer, reaching their peak in fall and then showing marked declines associated with the stressful daytime low tide periods of late fall and winter. This trend may have been particularly pronounced during the drought years of 1975–1976 and 1976–1977, when winter desiccating ("Santa Ana") wind conditions prevailed, coinciding with early afternoon low tides. Cover increases over 1975–1976 values (Table IV) ranged from 11% to 32% and occurred at all of the sites except Whites Point (no change), Coal Oil Point (decrease of 1%) and Santa Catalina Island (decrease of 5%).

Table V illustrates macroinvertebrate cover (seasonal and annual) for all sites. The mean overall intertidal macroinvertebrate cover for the 10 sites sampled during 1975–1976 was slightly greater (1.5%) than for the same sites during 1976–1977. Coal Oil Point no longer supported the greatest cover of macroinvertebrates (decrease of 12%), as had been the case for 1975–1976. All other sites remained about the same as during 1975–1976 in terms of total macroinvertebrate cover (ranging from a decrease of 2% to an increase of 4%). Seasonal change was slight among the 12 sites, being prominent only at Coal Oil Point (average range of 10%) and San Nicolas Island (annual range of 7%), both of which experienced important sand-inundation effects. Several of the sites showed a late winter to early

Table VII. Seasonal and mean yearly macroinvertebrate density (no./m^2); comparisons between sites

	Months				
Sites	MJJA	SON	DJ	FMA	Mean
Santa Rosa Island	8577	7160	6698	6468	7226
Government Point	6242	7322	6468	6580	6653
Coal Oil Point	3959	4527	5484	1676	3912
Santa Barbara Island	3500	2853	2816	3583	3188
San Nicolas Island	3270	3351	3042	2652	3079
Ocean Beach	3583	1823	2130	2056	2398
Corona del Mar	824	420	1221	5997	2116
San Clemente Island	2795	1853	1539	2076	2066
Whites Point	4971	1168	694	1266	2025
Santa Cruz Island	2942	1399	1572	2129	2010
Santa Catalina Island	1960	1961	2038	1846	1951
San Miguel Island	1865	1916	1863	1784	1857
Mean	3707	2979	2964	3176	3207

spring increase in macroinvertebrate cover associated with the recruitment of juvenile barnacles.

Seasonality in macroinvertebrate density occurred at all sites (Table VII). The winter months tended to be the times of minimal density (an average of 734 individuals/m^2 less than in summer months). Three sites showed striking annual ranges in numbers of individuals/m^2 (Corona del Mar, range of 5173/m^2; Whites Point, range of 4277/m^2; Coal Oil Point, range of 3808/m^2). These dramatic fluctuations in macroinvertebrate densities were associated with substrate instability and seasonal influxes of sand. Four sites showed marked increases in mean macroinvertebrate densities compared to 1975–1976 (Corona del Mar, increase of 1535/m^2; Whites Point, + 531/m^2; San Nicolas Island, + 403/m^2; Coal Oil Point, + 302/m^2), while two sites underwent considerable decreases (San Miguel Island, decrease of 441/m^2 and Santa Catalina Island, 331/m^2 fewer). Also, richness (D′) tended to increase slightly through recruitment during the winter months at many sites; this was presumably a result of stressful conditions, caused by daytime low tides, which in turn decreased the abundances of certain dominant canopy species.

7. *Response of Intertidal Communities to Natural Disturbances*

During the present investigation, two of the study sites were subjected to natural disturbances. Corona del Mar became flooded by an unusually heavy rainfall in May 1977, while Santa Catalina Island was disturbed by a large storm during May 1976. Such natural events are disturbing factors recurrent in biological communities (Connell, 1978) and their effects have not been adequately documented. The unpredictable occurrences of storms or high waves have been correlated with subtidal standing-stock fluctuations in the tropics (Doty, 1971), in which seasonality was obscured. Studies of the responses of intertidal communities to natural perturbations may give information on the recoverability of different components and thus provide one method of measuring community stability (resilience).

