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Chapter 11

SOUTHERN CALIFORNIA ROCKY INTERTIDAL ECOSYSTEMS

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INTRODUCTION

The Southern California Bight (Fig. 11.1) is defined as the triangular area with its apex at Pt. Conception and its southeastern and southwestern corners at the U.S./Mexico international border and the Tanner and Cortez submarine banks, respectively (Anonymous, 1973). This region is one of the most physiographically intriguing continental shelves of the world's oceans. Sheppard and Emery (1941) aptly termed this area the Southern California Borderland, due to its submarine relief as an expanded continental shelf. Topographically, the Borderland consists of about fourteen deep basins separated by a series of ridges, banks and offshore islands formed during the Miocene between 11 and 20 million years ago (Valentine and Lipps, 1967).

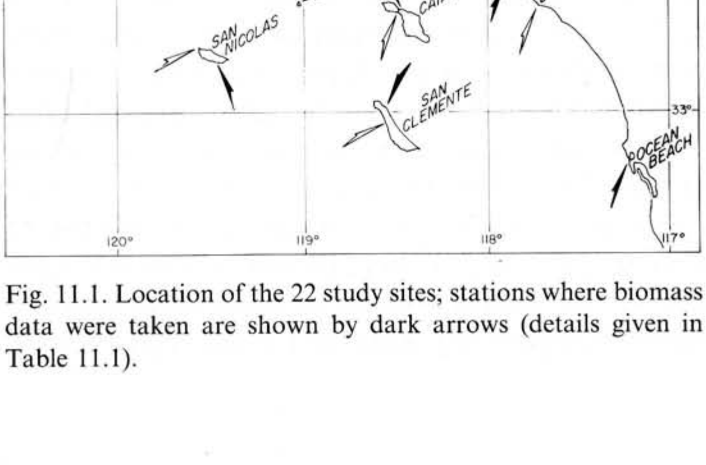

Fig. 11.1. Location of the 22 study sites; stations where biomass data were taken are shown by dark arrows (details given in Table 11.1).

Much is known about the climatology of the Bight (Kimura, 1974); however, published biological information still remains scarce. Cockerell (1939) was among the first to point out the biological importance of unusual mixing of cold and warm waters in the region. Changing climatic patterns results in a complex intermingling of physical conditions, which are reflected in the broad spectrum and variability of the biological systems within the Bight (Littler, 1980a, b) and the mixing of cold and warm temperate floras (Murray and Littler, 1981) and faunas (Seapy and Littler, 1980).

The predominant driving force of water circulation in the Southern California Bight is the California Current. This system, a portion of the eastern limb of the clockwise North Pacific Gyre, flows southward along the western coast of the United States. At Pt. Conception, the coastline turns toward the east, but the California Current continues to flow south to southeast. In a broad area to the south of Cortez Bank, surface flow is turned eastward and then northward through the Channel Islands, forming the Southern California Eddy or Countercurrent (Fig. 11.2). The development and strength of the Southern California Eddy are seasonal (Hickey, 1979), being strongest in the summer and weakest in the winter.

In addition to the southerly flowing California Current, the west coast of the United States is influenced by the deep California Undercurrent (core of flow at −200 to −300 m), which originates by the submergence of northward-flowing equatorial surface water beneath the California Current along a front extending southwestward off southern Baja California (Reid et al., 1958). During late fall and early winter, the

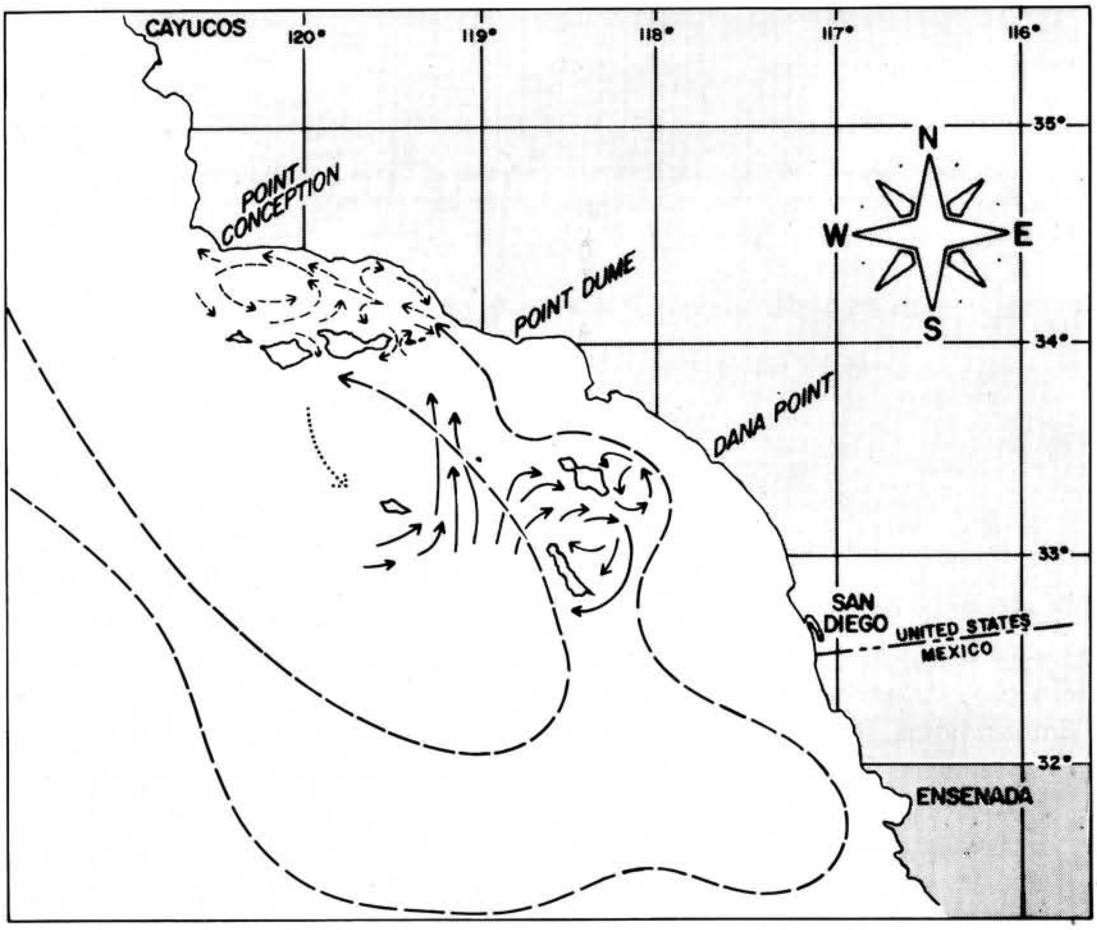

Fig. 11.2. Surface current patterns. Long dashed lines are mean geostrophic flow contours for August averaged for a 16-yr period; short dashed lines indicate surface current flow during August 1969 based on drift bottle studies; solid lines are surface currents derived from 10 m drogue releases during October 1958, while the single dotted line indicates a current system proposed by Neushul et al. (1967). (From Seapy and Littler, 1980.)

northerly winds decrease and are replaced by winds from the south to southwest to the north of Cape Mendocino and by northwesterly or southerly winds from Cape Mendocino to Pt. Conception (Hickey, 1979). North of Pt. Conception the California Undercurrent rises to the surface (Hickey, 1979) and flows northward along the coast as far as Vancouver Island, British Columbia (Schwartzlose, 1963). This northward surface flow is the Davidson Current, which is maximal (to 25 cm s^{-1}) in January (Reid and Schwartzlose, 1962). Whether the core of the California Undercurrent remains at a depth of -200 to -300 m to the south of Pt. Conception is unknown (Hickey, 1979). However, during winter months the northerly flow of the Southern California Eddy along the coast can be continuous with the Davidson Current at Pt. Conception (Hickey, 1979).

The mean monthly surface-water temperatures over the Southern California Borderland range from a low of 13°C in March and April to 20°C in August and September (Jones, 1971). 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).

Another hydrographic feature is the pattern of wind-driven upwelling. In southern California this process occurs in localized areas along both mainland and island shores, where strong steady winds displace surface water offshore to be replaced by cooler subsurface water containing high levels of nutrients. Upwelling is most intense in April, May and June, although wind conditions occasionally result in non-seasonal upwelling (Jones, 1971). Upwelling is most intense south of capes and points (for example, Pt. 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 biotic richness within the Southern California Bight. Wind conditions are also important, in that major reversals occur predominantly throughout late fall and winter (Kimura, 1974). These result in strong, hot and dry "Santa Ana" winds arising from the inland desert regions. For southern California intertidal areas, daytime tidal emersion is pronounced during the fall and winter months (Seapy and Hoppe, 1973; Sousa, 1979a; Littler, 1980a, b; Seapy and Littler, 1982) when low tides occur during afternoon hours. Consequently, when "Santa Ana" wind conditions are severe during these periods of daytime aerial exposure, extreme desiccation stress can result (Gunnill, 1979, 1980a; Seapy and Littler, 1982).

An important ecological factor related to water movement in the Southern California Bight is the protection of certain mainland shores and the mainland sides of islands from open ocean swell and storm waves. This leads to higher wave-energy regimes on the unprotected outer island shores, with marked effects on their biological communities (Table 11.1). Nearly all of the southern California mainland coastline is protected to some degree by the outlying islands (Ricketts et al., 1968). The only mainland areas receiving direct westerly swell are those near Los Angeles and San Diego (Fig. 11.1). The combination of the prevailing Southern California Eddy and its secondary eddies (Fig. 11.2), the deflection of currents and swell by the islands and local, wind-driven coastal upwelling result in a complex hydrographic environment.