At the Corona del Mar study site, the encrusting algae *Hydrolithon decipiens*, blue-green algae, and the red algae *Gelidium coulteri*/*pusillum*, showed declines of 1.3%, 7.8%, and 5%, respectively. following the flood. However, several macrophyte taxa characteristic of disturbed environments, *Ulva californica*/*Enteromorpha* sp. and Ectocarpaceae, showed sizable increases in mean cover (mean increases of 14.6% and 8.9%, respectively) after the disturbance. The most striking effect of the storm was on the purple sea urchin, *Strongylocentrotus purpuratus* (Stimpson). This species decreased dramatically from about 2.0% cover to less than 0.1% in the lower intertidal (MLLW to + 0.3 m) and disappeared entirely from the + 0.3 to 0.6 m interval. Belt transects in the flooded area recorded an average of 90.5% urchin mortality (19 recently killed out of 21 urchins) while a census of the total area between the two permanent transect lines revealed 93.6% mortality (52 dead out of 54 urchins). A comparable area just beyond the flooded region (20 m north of the north transect line) contained only 1.1% mortality of *S. purpuratus* (6 dead out of 539 urchins). These observations indicate that freshwater inundation of the intertidal due to severe rainstorms can have highly localized catastrophic effects on intertidal populations, which may have important implications for subsequent interpretations of community changes.

The distribution, abundance and community structure of the Santa Catalina Island site were studied one month after a large storm disturbed the area. The storm lasted for three days (13–15 April 1976).

During this period, the combination of extreme high tides and heavy westerly swells resulted in waves striking the bluff surface + 6.5 m above MLLW. The storm caused a dramatic thinning of the kelp beds immediately seaward of the study area and broke away a large portion of the bluff that rises 3.0 m above the west and center transect lines. In addition, the substrate along the center transect line showed evidence of abrasion due to the seaward transport of broken rubble. One of the immediate outcomes of the storm was a reduction in standing stocks. Macrophyte cover was reduced by 8.7% with dramatic decreases in cover of the articulated coralline alga *Corallina officinalis* var. *chilensis* and of the canopy-forming brown algae *Egregia menziesii* and *Eisenia arborea*. Decreases were also determined for the red alga *Gelidium purpurascens* and the encrusting coralline alga *Lithophyllum proboscideum* along the lower shoreline, where they had developed beneath the brown algal canopies prior to the storm. The larger canopy-forming algae were probably removed from their anchorage by the strong wave action, while the shade-acclimated *G. purpurascens* and *L. proboscideum* may have suffered from increased insolation received in the absence of a canopy.

Drift seaweed biomass consisting predominantly of the larger kelps increased (Zobell, 1971) on Southern California beaches during the period of most frequent storms (November through February). A strong positive correlation was noted (Zobell, 1971) between the quantity of seaweed on shores and wave height, as well as wind velocity, thereby providing additional evidence of the significance of storm conditions to seaweed communities.

The decreases in abundance of these dominant algal populations were partially offset by cover increases in opportunistic seaweed species. *Scytosiphon dotyi*, *Enteromorpha* sp., *Colpomenia sinuosa* and benthic diatoms were most abundant on disturbed surfaces after the storm and showed large increases over their previous cover values. These species are known (O. Wilson, 1925; Emerson and Zedler, 1978; Murray and Littler, 1978a) readily to occupy vacated patches within relatively mature biotic communities.

An overall 24.5% decrease in macroinvertebrate density occurred due to the storm. Suspension feeding organisms such as barnacles and tube-forming mollusks suffered the greatest decreases. These sessile species were presumably killed by abrasion and dislodgement from the substrate. Many members of the grazing guild were reduced in numbers following the storm although, of the dominants, only *Littorina planaxis* suffered a large (35.8%) decrease. Overall, the short-term effects of the storm resulted in abrupt localized declines in several of the abundant organisms, whereupon newly vacated space became occupied by short-lived opportunistic species of algae. Large-scale changes in overall community patterns did not result, nor were they interpreted as likely to occur over a longer term since abundances of the dominants showed little change beyond normal seasonal variability.

8. Recovery of Disturbed Quadrats

The successional study was designed to determine biological recovery rates in fixed quadrats following severe mechanical disturbances, i.e. the removal of all fleshy and upright organisms. A primary objective was to identify sensitive species which would be slow to re-establish. While this research did not directly address the potential effect of oil on natural intertidal communities, certain effects of oil are highly mechanical (e.g. smothering; Crapp, 1971) and the resultant mortality suffered by populations provides free space such as that produced by natural physical disturbances.