Rocky shorelines occur intermittently throughout the entire coastal area of the Southern California Bight, and are interspersed with sandy beaches and inlets to lagoons, estuaries and marinas. The intertidal habitats of the offshore Southern California islands consist of approximately 62.5% bedrock, 16.0% boulder beaches and 21.5% sandy beaches (Table 11.2). On the mainland, in the upper half of the intertidal zone, sandy beaches total 75.1% of the shoreline with the remainder comprised of 16.5% bedrock and 8.4% boulder beach. Sandy beaches on the mainland constitute 64.2% of the lower intertidal zone, bedrock 29.1% and boulders 6.7%.

A number of substratum types are represented among the rocky intertidal habitats (Table 11.1), ranging from hard, irregular 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. At some sites, sand consistently inundates the upper intertidal zone (Stewart, 1983), especially in many mainland habitats, thereby eliminating an entire zonal component from the biota. The widespread presence of extensive loose boulder fields (for example, at Whites Point, Corona del Mar and Dana Point) constitutes another form of environmental instability, curbing community development. The existence of such natural disturbances in rocky intertidal habitats (Sousa, 1979a; Littler and Littler, 1984) has important implications in interpreting changes associated with coastal exploitation and resource development.

The 22 study sites sampled during 1977–1978 (Littler, 1979) under the Bureau of Land Management (now Minerals Management Services) Outer Continental Shelf Program (Fig. 11.1, Table 11.1) form the basis for this synopsis. Fifteen of these sites were situated on the eight islands, while the remainder were located on the mainland (Fig. 11.1). The islands range in size from 2.5 to 249 km^2 and are positioned from 20 to 90 km from the mainland (Power, 1980). 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 four sites to the south of Santa Monica Bay (Whites Point, Corona del Mar, Dana Point and Ocean Beach) may be considered a discrete unit. A general trend of increasing water temperatures to the south is largely offset by exposure of the outermost islands (San Miguel and San Nicolas) to the eastern margin of the cold California Current system (Fig. 11.2). Thus, a division of island sites into northern and southern on the basis of geographic location related to the temperature regime is not accurate. This differential in surface temperatures mediated by water circulation patterns has also been substantiated by satellite thermal imagery (Hendricks, 1977).

Before 1970, relatively little information was available concerning the structure of the intertidal

TABLE 11.1

Physiographic attributes of the 22 rocky intertidal habitats studied

Study area	Latitude and 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 eulittoral
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
Malibu	34°00′42″N 118°47′30″W	Warm (moderate)	Monterey shale/ siltstone	−0.3 to +2.4	Moderate	None	Low eulittoral
Whites Point	33°34′11″N 118°19′39″W	Warm to intermediate	Diatomaceous Monterey shale and unstable boulders	−0.3 to +0.9	Exposed (moderate)	Domestic wastes	High eulittoral 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)	High eulittoral
Dana Point	33°35′25″N 117°42′44″W	Warm (moderate)	Granitic boulders	0.0 to +2.1	Moderate	None	Low eulittoral
Ocean Beach, San Diego	32°44′35″N 117°15′15″W	Warm to intermediate	Poorly consolidated friable sandstone	+0.3 to +4.0	Exposed	None	None
Cuyler Harbor, San Miguel Island	34°02′55″N 120°20′08″W	Cold	Irregular volcanic flow breccia	−0.3 to +2.7	Exposed (moderate)	None	Low eulittoral
Crook Point, San Miguel Island	34°01′28″N 120°22′43″W	Cold	Sandstone	+0.3 to +2.7	Heavy	None	None
Santa Rosa Island	33°53′31″N 120°06′31″W	Cold (moderate)	Smooth sandstone	+0.3 to +3.4	Exposed (moderate)	None	Low eulittoral
Willows Anchorage, Santa Cruz Island	33°57′43″N 119°45′16″W	Intermediate	Irregular volcanic breccia	+0.3 to +4.0	Surge	None	None

Prisoners Cove, Santa Cruz Island	34°01′14″N 119°41′14″W	Intermediate	Volcanic rock	−0.6 to +2.4	Low	None	None
Frenchys Cove, Anacapa Island	34°00′31″N 119°24′21″W	Intermediate	Volcanic boulders	−0.3 to +2.7	Low	Human usage (light)	None
Cat Rock, Anacapa Island	34°00′19″N 119°25′05″W	Intermediate	Volcanic rock	0.0 to +2.1	Moderate	None	None
Disturbed, Anacapa Island	34°00′24″N 119°24′38″W	Intermediate	Volcanic rock	−0.3 to +2.7	Moderate	Human usage (heavy)	High eulittoral
Dutch Harbor, San Nicolas Island	33°12′54″N 119°28′22″W	Cold	Sandstone	−0.3 to +1.5	Exposed (moderate)	None	Extensive
West Point, San Nicolas Island	33°16′43″N 119°34′41″W	Cold	Sandstone	0.0 to +1.5	Heavy	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
Fisherman Cove, Santa Catalina Island	33°26′47″N 118°29′04″W	Warm	Vesicular volcanic rock	−0.6 to +3.0	Protected	None	None
Catalina Harbor, Santa Catalina Island	33°25′42″N 118°30′42″W	Warm	Vesicular volcanic rock	−0.3 to +2.1	Protected	None	None
Wilson Cove, San Clemente Island	33°00′06″N 118°33′03″W	Warm	Stable granitic boulders	−0.3 to +2.1	Protected	None	None
Northwest Coast, San Clemente Island	33°58′06″N 118°34′18″W	Warm	Large volcanic boulders and rocks	−0.3 to +1.5	Moderate	None	None

TABLE 11.2

Relative amounts of substratum types observed in the rocky intertidal zone of the Southern California Bight. Based on aerial survey by helicopter during low-tide periods (From Littler and Littler, 1978, 1979.)

System	Bedrock	Boulder	Sand
Islands			
San Miguel Island	63.7	0.2	36.1
Santa Rosa Island	61.8	5.0	33.3
Santa Cruz Island	66.2	14.8	19.2
Anacapa Island	70.0	14.8	15.2
Santa Barbara Island	73.6	22.2	4.2
Santa Catalina Island	35.3	49.5	15.3
San Nicolas Island	60.7	4.6	34.7
San Clemente Island	68.6	17.3	14.0
Island mean	62.5	16.0	21.5
Mainland			
Upper intertidal	16.5	8.4	75.1
Lower intertidal	29.1	6.7	64.2
Mainland mean	22.8	7.5	69.6

ecosystems of the Southern California Bight. Reviews of the existing literature (Bright, 1974; Murray, 1974) pointed out the paucity of data (mostly biological), particularly for the offshore islands. For these eight islands, limited taxonomic lists were available only for a few isolated localities (Hewatt, 1946; Dawson, 1949; Dawson and Neushul, 1966; Neushul et al., 1967; Nicholson and Cimberg, 1971; Seapy, 1974; Sims, 1974). Quantitative ecological data could be found in only a few published papers (see, for instance, Hewatt, 1946; Caplan and Boolootian, 1967; Murray and Littler, 1974; Littler and Murray, 1974, 1975). Knowledge of biological communities inhabiting rocky intertidal habitats along the southern California mainland was also very limited (e.g., Dawson, 1959, 1965; Widdowson, 1971; Nicholson and Cimberg, 1971).

During the past ten years, however, there has been a dramatic increase in ecological information for rocky intertidal habitats of the Southern California Bight. A number of accounts of ecological research performed on island (Littler and Murray, 1977, 1978; Murray and Littler, 1978; Seapy and Littler, 1982; Taylor and Littler, 1982; Littler et al., 1983) and mainland (Emerson and Zedler, 1978; Sousa, 1979a, b, 1980; Gunnill, 1980a, b, 1983, 1985; Stewart and Myers, 1980; Sousa et al., 1981; Murray and Littler, 1984) rocky intertidal habitats have been published. A significant increase in the understanding of southern California intertidal communities resulted from an extensive three-year sampling program sponsored by the U.S. Department of Interior, Bureau of Land Management (now Minerals Management Service). The data obtained during 1975–1978 as part of this program represent quantitative ecological accounts of the distributions and abundances of the macrobiota for representative sites (Fig. 11.1), and provide the best single source of information on the structure of rocky intertidal communities within the Southern California Borderland. This is because identical field methodologies and analytical techniques were employed to obtain and compare populational and community data over the entire geographic extent of the Bight. For these reasons, this research, which to date has been available in its entirety only in governmental reports of limited distribution, forms the basis of our review. The reader is referred to more limited accounts of the results of earlier phases of this program (Littler, 1980a, b) for a detailed description of the sampling and analytical methods used consistently for all 22 sites.

COMMUNITY COMPOSITION AND STRUCTURE

Ecological assessments of the macro-epibiota inhabiting each site were performed throughout different seasons using a quadrat sampling technique (Littler, 1980a, b). These assessments provided data concerning the variable species compositions as well as distributions and abundances of the rocky intertidal communities for each of the stations. Both undisturbed (photogrammetric) and disturbed (harvest) samples were taken to provide data on population coverage (%) and biomass (wet and dry).