Generally, intertidal macrophytes were effective at rapidly re-establishing their overall cover on disturbed surfaces, while the macroinvertebrate populations recovered much more slowly. All of the sites (except Santa Cruz Island and Santa Catalina Island) re-attained their pre-harvest mean macrophyte cover values after 12 months, whereas none of the macroinvertebrate species attained pre-harvest levels of cover and overall pre-harvest densities were matched only at Whites Point. After 12 months, an average of only 55.4% of the pre-harvest densities and 64.4% Bray–Curtis cover similarity was recorded at the nine sites.

Certain species showed a high degree of resilience and quickly re-established on the disturbed areas. The articulated coralline algae (e.g. *Corallina officinalis* var. *chilensis*) showed remarkably rapid recovery rates from remnant basal-crust portions, particularly where they had previously formed a dense turf. Certain of the frondose forms such as *Gigartina canaliculata* also showed rapid recovery following plot clearance. *Egregia menziesii* began to recolonize disturbed surfaces soon after harvesting at several sites; however, sites subjected to other disturbances (such as Whites Point, Coal Oil Point and Corona del Mar) were not readily recolonized by *Egregia*. Filamentous algae (e.g. rhodophycean turf at Coal Oil Point) showed rapid re-establishment to pre-harvest levels. Among the macroinvertebrates that appeared to be most rapid in recolonizing disturbed surfaces were the tube worms *Phragmatopoma californica* and *Dodecaceria fewkesi*.

Several populations of macrophytes and macroinvertebrates were very slow to recover at all sites and are, thus, heavily impacted by disturbance. The upper intertidal rockweeds *Hesperophycus harveyanus* and *Pelvetia fastigiata* consistently failed to re-establish. These species were generally abundant adjacent to the disturbed plots; however, vegetative encroachment by them or by other large frondose seaweeds such as *Halidrys dioica* and *Prionitis lanceolata* was also extremely slow, particularly at the island sites. Populations of sessile bivalves were similarly quite slow to recover. For example, the mussels *Mytilus californianus*, *M. edulis* L., *Septifer bifurcatus* (Conrad) and *Brachidontes adamsianus* (Dunker) all revealed virtually negligible recovery after 12 months, as did the rock oyster *Pseudochama exogyra*.

ACKNOWLEDGEMENTS

This project would have been impossible without the high level of skills, dedication and perseverance shown by such individuals as: Keith E. Arnold, Rebecca L. Baugh, Martin J. Byhower, Joyce E. Cook, Charles A. Currie, Jr., Cally A. Curtis, Sally L. Dean, William M. Dunstan, Steven R. Fain, Steven D. Gaines, Phyllis Y. Ha, Roxanna R. Hager, Mark E. Hay, John N. Heine, Maurice L. Hill, Jeff F. Karnes, Richard A. Kendall, Andrew C. Kindig, Robert E. Kleban, Diane S. Littler, Greg S. MacKay, Donn L. Marrin, David R. Martz, Martina M. McGlynn, Wayne N. McMahon, Ronald K. Mizusawa, Lisa J. Morgan, Jane B. Norman, Shirlianne Ouimette, Debra S. Printy, Michael S. Rios, Greg T. Ruggerone, Sally A. Russell, Mark P. Schildhauer, Robert H. Sims, Lawrence H. Solomon, Frank M. Sweeney, Edward R. Tomasek, Peggy J. Trabue, Lynnette L. Vesco, Deborah J. Wilson, William F. White, Susan A. Yamada, Karen K. Yoshihara and John R. Ysais.

Andrew C. Kindig participated very ably as coordinator of the overall field and laboratory efforts while Diane S. Littler served as administrative and materials organizer as well as project illustrator. Special acknowledgements are given to my colleagues Dr Steven N. Murray and Dr Roger R. Seapy, who identified macrophyte and macroinvertebrate specimens, respectively, throughout the project and also provided technical and scholarly expertise which contributed immeasurably to overall quality control. The credibility of the information gathered was elevated greatly through the efforts of Dr Isabella A. Abbott, who annotated and confirmed most of our algal identifications. Special thanks are given to the following people for verification and identification of macroinvertebrate species: Dr Gerald Bakus (Porifera), Dr Gilbert Jones (Mollusca and Crustacea), and Dr Charles Lambert (Ascidiacea). We are indebted to Cecil W. Robinson for the time and care he spent characterizing the samples of substrate. Funding for this research was provided by the Bureau of Land Management, U.S. Department of the Interior through Contract No. AA 550-CT6-40 awarded to Science Applications, Inc.