Species composition

A total of 539 taxa of macrophytes and macroinvertebrates was recorded during the three

TABLE 11.3

Numbers of taxa by major taxonomic groups

Major groups		Number of taxa collected
Macrophytes		
Bacillariophyta		1
Chlorophyta		23
Cyanophyta		2
Phaeophyta		47
Rhodophyta		149
Spermatophyta		2
Total		224
Macroinvertebrates		
Annelida	– Polychaeta	10
Arthropoda	– Crustacea	25
Cnidaria	– Anthozoa	11
Cnidaria	– Hydrozoa	19
Chordata	– Ascidiacea	20
Echinodermata	– Asteroidea	10
Echinodermata	– Echinoidea	2
Echinodermata	– Holothuroidea	3
Ectoprocta (Bryozoa)		4
Entoprocta		1
Mollusca	– Bivalvia	16
Mollusca	– Cephalopoda	1
Mollusca	– Gastropoda	131
Mollusca	– Polyplacophora	20
Porifera	– Calcarea	5
Porifera	– Demospongiae	37
Total		315

TABLE 11.4

Taxa common to all 22 study sites throughout 1975–1978

Blue-green algae
Bossiella orbigniana spp. *dichotoma*
Ceramium eatonianum
Ceramium sinicola
Corallina officinalis var. *chilensis*
Corallina vancouveriensis
Cryptopleura spp. (4)
Crustose Corallinaceae (2)
Egregia menziesii
Gelidium coulteri
Gelidium pusillum
Gigartina canaliculata
Polysiphonia spp. (6)
Rhodoglossum affine
Ulva californica
Ulva lobata

Acmaea (Collisella) limatula
Acmaea (Collisella) pelta
Acmaea (Collisella) scabra
Anthopleura elegantissima
Balanus glandula
Chthamalus dalli
Chthamalus fissus
Cyanoplax hartwegii
Littorina planaxis
Littorina scutulata
Nuttallina californica
Nuttallina fluxa
Pachygrapsus crassipes
Pagurus spp. (2)
Phragmatopoma californica
Tetraclita rubescens

years of research. The number of macrophyte taxa (224) was considerably less than the number of macroinvertebrates (315 taxa, Table 11.3). Over half of the macrophytes belonged to the Rhodophyta (149), followed by the Phaeophyta (47). Two species of seagrasses (Spermatophyta) and 23 Chlorophyta accounted for virtually all of the remaining taxa; efforts were made to quantify the abundances of encrusting blue-green algae, but these were all treated as a single entity for ecological analyses. Of the macroinvertebrates (Table 11.3), Mollusca (168) and particularly Gastropoda (131) contributed the most taxa, followed by Porifera (37), Cnidaria (30) and Arthropoda (25). Thirteen macrophyte and 14 macroinvertebrate taxa were found at all 22 study sites (Table 11.4). Ubiquitous macrophytes were mostly coralline red algae, or small filamentous and sheet-like species, while the macroinvertebrate taxa common to all sites were mostly species of limpets, littorine gastropods and barnacles. Relatively more taxa had restricted distributions (that is, found at fewer than four sites) compared to those that were broadly distributed (that is, present at more than four different localities, Fig. 11.3). This may reflect a high degree of environmental variation between habitats throughout the Bight.

Abundances of macrophyte and macroinvertebrate populations

Because space and light are believed (Connell, 1972) to be the primary limiting resources in rocky intertidal habitats, cover measurements probably represent the most meaningful method of quantifying abundances of macrophytes and sessile macroinvertebrates. Nearly all of the sites investigated were characterized by an upper intertidal zone of encrusting blue-green algae; thus, this taxonomic category averaged the greatest cover (41.4%). Blue-green algae were followed by the red alga *Gigartina canaliculata* (mean of 7.2% cover), the surf grasses *Phyllospadix scouleri* and *P. torreyi* (5.5%), the articulated coralline alga *Corallina officinalis* var. *chilensis* (5.3%) and the multi-

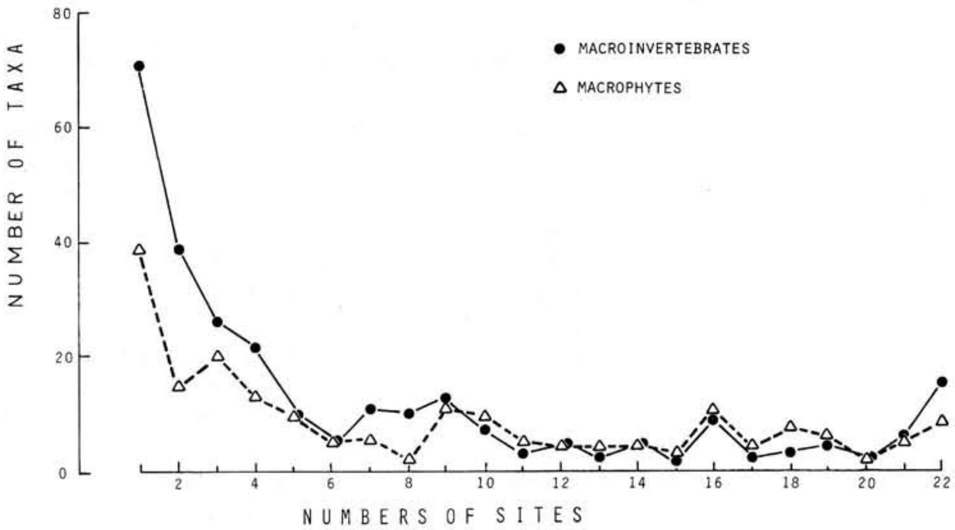

Fig. 11.3. Distribution of numbers of taxa as a function of the numbers of study sites in which they occurred.

species crustose Corallinaceae (5.0%). Sessile macroinvertebrates with the greatest mean cover were the sand-castle worm *Phragmatopoma californica* (6.3%), the small acorn barnacles *Chthamalus dalli* and *C. fissus* (4.5% combined) and the mussel *Mytilus californianus* (3.8%).

For the mobile macroinvertebrates, abundances are probably best represented by estimates of density (numbers of individual animals). Mobile macroinvertebrates with the greatest mean densities were the periwinkle *Littorina planaxis* (311 m^{-2}) and the limpets *Acmaea (Collisella) conus* and *A. scabra* (79 m^{-2}). Sessile macroinvertebrates were, however, more numerous with *Chthamalus dalli* and *C. fissus* having a combined average density of 3642 m^{-2}; other numerous sessile forms included *Phragmatopoma californica* (625 m^{-2}), the barnacles *Balanus glandula* (205 m^{-2}) and *Tetraclita squamosa rubescens* (204 m^{-2}), *Mytilus californianus* (162 m^{-2}) and the anemone *Anthopleura elegantissima* (87 m^{-2}).

Harvested samples taken at 12 of the sites provide important biomass information. Organic dry weight (biomass in g m^{-2}, after drying at 60°C, less inorganic parts and ash) constitutes an ecologically meaningful estimate of abundance, as it represents the quantity of bound food energy available to higher trophic levels. *Egregia menziesii*, a large brown kelp, had by far the greatest average organic dry biomass (119 g m^{-2}), followed by *Phyllospadix scouleri* (86 g m^{-2}), the rockweed *Pelvetia fastigiata* (64 g m^{-2}), *Gigartina canaliculata* (50 g m^{-2}), *Phyllospadix torreyi* (46 g m^{-2}) and *Eisenia arborea* (45 g m^{-2}). The combined figures for *Phyllospadix* make this seagrass genus the greatest contributor of biomass in the southern California rocky intertidal. Of the macroinvertebrates, *Mytilus californianus* averaged the greatest organic dry biomass (51 g m^{-2}), followed by *Anthopleura elegantissima* (26 g m^{-2}), the bivalve *Pseudochama exogyra* and the related *Chama arcana* (6 g m^{-2}), the tube worm *Dodecaceria fewkesi* (5 g m^{-2}), the purple sea urchin *Strongylocentrotus purpuratus* (4 g m^{-2}) and *Tetraclita rubescens* (4 g m^{-2}).

Species assemblages and intertidal zonation

The population data obtained for the individual quadrats were subjected to classification analysis to determine species assemblages and zonation patterns throughout the Bight. The Bray–Curtis similarity index (Bray and Curtis, 1957) was used to establish affinities between samples (after Smith, 1976). Classification analysis of the cover data revealed a total of 46 discrete biotic assemblages, which were used to characterize the zonation patterns for each of the sites (Table 11.5). This revealed 11 groupings characteristic of the supralittoral and upper intertidal zones, 23 found in the mid-intertidal and 12 in the lower intertidal zone.

The dendrogram generated from classification of the cover data for all stations (Fig. 11.4) separates the sites into two subgroups related largely to the influence of sand. Most of the stations assigned to

TABLE 11.5.

Distributional patterns of dominant species assemblages (as determined by Bray–Curtis cluster analysis based on cover) in relation to tidal height for each of the 22 study sites (abbreviations as in Table 11.1)

	High intertidal											High eulittoral filamentous epiphytes; turfs						Mid intertidal																	Low intertidal											
	Blue-green algae	*Chthamalus fissus/dalli*	*Peyssonneliaceae/Hildenbrandiaceae*	*Endocladia muricata*	Chlorophycean crust	*Pseudolithoderma nigra*	*Enteromorpha* spp.	*Chaetomorpha linum*	*Acmaea* spp.	Bare rock	*Littorina* spp.	*Polysiphonia* spp.	*Herposiphonia* spp.	Rhodophycean turf	Gelidium turf	*Centroceras clavulatum*	*Ceramium* spp.	*Anthopleura elegantissima*	*Gigartina leptorhynchos*	*Pelvetia fastigiata*	*Corallina* spp.	Crustose coralline	*Hesperophycus harveyanus*	*Mytilus californianus*	*Tetraclita squamosa rubescens*	*Phragmatopoma californica*	Sand	*Gigartina canaliculata*	*Rhodoglossum affine*	Articulated coralline crust	*Balanus glandula*	*Chondria californica*	Ralfsiaceae	*Ulva* spp.	*Lithothrix aspergillum*	*Cryptopleura* spp.	*Phyllospadix torreyi/scouleri*	*Halidrys dioica*	*Laminaria* spp.	*Egregia menziesii*	*Eisenia arborea*	*Bossiella* spp.	*Gelidium purpurascens*	*Pterocladia capillaceae*	*Strongylocentrotus purpuratus*	*Dodecaceria fewkesi*
Government Point	●	●								●								●		●						●		●							●		●		●							
Coal Oil Point														●				●										●									●	●									
Cuyler Harbor, SMI	●	●		●							●									●	●			●		●		●									●									●
Crook Point, SMI	●			●																●				●		●		●						●												
Prisoners Cove, SCR	●	●					●																	●				●			●						●									
Willows Anchorage, SCR	●																				●	●			●			●									●									
Malibu	●	●		●																	●			●		●		●									●									●
Frenchys Cove, ANA	●										●										●		●			●		●	●				●				●									
Cat Rock, ANA	●	●																		●						●		●																		
Disturbed, ANA	●	●											●							●				●		●			●								●									
Santa Rosa Island	●			●																				●		●											●									
Whites Point	●								●				●				●		●		●						●	●		●		●	●		●										●	
Corona Del Mar	●												●		●	●					●	●																		●						
Santa Barbara Island	●										●										●	●			●			●										●				●				
Dana Point	●	●														●				●	●	●						●					●			●								●		
Fisherman Cove, SCA	●	●				●														●	●	●	●		●			●										●		●	●					
Catalina Harbor, SCA	●	●										●								●	●	●			●																●			●		
Dutch Harbor, SNI	●	●						●										●			●							●									●									●
West Point, SNI	●		●		●													●			●	●																							
Wilson Cove, SCL	●	●				●															●				●			●	●									●		●						
Northwest Coast, SCL	●	●		●		●															●	●				●		●									●				●		●			
Ocean Beach, San Diego	●						●														●	●				●											●									

subgroup A (Fig. 11.4) were exposed to seasonal sand inundation and scouring, whereas those belonging to subgroup B were characteristically associated with more consistently sand-free habitats. The stations in subgroup A all contained relatively large populations of the sand-castle worm *Phragmatopoma californica*, along with abundant *Mytilus californianus*, *Chthamalus dalli* and *C. fissus*; in contrast, subgroup B sites were dominated by cover of the articulated coralline algae *Corallina officinalis* var. *chilensis* and *C. vancouveriensis*.

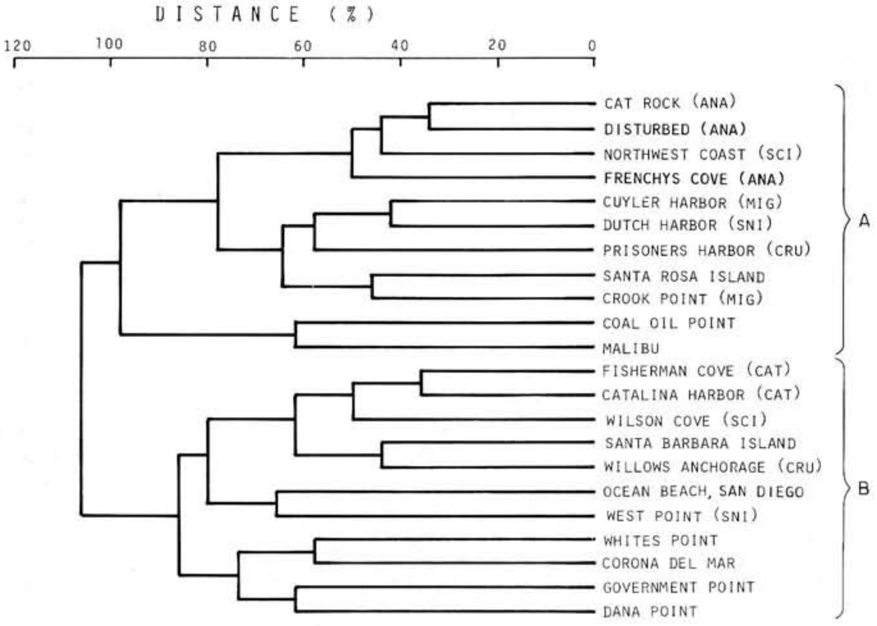

Fig. 11.4. Dendrogram of differential clustering of the 22 study sites based on mean cover values of individual macrophytes and macroinvertebrates (level of similarity indicated by Bray–Curtis percent distance). ANA: Anacapa Island; SCI: San Clemente Island; MIG: San Miguel Island; SNI: San Nicolas Island; CRU: Santa Cruz Island; CAT: Santa Catalina Island.

Biogeography

The Southern California Borderland has historically been regarded as part of the warm-temperate biogeographic province of the eastern North Pacific (Fig 11.5), a region commonly reported (see, for instance, Briggs, 1974; Hayden and Dolan, 1976; Brusca and Wallerstein, 1979) to extend from Pt. Conception to Punta Eugenio, Mexico. Previous biogeographic studies (Newell, 1948; Newman, 1979), however, have emphasized the transitional nature of the biotic assemblages in the Bight (Fig. 11.5), because species indicative not only of the warm-temperate zone but also of the cold-temperate province to the north of Point Conception co-occur in waters off southern California. Distributional analyses of binary (presence/absence) data for macrophytes (Murray et al., 1980; Murray and Littler, 1981) and macroinvertebrates (Seapy and Littler, 1980) sampled from mainland and island sites during our three-year program support this viewpoint and confirm that the southern California rocky intertidal zone contains a mixture of cold- and warm-temperate biotic associations. Island (San Miguel, San Nicolas, Santa Rosa) and mainland (Government Point) sites closest to the cold California Current (Fig. 11.2) generally had intertidal communities comparable to those of the cold-temperate coastline north of Pt. Conception (see Seapy and Littler, 1979; Horn et al., 1983). In contrast, southern mainland (Dana Point, Corona Del Mar, Whites Point) and island (San Clemente, Santa Catalina) sites most remote from California Current waters contained warm-water biotic associations (Murray et al., 1980; Murray and Littler, 1981; Seapy and Littler, 1980). The communities of island sites (Santa Cruz, Santa Barbara, Anacapa) and mainland localities (Malibu, Ocean Beach, Coal Oil Point) receiving variable and mixed exposure to the cold- and warm-water currents had intermediate biological affinities.

The dendrogram exhibiting the relationship between the 12 sites for which organic dry biomass data were obtained (Fig. 11.6) showed remarkable comparability with the biogeographic patterns described above derived solely from binary data. The more southeasterly sites exposed to the warmer waters of the Southern California Countercurrent (Fig. 11.2; Corona Del Mar, Whites Point, San Clemente Island, Santa Catalina Island) grouped together. The more northerly sites (Government Point, Coal Oil Point) and those islands with greatest proximity to California Current influence (San Miguel, San Nicolas, Santa Rosa) sorted as a unit along with the stations at Ocean