REFERENCES

Abbott, I. A. and Hollenberg, G. J. (1976). "Marine Algae of California". Stanford University Press, Stanford, California.

Abe, N. (1937). Ecological survey of Iwayama Bay, Palao. *Palao Trop. Biol. Stn Stud.* **1**, 217–324.

Bray, J. R. and Curtis, J. T. (1957). An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* **27**, 325–349.

Bright, D. B. (1974). Benthic invertebrates. *In* "A Summary of Knowledge of the Southern California Coastal Zone and Offshore Areas, Vol. II" (M. D. Dailey, B. Hill and N. Lansing, eds), pp. 10–1 to 10–29. U.S. Department of the Interior, Bureau of Land Management, Washington, D.C.

Caplan, R. I. and Boolootian, R. A. (1967). Intertidal ecology of San Nicolas Island. *In* "Proceedings of the Symposium on the Biology of the California Islands" (R. N. Philbrick, ed.), pp. 201–217. Santa Barbara Botanic Gardens, Santa Barbara, California.

Cockerell, T. D. A. (1939). The marine invertebrate fauna of the Californian islands. *Proc. 6th Pac. Sci. Congr.* **3**, 501–504.

Connell, J. H. (1972). Community interactions on marine rocky intertidal shores. *Ann. Rev. Ecol. Syst.* **3**, 169–192.

Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science, N.Y.* **199**, 1302–1310.

Crapp, G. B. (1971). The ecological effects of standard oil. *In* "The Ecological Effects of Oil Pollution on Littoral Communities" (E. B. Cowell, ed.), pp. 181–207. Applied Science Publications, Essex, England.

Dawson, E. Y. (1949). "Contributions toward a Marine Flora of the Southern California Channel Islands, I–III". Allan Hancock Foundation Occasional Paper No. 8. University of Southern California, Los Angeles, California.

Dawson, E. Y. (1959). A primary report on the benthic marine flora of southern California. *In* "Oceanographic Survey of the Continential Shelf Area of Southern California", pp. 169–264. California State Water Pollution Control Board Publ. No. 20. Sacramento, California.

Dawson, E. Y. (1965). Intertidal algae. *In* "An Oceanographic and Biological Survey of the Southern California Mainland Shelf", pp. 220–231, Appendix

351–438. California State Water Control Board Publ. No. 27. Sacramento, California.

Dawson, E. Y. and Neushul, M. (1966). New records of marine algae from Anacapa Island, California. *Nova Hedwigia* **12**, 173–187.

Dayton, P. K. (1971). Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* **41**, 351–389.

Dayton, P. K. (1975). Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecol. Monogr.* **45**, 137–159.

Doty, M. S. (1971). Antecedent event influence on benthic marine algal standing crops in Hawaii. *J. exp. mar. Biol. Ecol.* **6**, 161–166.

Emerson, S. E. and Zedler, J. B. (1978). Recolonization of intertidal algae: an experimental study. *Mar. Biol., Berl.* **44**, 315–324.

Emery, K. O. (1960). "The Sea off Southern California; a Modern Habitat of Petroleum". Wiley, New York.

Foster, M., Neushul, M. and Zingmark R. (1971). The Santa Barbara oil spill, part 2: initial effects on intertidal and kelp bed organisms. *Environ. Pollut.* **2**, 115–134.

Hendricks, T. J. (1977). Satellite imagery studies. *In* "Coastal Water Research Project, annual report for the year ended 30 June 1977", pp. 75–78. Southern California Coastal Water Research Project. El Segundo, California.

Hewatt, W. G. (1946). Marine ecological studies on Santa Cruz Island, California. *Ecol. Monogr.* **16**, 187–208.

Jones, J. H. (1971). "General Circulation and Water Characteristics in the Southern California Bight". Southern California Coastal Water Research Project. El Segundo, California.

Kimura, J. C. (1974). Climate. *In* "A Summary of Knowledge of the Southern California Coastal Zone and Offshore Areas, Vol. II" (M. D. Dailey, B. Hill and N. Lansing, (eds), pp. 2–1 to 2–70. U.S. Department of the Interior, Bureau of Land Management. Washington, D.C.

Kindig, A. C. and Littler, M. M. (1980). Growth and primary productivity of marine macrophytes under exposure to domestic sewage effluents. *Mar. Environ. Res.* **3**, 81–100.

Littler, M. M. (1968). Development of reef-building crustose coralline algae measurement techniques. *Western Society of Naturalists 49th Meeting Abstracts* **17**.