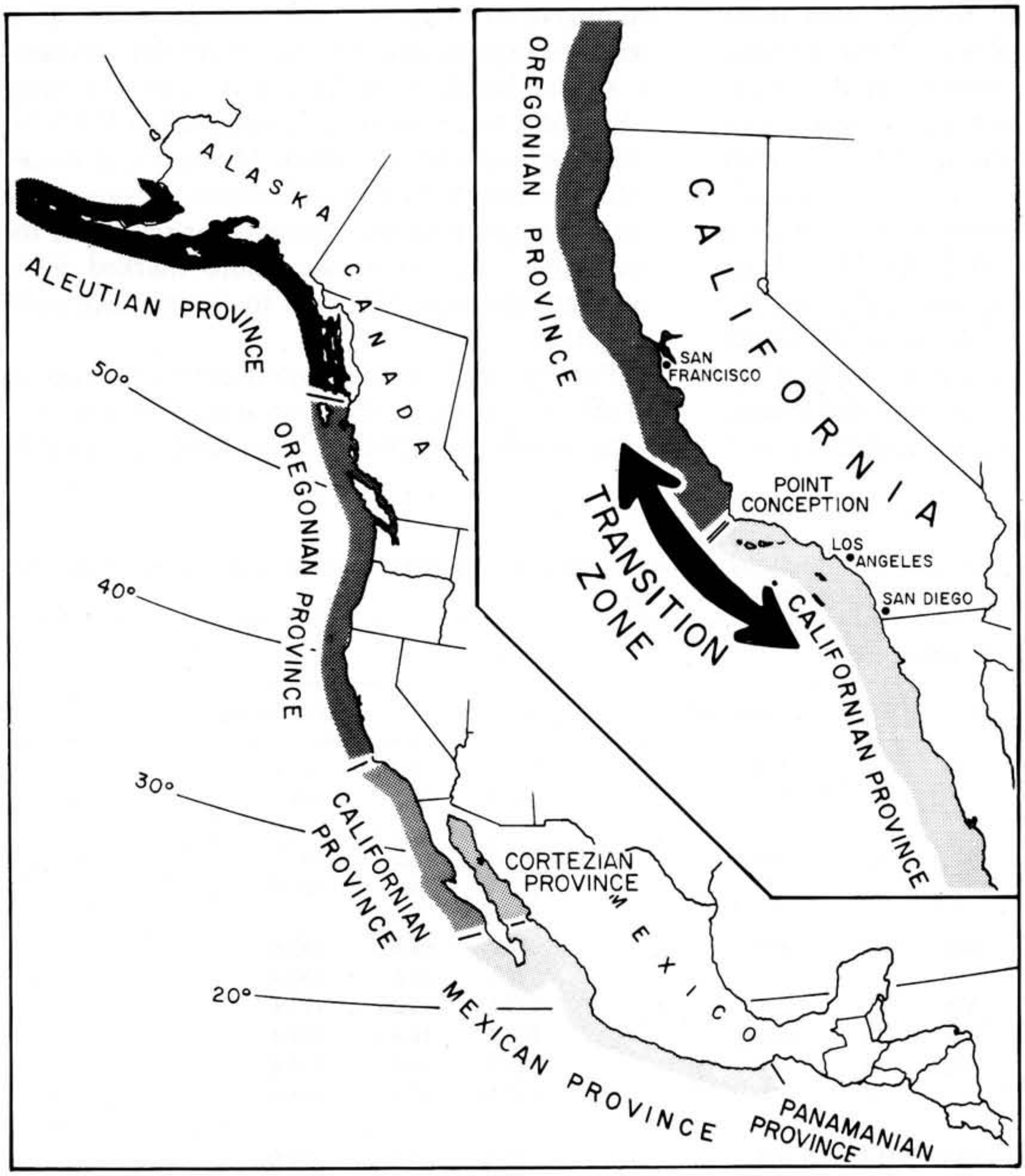

Fig. 11.5. Zoogeographic provinces of the Pacific coast of North America. (From Seapy and Littler, 1980.)

Beach, Santa Barbara Island and Santa Cruz Island, all of which receive mixed exposure to warm- and cold-water currents.

Cover and biomass

The overall abundances of the macro-epibiota varied concurrent with differences in the species composition and zonation patterns. Since the data were averaged by tidal interval over the entire intertidal range (see Littler, 1980a, b), individual abundance means were affected by the vertical extent of the shoreline. For example, biota were not present within the upper intertidal and supra-

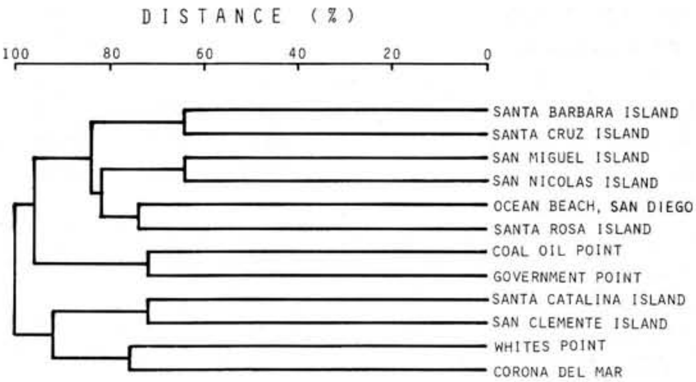

Fig. 11.6. Dendrogram of differential clustering of the 12 study sites based on mean dry organic biomass values of individual macrophytes and macroinvertebrates (Bray–Curtis percent distance).

littoral at one island (San Nicolas) and three mainland (Coal Oil Point, Whites Point, Corona Del Mar) sites because of persistent sand inundation or boulder cover of the uppermost rocky substrata. The absence of fixed and uncovered rocky substrata on the upper shore is of frequent occurrence in southern California, particularly for mainland localities (Table 11.2; Littler, 1978a, 1979). Consequently, many habitats are characterized by poor development or lack of upper shoreline biota. The grand means for each of the mainland and island sites reflect these differences. For example, the island biotas averaged 814 g m^{-2} compared to 614 g m^{-2} for the mainland sites in terms of organic dry biomass; cover data revealed a similar trend, with the island sites averaging 130% (due to stratification) compared to 119% for the mainland stations. These differences, although influenced by the lack of well-populated supralittoral and upper intertidal habitats for several of the mainland sites, were even more marked when comparisons were restricted to lower shore communities.

For the mid through lower intertidal regions (Table 11.6), island sites averaged 1496 g m^{-2}, a value nearly twice that for mainland stations (788

TABLE 11.6

Mean yearly macrophyte (M) and macroinvertebrate (I) dry organic biomass (g m^{-2}) and cover (%) comparisons between sites averaged for the three lower 0.3 m wide eulittoral intervals

Sites	Biomass (g m^{-2})			Cover (%)		
	M	I	Combined	M	I	Combined
San Clemente Island	1109	5	1114	181.2	3.9	185.1
San Clemente Island outer coast				145.6	23.7	169.3
Santa Catalina Island	2507	42	2549	187.8	5.9	193.7
Santa Catalina Island outer coast				157.6	8.4	166.0
Whites Point (2)	960	32	992	85.0	68.6	153.6
Dana Point				139.1	21.6	160.7
San Diego	578	61	639	135.1	42.0	177.1
Santa Barbara Island	988	114	1102	107.5	16.9	124.4
Santa Cruz Island	366	178	544	121.3	34.8	156.1
Santa Cruz Island inner coast				132.1	12.3	144.4
Coal Oil Point	546	112	658	89.6	15.0	104.6
Malibu				137.0	15.6	152.6
San Nicolas Island	1399	56	1455	102.6	42.6	145.2
San Nicolas Island northwest coast				97.0	16.3	113.3
San Miguel Island	775	284	1059	111.2	31.7	142.9
San Miguel Island outer coast				108.5	63.1	171.6
Corona del Mar	369	46	414	102.0	3.3	105.3
Santa Rosa Island	2077	572	2649	113.0	67.1	180.1
Pt. Conception	1179	60	1239	117.6	28.9	146.5
Anacapa Island outer coast				115.8	35.8	151.6
Anacapa Island inner coast				123.4	40.0	163.4
Anacapa Island outer disturbed				117.6	46.7	164.3
Island mean	1317.3	178.7	1496.0	128.1	29.9	158.1
Mainland mean	726.4	62.2	788.4	115.1	27.9	142.9
Combined mean	1091.1	130.2	1201.2	124.0	29.3	153.3

g m^{-2}); comparable trends were apparent from the mean cover data (158% for island *vs.* 143% for mainland sites). In addition to the greater cover on islands, *H*′ diversity (Shannon and Weaver, 1949) was 3% higher, *D*′ richness (Margalef, 1968) was 19% greater and organic dry weight was 33% higher (organic dry weight in the lower intertidal was nearly double that of mainland means).

Much of the difference between the island and mainland communities is due to considerable differences in the standing stocks of lower intertidal macrophytes, that is, the large brown algae *Egregia menziesii, Eisenia arborea* and *Halidrys dioica*, and the surf grasses *Phyllospadix scouleri* and *P. torreyi*. These macrophytes, particularly the large brown algae, are often depauperate and patchy at mainland sites near cities. This apparent reduction in algal biomass is likely attributable to water quality (see discussion under Human Influences below).

In addition to the notable differences in the abundances of kelps and rockweeds between island and mainland habitats, there were also differences in the algal assemblages that dominated in the mid-intertidal zone (see Table 11.5). This region was occupied by tightly compacted articulated coralline algae and their algal epiphytes (see Stewart, 1983). While extensive algal turf communities were prevalent in the mid and low intertidal at nearly all sites, island habitats contained considerably larger and more robust forms. Conversely, mainland turf communities, particularly those near metropolitan areas, were characterized by smaller and simpler algal forms and more compact structure. These mainland turfs were often composed of fine filamentous epiphytes in conjunction with smaller thalli of articulated coralline algae. Such filamentous turf populations may in fact be highly useful in identifying intermediate successional communities maintained in subclimax by lack of environmental constancy or some form of physiological stress, as shown by Littler and Murray (1975) for a sewage-stressed system on San Clemente Island. Stewart (1983) has characterized this unique and taxonomically complex coralline–algal turf community of southern California, particularly in terms of its variability and role in trapping sediments.

PRIMARY PRODUCTIVITY AND FUNCTIONAL FORM RELATIONSHIPS

Productivity

The importance of intertidal seaweeds in fixing energy in coastal waters has been well documented (see, for instance, Blinks, 1955; Kanwisher, 1966; Mann, 1973; Littler et al., 1979). Standing stocks and net photosynthetic performances were determined concurrently (Littler et al., 1979) for the 13 most abundant intertidal macrophytes from a pristine habitat (San Clemente Island, southern California) over a four-season period. Highest net production rates were observed during summer for nine of the 13 species and minimum rates were recorded in spring and to a lesser extent during winter. Correlations between seasonal fluctuations in standing stock and net productivity were evident for only eight species. Total daily community production reached a peak in the fall (1.22 g C fixed per square meter of substratum per day) and declined sharply through winter to a spring low (0.47 g C m^{-2} day^{-1}), closely paralleling changes in ambient water temperature. Blue-green algae, *Corallina officinalis* var. *chilensis, Pterocladia capillacea* and *Egregia menziesii* contributed 76% of the total community primary productivity for the year. Seasonal patterns of photosynthetic performances were highly variable, with a tendency for most species to attain peak daily photosynthetic rates when temperatures were high and days long.