Littler, M. M. (1971). Standing stock measurements of crustose coralline algae (Rhodophyta) and other saxicolous organisms. *J. exp. mar. Biol. Ecol.* **6**, 91–99.

Littler, M. M. (1978). "Assessments of Visitor Impact on Spatial Variations in the Distribution and Abundance of Rocky Intertidal Organisms on Anacapa Island, California". U.S. National Parks Service, Washington, D.C.

Littler, M. M. (1980). Overview of the rocky intertidal systems of Southern California. *In* "The California Islands: Proceedings of a Multidisciplinary Symposium" (D. M. Power, ed.). Santa Barbara Museum of Natural History, Santa Barbara, California.

Littler, M. M. and Murray, S. N. (1974). The primary productivity of marine macrophytes from a rocky intertidal community. *Mar. Biol., Berl.* **27**, 131–135.

Littler, M. M. and Murray, S. N. (1975). Impact of sewage on the distribution, abundance and community structure of rocky intertidal macro-organisms. *Mar. Biol., Berl.* **30**, 277–291.

Littler, M. M. and Murray, S. N. (1978). Influence of domestic wastes on energetic pathways in rocky intertidal communities. *J. appl. Ecol.* **15**, 583–595.

Maloney, N. J. and Chan, K. M. (1974). Physical oceanography. *In* "A Summary of Knowledge of the Southern California Coastal Zone and Offshore Areas, Vol. I" (M. D. Dailey, B. Hill and N. Lansing, eds), pp. 3–1 to 3–65. U.S. Department of the Interior, Bureau of Land Management, Washington, D.C.

Manton, S. M. (1935). Ecological surveys of coral reefs. *Scient. Rep. Gt. Barrier Reef Exped.* **3**, 273–312.

Margalef, R. (1968). "Perspectives in Ecological Theory". University of Chicago Press, Chicago.

Murray, S. N. (1974). Benthic algae and grasses. *In* "A Summary of Knowledge of the Southern California Coastal Zone and Offshore Areas, Vol. II" (M. D. Bailey, B. Hill and N. Lansing, eds), pp. 9–1 to 9–61. U.S. Department of the Interior, Bureau of Land Management, Washington, D.C.

Murray, S. N. and Littler, M. M. (1978a). Patterns of algal succession in a perturbated marine intertidal community. *J. Phycol.* **14**, 506–512.

Murray, S. N. and Littler, M. M. (1978b). Analysis of the patterns of recovery of intertidal and subtidal communities. *In* "The Annual and Seasonal Ecology of Southern California Rocky Intertidal, Subtidal and Tidepool biotas. Southern California baseline study, year two, final report, Vol. III, rept. 1.1" (M. M. Littler, ed.), pp. III–1.1.20–1 to III–1.1.20–226. U.S. Department of the Interior, Bureau of Land Management, Washington, D.C.

Murray, S. N., Littler, M. M. and Abbott, I. A. (1980). Biogeography of the California marine algae with emphasis on the southern California Islands. *In* "The California Islands: Proceedings of a Multidisciplinary Symposium" (D. M. Power, ed.). Santa Barbara Museum of Natural History, Santa Barbara, California.

Neushul, M., Clarke, W. D. and Brown, D. W. (1967). Subtidal plant and animal communities of the Southern California Islands. *In* "Proceedings of the Symposium on the Biology of the California Islands" (R. N. Philbrick, ed.), pp. 37–55. Santa Barbara Botanic Garden, Santa Barbara, California.

Nicholson, N. L. (1972). The Santa Barbara oil spills in perspective. *Calif. Mar. Res. Comm., CalCOFI Report* **16**, 130–149.

Nicholson, N. L. and Cimberg, R. L. (1971). The Santa Barbara oil spill of 1969: post-spill survey of the rocky intertidal. *In* "Biological and Oceanographic Survey of the Santa Barbara Channel oil spill 1969–1970, Vol. I" (D. Straughan, ed.), pp. 325–399. Allan Hancock Foundation, University of Southern California, Los Angeles, California.

North, W. J., Stephens, G. C. and North, B. B. (1972). Marine algae and their relations to pollution problems. *In* "Marine Pollution and Sea Life" (M. Ruivo, ed.), pp. 330–340. F.A.O. Fishing News (Books) Ltd., London.

Paine, R. T. (1966). Food web complexity and species diversity. *Am. Nat.* **100**, 65–75.

Pielou, E. C. (1975). "Ecological Diversity". Wiley, New York.

Poole, R. W. (1974). "An Introduction to Quantitative Ecology". McGraw-Hill, New York.

Reid, J. L., Jr., Roden G. I. and Wyllie, J. G. (1958). Studies of the California Current System. *Calif. Mar. Res. Comm., CalCOFI Report* **6**, 27–56.

Ricketts, E. F., Calvin, J. and Hedgpeth, J. W. (1968). "Between Pacific Tides" (4th edn.). Stanford University Press, Stanford, California.

Schwartzlose, R. A. (1963). Nearshore currents of the western United States and Baja California as measured by drift bottles. *Calif. Mar. Res. Comm., CalCOFI Report* **9**, 15–22.

Seapy, R. R. (1974). Macro-invertebrates. *In* "Biolgocal Features of Intertidal Communities near the U.S. Navy sewage Outfall, Wilson Cove, San Clemente Island, California" (S. N. Murray and M. M. Littler, eds), pp. 19–22. Naval Undersea Center Technical Paper 396, San Diego, California.

Seapy, R. R. and Littler, M. M. (1980). Biogeography of rocky intertidal macroinvertebrates. *In* "The California Islands: Proceedings of a Multidisciplinary Symposium" (D. M. Power, ed.). Santa Barbara Museum of Natural History, Santa Barbara, California.

Shannon, C. E. and Weaver, W. (1949). "The Mathematical Theory of Communication". University of Illinois Press, Urbana.

Sheppard, F. P. and Emery, K. O. (1941). Submarine topography off the California coast: canyons and tectonic interpretations. Geological Society of America, Special Paper 31.

Sims, R. H. (1974). Macrophytes. *In* "Biological Features of Intertidal Communities near the U.S. Navy sewage Outfall, Wilson Cove, San Clemente Island, California" (S. N. Murray and M. M. Littler, eds), pp. 13–17. Naval Undersea Center Technical Paper 396, San Diego, California.

Smith, R. W. (1976). "Numerical analysis of ecological survey data". Ph.D. Dissertation, University of Southern California, Los Angeles.

Southern California Coastal Water Research Project. (1973). "The Ecology of the Southern California Bight: Implications for Water Quality Management". Southern California Coastal Water Research Project, Technical Report 104. El Segundo, California.

Stephenson, T. A. and Stephenson, A. (1972). "Life between Tidemarks on Rocky Shores". W. H. Freeman, San Francisco.

Straughan, D. (ed.) (1971). "Biological and Oceanographical Survey of the Santa Barbara Channel oil spill 1969–70. Vol. I. Biology and Bacteriology". Allan Hancock Foundation, University of Southern California, Los Angeles, California.

Thom, R. M. (1976). "Changes in the intertidal flora of the southern California mainland". M. A. Thesis, California State University, Long Beach, California.

Thom, R. M. and Widdowson, T. B. (1978). A resurvey of E. Yale Dawson's 42 intertidal algal transects on the southern California mainland after 15 years. *Bull. S. Calif. Acad. Sci.* **77**, 1–13.

U.S. Department of Commerce (1976). "Tidal Tables 1976, West Coast of North and South America". National Ocean Survey, Rockville, Maryland.

U.S. Department of Commerce (1977). "Tidal Tables 1977, West Coast of North and South America". National Ocean Survey, Rockville, Maryland.

Widdowson, T. B. (1971). Changes in the intertidal algal flora of the Los Angeles area since the survey by E. Yale Dawson in 1956–1959. *Bull. S. Calif. Acad. Sci.* **70**, 2–16.

Wilson, J. L. (1976). Data synthesis. *In* "Southern California Baseline Study, final report, Vol. III, rep. 5.2". U.S. Department of the Interior, Bureau of Land Management, Washington, D.C.

Wilson, O. T. (1925). Some experimental observations of marine algal successions. *Ecology* **6**, 303–311.

Zobell, C. E. (1971). Drift seaweeds on San Diego County beaches. *Beih. Nova Hedwigia* **32**, 269–314.

Littler M. M. 1980.

Southern California rocky intertidal ecosystems: methods, community structure and variability. *In* Price J. H., Irvine D. E. and Farnham W. F. eds. The shore environment, Vol. 2: Ecosystems, pp. 565-608. Academic Press, London