The impact of a low-volume discharge of domestic sewage on net community productivity and ecological energetics was studied (Littler and Murray, 1974) near Wilson Cove, San Clemente Island. The mean primary productivity of the macrophyte community at the outfall (127.1 mg C m^{-2} h^{-1}) was not appreciably different from that measured for nearby unpolluted controls (123.4 mg C m^{-2} h^{-1}), even though there was 11.7% less cover and fewer than half as many species in the sewage-affected area. The above rates are comparable to those reported for other intertidal systems. For example, a wave-exposed sea stack and a protected boulder beach at Cayucos Point, central California, were compared (Seapy and Littler, 1979); macrophytes contributed approximately one-third more to total community primary production on the boulder beach than did those of the sea stack (169.7 versus 116.5 net mg $C\,m^{-2}\,h^{-1}$), due mainly to the greater cover and concomitant production of Cyanophyta and Fucaceae.

Functional forms

Littler and Littler (1980) developed a functional-form model for understanding and predicting patterns of primary productivity (see also Littler, 1980b; Littler and Littler, 1981, 1983; Littler and Arnold, 1982; Littler and Kauker, 1984). Their paradigm was based on studies within diverse floras from a broad spectrum of rocky intertidal environments in southwestern North America, including several habitats within the Southern California Bight. Specifically, macroalgae having thin sheet-like thalli showed the highest productivity (mean apparent net photosynthetic performance = 5.16 mg $C\,g^{-1}\,h^{-1}$) with a reduction by a factor of about two between each of the following four groups: filamentous forms (2.47), coarsely branched forms (1.30), thick leathery forms (0.76) and jointed calcareous algae (0.45). The crustose group had by far the lowest mean net productivity of only 0.07 mg $C\,g^{-1}\,h^{-1}$ (Littler and Arnold, 1982). The functional-form group approach is a promising tool for interpreting physiological and morphological co-evolved interrelationships. Specifically, it has demonstrated (Littler and Littler, 1984) considerable credibility in predicting the outcome of productivity-related ecological processes without being bound to a particular geographic region or phylogenetic line.

ENERGETIC AND FOOD-WEB RELATIONSHIPS

Calorific values

Littler and Murray (1977) examined the factors controlling food-web structure, and how natural intertidal communities in southern California deal with high-energy inputs from sewage-derived particulate matter. Much of the variation in the calorific values of intertidal macrophytes was related (Littler and Murray, 1977) to differences in life-form strategies. In agreement with data for colder north-temperate species (Paine and Vadas, 1969), those forms with relatively more structural tissues (presumably selected for by competition for space and light, predation or physical shearing stress) tended to contain fewer total calories per unit weight. On the other hand, fugitive or opportunistic species selected for rapid growth and high productivity and containing few predator or competitor defenses had relatively greater calorific values. Encrusting intertidal forms that are easily accessible to herbivores may have evolved reduced palatability through selection for thallus constituents with reduced calorific values. In nearly every case, macroinvertebrate populations near the outfall had higher energy contents than did unpolluted control populations. The potential ability of certain seaweeds to utilize and recycle organic materials back through the food web has been stressed (see Prince, 1974). Energy-rich sewage compounds appeared to enter the intertidal food web through populations of omnivores and suspension feeders (Fig. 11.7), which may explain the enhanced standing stocks of these organisms in the peripheral region of the effluent plume.

Food webs

There were two distinct food sub-webs characteristic of the rocky intertidal systems of the leeward coast of San Clemente Island (Fig. 11.7; Littler and Murray, 1978). The first is a macrophyte-based grazing sub-web near the outfall area

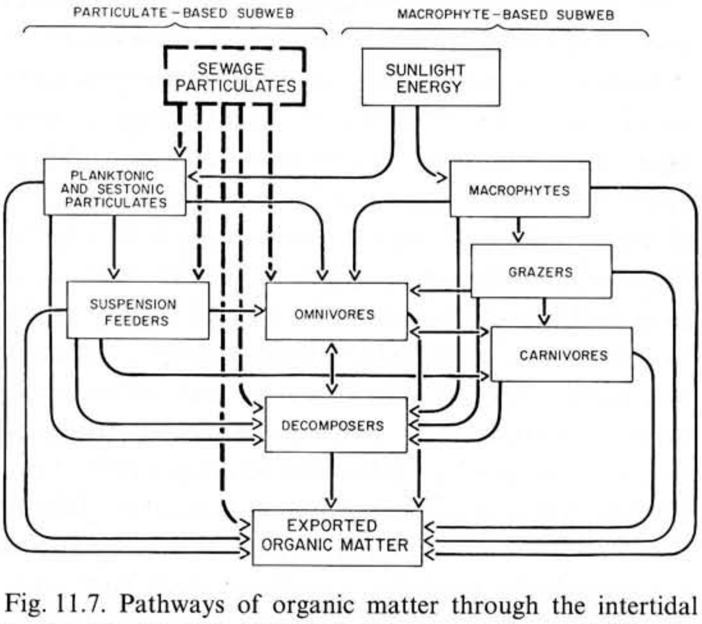

Fig. 11.7. Pathways of organic matter through the intertidal food web on San Clemente Island, southern California. Pathways unique to the San Clemente Island sewage outfall are shown by dashed lines. (From Littler and Murray, 1978.)

in which *Acmaea (Collisella)* spp., *Littorina planaxis, Lottia gigantea* and the omnivorous shore crab *Pachygrapsus crassipes* were the important herbivores. The same sub-web was also present on the unpolluted shoreline, where a similar guild of grazers was apparent, differing in the much lower numbers of *L. gigantea*. Hypothetically (Littler and Murray, 1978), the populations of grazers were enhanced energetically by the increased standing stocks of eurytolerant primary producers such as blue-green algae, *Gelidium pusillum* and *Ulva californica*, including their epiphytic filamentous brown algae, diatoms and bacteria.

The second food sub-web in the outfall and control areas (Fig. 11.7) utilized suspended and settled particulate materials as the primary energy source. In both the outfall and control areas, plankton and seston were available to suspension feeders. Populations of barnacles — *Chthamalus* spp. and *Tetraclita rubescens* — occurred commonly in the control areas and were the dominant suspension feeders.

However, in the outfall area, discharged organic particles served as the primary food source to the suspension-feeder sub-web, and organisms capable of utilizing sewage particulates predominated. These populations included *Pachygrapsus crassipes*, which was observed near the outfall to feed consistently on solid organic particles as well as algae during periods of low tide. The anemone *Anthopleura elegantissima* was also abundant in the area immediately fringing the point of discharge, but was rarely encountered in the unpolluted habitat. Also occurring in the outfall fringing area was an extremely dense population of very large individuals of the vermetid gastropod *Serpulorbis squamigerus*. This mollusc, which characteristically feeds upon detrital particles trapped from suspension, had formed an extensive bed at the lower intertidal margin of the outfall area and had been abundant in the sewage-impacted zone for many years, as evidenced by the reef-like build-up of dead calcareous tubes.

There was a much higher concentration of fishes in the vicinity of the San Clemente Island outfall than in a nearby unpolluted area (Horn, 1977). On average, gillnets in the outfall area trapped a larger number of fish species (1.4 times as great), higher densities (3 times as many individuals) and greater biomass (4.5 times) than were obtained in the control area. Horn (1977) concluded that the outfall served as both an attractant and food source for fishes that are generalized feeders.

Gut analyses

Pachygrapsus crassipes taken from the outfall area was found (see Littler and Murray, 1978 for details) to consume 18% more sewage particulates, as well as greater amounts of opportunistic primary producers, than *P. crassipes* from control areas, whose diet was more diverse and included calcareous algae as important constituents. Other grazers such as *Acmaea (Collisella) limatula, A. (Collisella) scabra* and *Lottia gigantea*, were found (Littler and Murray, 1978) to utilize preferentially high-energy ephemeral forms of algae in the outfall system. There was little qualitative difference in the gut contents of populations of *Littorina planaxis, L. scutulata* and *Serpulorbis squamigerus* in the outfall and control areas.

The omnivorous suspension feeder *Anthopleura elegantissima* occurred only rarely outside of the outfall fringe zone, where it regularly contained sewage in its gut. The outfall grazers consumed high-energy disclimax algal forms. For example, *Acmaea (Collisella) digitalis* utilized considerable amounts of *Enteromorpha* sp., while the diets of *A. (Collisella) limatula, A. (Collisella) scabra* and *Lottia gigantea* consisted of relatively large quantities of blue-green algae near the outfall. Specimens of *Acmaea (Collisella) digitalis*, a limpet occurring higher in the upper intertidal than other limpets and, consequently, nearer the outfall terminus, were found to be feeding considerably more on bacteria than were other gastropods.

ENVIRONMENTAL ASPECTS

Sand movement

Island sites tended to be dominated by the larger perennial species characteristic of mature communities. The habitat investigated on the western coast of San Nicolas Island near Dutch Harbor was unusual because of periodic episodes of sand movement and inundation, which occurred throughout the three years of the research program. In places where sand scouring was frequent (see Taylor and Littler, 1982; Littler et al., 1983 for detail), opportunistic organisms associated with early stages of community development (for example, seaweeds such as *Chaetomorpha linum, Cladophora columbiana, Enteromorpha intestinalis* and *Ulva lobata* and macroinvertebrates *Chthamalus dalli, Chthamalus fissus, Phragmatopoma californica* and *Tetraclita rubescens*) dominated the standing stocks. In contrast, elevated rocky substrata provided spatial escapes from sand inundation; these raised areas were occupied by relatively mature community assemblages, including long-lived molluscs such as *Haliotis cracherodii, Lottia gigantea* and *Mytilus californianus*. Santa Rosa Island also contained a highly variable zone below + 0.9 m, which appeared to be affected similarly by sand deposition. All three mainland areas that were subjected to a high degree of substratum instability (Corona del Mar, Whites Point and Coal Oil Point) also were distinguished by opportunistic species assemblages.

Wave exposure

There tended to be fewer macroinvertebrate taxa in samples from sites with heavy wave exposure (Fig. 11.8), while the greatest number of macroinvertebrates was encountered on Santa Catalina Island, a relatively sheltered habitat. Macrophyte species showed increased numbers at sites with prominent surge or swell, possibly due to less desiccation stress (Fig. 11.8), allowing a greater number of normally subtidal species to inhabit higher regions. The Ocean Beach community was relatively constant but lacked the large brown seaweeds usually found in other mature communities (see also Stephenson and Stephenson, 1972). 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 soft sandstone substratum. It was observed frequently that the large seaweeds and barnacles were easily torn loose during periods of high wave energy.

Temporal variation

Seasonal patterns of distribution and abundance have often been described for populations inhabiting rocky intertidal habitats of temperate seas. For macrophytes, seasonality commonly has been associated with fluctuations in environmental variables such as light, temperature and frequency of storms (see, for instance, Conover, 1958; Edwards, 1969; Doty, 1971; Horn et al., 1983). However, as demonstrated by several recent studies (Raffaelli, 1979; Lubchenco and Cubit, 1980; Dethier, 1981), biotic factors such as competition and predation may also contribute to seasonal patterns. For southern California, predictable seasonal cycles of certain abiotic features are apparent. For example, summer is characterized by longer daylight hours, warmer seawater and air temperatures, lower precipitation levels and fewer periods of stressful daytime aerial exposure than is the case during the winter.

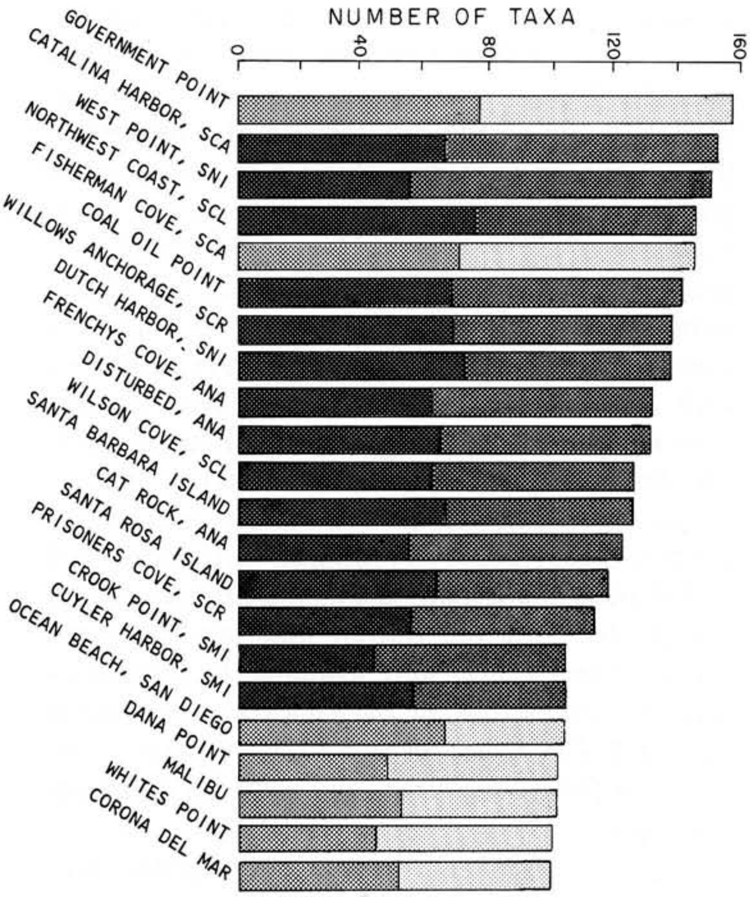

Fig. 11.8. Numbers of macrophyte taxa (left portions of histograms) and macroinvertebrate taxa (right portions of histograms) at each of the 22 study areas. Mainland stations are shaded lighter overall than island sites. The five stations below, located near large centers of human population, tended to have lower numbers of species. SCA: Santa Catalina Island; SNI: San Nicolas Island; SCL: San Clemente Island; SCR: Santa Cruz Island; ANA: Anacapa Island; SMI: San Miguel Island.

Throughout 1975–1978 in southern California there were few widespread or consistent seasonal fluctuations of rocky intertidal populations except for (1) a slight lowering of most biological parameters at all stations following the daytime low-tide emersions preceding the winter months; (2) sporadic recruitment of barnacles and several other macroinvertebrates (such as *Aplysia*) at various sites during the winter through spring period; and (3) growth and accumulation of standing stocks of large seaweeds throughout the summer. Distinct seasonal patterns were most pronounced at the relatively protected, physically benign, southern island stations (for example, Santa Catalina Island, Fisherman Cove; San Clemente Island, Wilson Cove). At these sites, macrophyte standing stocks were greatest during the late summer and least during the winter when harsher environmental conditions probably resulted in lower growth rates. Reductions in intertidal standing stocks during periods of increased physical harshness have also been shown for New South Wales, Australia (Underwood, 1981) and central California (Horn et al., 1983). The overall lack of consistent temporal tendencies strongly suggests that local-scale or even site-specific conditions tend most often to predominate and obscure broad climatic effects. This agrees with other descriptions (Stephenson and Stephenson, 1972; Jernakoff, 1985) of rocky intertidal systems that also have a high degree of autonomy.

However, as is the case for many biological systems, major stochastic abiotic disturbances appear to be paramount in restructuring southern California intertidal communities. The most important of these during our study were (1) unusually heavy precipitation and flooding events that exposed intertidal organisms to reduced salinities and sediment loading; (2) conditions of extreme heat, low humidity and high winds that occurred during periods of daytime tidal emersion; (3) exceptionally large storm-generated waves; and (4) patterns of longshore sand transport that scoured and buried various organisms. The first two disturbances typically occur during the late fall and winter; however, large waves can strike the southern California coastline at any time, and the patterns of sand movement within stations appear to be quite variable, as well as differing from site to site (Littler, 1980b). Therefore, subtle seasonal patterns in community composition and standing stocks may be difficult to detect, particularly for systems that are subjected to high levels of such unpredictable disturbance.

Community responses to natural disturbances

During the three-year investigation, several of the sites experienced major natural physical disturbances. For example, the Corona del Mar study area became flooded by an unusually heavy rainfall (2.56 cm within 3 hours) in May 1977 (Littler and Littler, 1987). As a result, the sea urchin *Strongylocentrotus purpuratus* underwent a twenty-fold decrease in cover (from about 2.0% to less than 0.1%) in the lower intertidal zone (MLLW to +0.3 m) and disappeared entirely within the +0.3 to +0.6 m interval. However, the most dramatic effects were revealed by the density counts of *S. purpuratus* over relatively broad areas. Belt transects documented an average of 90.5% mortality, and a census of the total area between two permanent transect lines showed 93.6% of the *S. purpuratus* to be dead. A biotically similar area beyond the periphery of the region that was flooded (20 m north of the north transect line) experienced only 1.1% mortality of *S. purpuratus* (Littler and Littler, 1987). The serpulid worm *Eupomatus gracilis* decreased in mean density by 74 m^{-2}. Species consistently present previously, but absent following the flood, included four gastropods, the crab *Pugettia producta*, the bivalve *Glans carpenteri* and an unknown bryozoan. Ephemeral macrophytes characteristic of disturbed environments, the green algae *Enteromorpha* sp. and *Ulva californica* and Ectocarpaceae, increased markedly in mean overall cover (14.5% and 8.9%, respectively) following the rain-storm, as did newly recruited barnacles. However, the majority of long-lived macrophytes, such as *Hydrolithon decipiens*, blue-green algal crusts and *Gelidium* spp. (*G. coulteri* and *G. pusillum*), showed declines in overall mean cover (1.3%, 7.8%, and 5.0%, respectively).

During afternoon low tides in the winter of 1976, rocky intertidal organisms inhabiting the Santa Cruz Island site at Willows Anchorage were subject to prolonged exposure to hot, dry "Santa Ana" winds (Seapy and Littler, 1982). Numerous species exhibited pronounced die-back, including the barnacles *Chthamalus dalli* and *C. fissus* and the seaweeds *Codium fragile, Corallina officinalis* var. *chilensis, C. vancouveriensis, Cylindrocarpus rugosus, Endocladia muricata* and *Pelvetia fastigiata* f. *gracilis*. The die-backs were succeeded by blooms of morphologically simple seaweeds such as *Porphyra perforata* and *Ulva californica*.

During May 1976, an unusually severe storm devastated the Santa Catalina Island, Fisherman Cove site, which is normally sheltered in the lee of the prevailing swell patterns. This protected site was dominated by high standing stocks of large morphologically complex seaweeds and other organisms characteristic of mature stages of community development. The storm waves ripped up many kelp plants immediately seaward of the study area, in addition to breaking off a large portion of the three-meter high rocky bluff above the supralittoral fringe. Short-term effects of the storm were largely confined to decreases in the standing stocks of larger long-lived seaweeds, such as *Corallina officinalis* var. *chilensis, Egregia menziesii, Eisenia arborea* and *Gelidium purpurascens*, and increases in the abundance of morphologically simple opportunists, such as *Colpomenia sinuosa, Enteromorpha* sp. and *Scytosiphon dotyi*. These opportunistic species are known (Wilson, 1925; Emerson and Zedler, 1978; Murray and Littler, 1978) to readily occupy newly vacated patches within mature southern California communities. Where disturbance is periodic and not too severe, southern California rocky intertidal communities appear to exhibit an overall increase in diversity, owing to the coexistence of mixed patches of early and late successional species (Sousa, 1979a). For example, overall community H' diversity at Fisherman Cove increased following the 1976 storm from 2.80 to 3.04, due to the greater abundance of opportunists and decreased abundance of community dominants.

Drift seaweed biomass, consisting predominantly of the larger kelps, increases dramatically (ZoBell, 1971) on southern California beaches during the periods 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. Such natural events remove biomass and are recurrent physical factors in biological communities (Connell, 1978); their effects have been partially documented in the cases of sand scouring and inundation (Seapy and Littler, 1982; Taylor and Littler, 1982; Littler et al., 1983), substratum instability (Sousa, 1979a, 1980; Murray and Littler, 1984; Littler and Littler, 1984), extreme aerial exposure (Seapy and Littler, 1982) and unusually severe, storm-generated waves (Murray and Littler, 1978).

The unpredictable occurrence of storms or high waves has been correlated with subtidal standing-stock fluctuations in the tropics (Doty, 1971), where normal seasonality is obscured. Similarly, catastrophic events were related (Paine, 1979) to biomass fluctuations in the temperate sea palm *Postelsia*. Such stochastic events can have highly localized species-specific catastrophic effects on littoral populations; they may set in motion subsequent changes to overall community structure that would be difficult to understand from a program of infrequent sampling. Therefore, studies of the responses of intertidal communities to natural perturbations (Sousa, 1980; Littler and Littler, 1984) may give information on the ability of different components to recover, and thus provide one method of measuring community stability (resilience).

Recovery from disturbances

Successional studies have been conducted (Murray and Littler, 1979) throughout southern California to determine biological recovery rates following severe mechanical disturbances, that is, the removal of all fleshy and upright organisms. A primary objective was to identify sensitive populations that would be slow to re-establish. The resultant mortality suffered by mechanically harvesting populations provided free space such as that produced by natural physical disturbances.

Generally, most intertidal macrophytes were effective in rapidly re-establishing their overall cover on disturbed surfaces, while most macroinvertebrate populations tended to recover much more slowly. All of the sites (except Santa Cruz Island and Santa Catalina Island) regained their pre-harvest levels of mean macrophyte cover after 12 months, whereas none of the macroinvertebrate species attained preharvest levels of cover, and overall pre-harvest densities of macroinvertebrates 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 experimental sites.

This evidence is in agreement with that of Murray and Littler (1978) and Sousa (1980) in demonstrating that the successional stages of intertidal algal communities differ significantly in their responses to disturbance. Early successional communities tend to suffer more damage from a given level of perturbation but recover more quickly than either middle or late successional communities. The long-lived articulated coralline algae (such as, for instance, *Corallina officinalis* var. *chilensis*) show remarkably rapid recovery rates from remnant basal-crust portions (Littler and Murray, 1978; Littler and Kauker, 1984), particularly where they have previously formed a dense turf. In agreement, Stewart (1982) found that experimentally scraped quadrats could be distinguished from unscraped turfs after 12 to 14 months only because the genus *Corallina* remained less dense and in some instances, large clumps of *C. vancouveriensis* were still absent. After 24 months, turf regrowth areas were indistinguishable from the surrounding community, and *Corallina* was re-established completely on surfaces where it had formerly predominated. Certain of the frondose forms such as *Gigartina canaliculata* also showed rapid recovery following plot clearance (Sousa, 1979b). In our studies, *Egregia menziesii* was found to initiate recolonization of disturbed surfaces soon after harvesting; however, habitats subjected to continual disturbances (such as Whites Point, Coal Oil Point and Corona del Mar) were not readily recolonized by *Egregia*. Filamentous algae (such as 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 *Dodecaceria fewkesi* and *Phragmatopoma californica*.

Several populations of macrophytes and macroinvertebrates were found to be exceptionally slow to recover, and are, thus, likely to be severely impacted by disturbance. The upper intertidal rockweeds *Hesperophycus harveyanus* and *Pelvetia fastigiata* consistently failed to re-establish. These species, even when abundant adjacent to disturbed plots, showed extremely slow vegetative encroachment or propagule recruitment. Other large frondose seaweeds, such as *Halidrys dioica* and *Prionitis lanceolata*, were also extremely slow to recruit or encroach. Populations of sessile bivalves were likewise quite slow to recover. For example, the mussels *Brachidontes adamsianus*, *Mytilus californianus*, *M. edulis* and *Septifer bifurcatus* all showed virtually negligible re-establishment on disturbed surfaces, as did the rock oyster *Pseudochama exogyra*.

HUMAN INFLUENCES

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

The most widely cited baseline information was that of Dawson (1959, 1965) for marine algae. Dawson noted reductions in algal species numbers ranging from 50 to 70% at sites near sewage outfalls. Because Dawson (1959, 1965) assessed only the "conspicuous" members of the seaweed flora, it has been difficult for subsequent researchers to make direct comparisons of richness (see Harris, 1980). Problems aside, other workers (Nicholson and Cimberg, 1971; Widdowson, 1971; Thom, 1976; Thom and Widdowson, 1978) have clearly substantiated further declines in macrophyte species numbers at many of the same areas studied by Dawson. Such declines were attributed to human influence but only circumstantial evidence was available. The declines do not seem to have been instantaneous (Nicholson, 1972), but probably are the result of human pressure that has been increasing markedly since the turn of the century.

Littler and Murray (1975) demonstrated considerable reductions in the standing stocks of large brown algae and seagrasses near a low-volume domestic sewage outfall on San Clemente Island. There were fewer species and less cover near the point of discharge (7 macroinvertebrates, 17.6% cover; 13 macrophytes, 91.7%) than in nearby "unpolluted" control areas (9 macroinvertebrates, 9.2%; 30 macrophytes, 103.4%). The outfall biota was less diverse than that of the controls, as shown by five different diversity indices. A great reduction in community stratification (spatial heterogeneity) and, hence, community complexity was noted near the outfall; this reduction in stratification was primarily due to the absence of large macrophytes such as *Egregia laevigata, Halidrys dioica, Phyllospadix torreyi* and *Sargassum agardhianum*. These were replaced in the mid intertidal near the outfall by a low turf of blue-green algae, *Gelidium pusillum, Ulva californica*, and small *Pterocladia capillacea*, and in the lower intertidal by *Serpulorbis squamigerus* covered with *Corallina officinalis* var. *chilensis*. As mentioned earlier, the enhancement of the suspension feeder *Serpulorbis squamigerus* and the omnivores *Anthopleura elegantissima, Ligia occidentalis* and *Pachygrapsus crassipes* in the outer fringe of the outfall plume appeared to be related to their ability to utilize sewage as a food source. A critical effect of the outfall was to decrease environmental stability, thereby favoring rapid colonizers and more sewage-tolerant organisms. The outfall macrophytes had relatively higher net primary productivity, smaller growth forms, and simpler and shorter life histories; most are components of early successional stages. The above findings (Littler and Murray, 1975) were in agreement with earlier observations (Widdowson, 1971; Thom and Widdowson, 1978) that there has been a shift from the more massive algal species towards turf and crustose taxa in southern California littoral communities since the surveys by Dawson (1959, 1965) in the 1950's. Additionally, Thom and Widdowson (1978) reported that these changes were most pronounced in habitats exposed to greatest disturbance, that is, localities near heavily populated metropolitan areas or in public parks subject to heavy human recreational usage.

Beauchamp and Gowing (1982) have shown that human trampling can cause serious degradation of littoral communities where usage is high. Murray and Littler (1984) have also documented a reduction of large brown and fleshy algae at Whites Point, a site exposed to extensive human traffic and inshore from the large (>300 million gal day^{-1}) sewage outfall operated by the Los Angeles County Sanitation District. Sousa et al. (1981) described reductions in standing stocks of long-lived, large brown algae for southern California intertidal habitats, and attributed their reduction to enhanced grazing pressure from sea urchins. However, our experience on the outer coastal habitats of the southern California islands is that abundant populations of the purple sea urchin *Strongylocentrotus purpuratus* commonly coexist with high standing stocks of large brown algae such as *Halidrys dioica* in the lower intertidal zone.

As a result of expansion of the human population in southern California, more of the marine communities on the relatively inaccessible offshore Channel Islands (for instance, Anacapa Island) are being altered (Littler, 1978b). By comparing an accessible station ("Anacapa-Disturbed"; Fig. 11.1; visited by approximately 50 000 boaters per year) with a relatively inaccessible habitat (Cat Rock) near Frenchys Cove, Anacapa Island, Littler (1978b) was able to show a community shift, from long-lived invertebrate and algal populations toward turfy opportunistic algae and the tube-worm *Phragmatopoma*, correlated with activities of visitors. Already most of southern California's rocky intertidal systems have been exposed to different degrees of anthropogenic influence; collecting, rock-turning, trampling, oil spills and sewage pollution have been so intensive that the conspicuous invertebrates and plant life have been severely reduced or eliminated near many of the heavily populated regions. Despite extensive research, human influence on intertidal coastal environments continues to outpace understanding of the ecological changes that are taking place.

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