

Biogeographical analysis of intertidal macrophyte floras of southern California

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ABSTRACT. The macrophyte floras of California mainland and island sites south of Point Conception form five discrete biogeographic units based on individual between-site similarity comparisons, hierarchical classification (cluster) analysis and principal coordinates ordination. These site assemblages correlate well with the complex patterns of surface water circulation and temperature. Sites bathed more regularly by the warm waters of the Southern California Countercurrent tend to group and exhibit relatively low overlap in species composition with the cold-temperate flora characteristic of the central California coast north of Point Conception. Greater cold water floristic affinities were found for the sites proximal to cold California Current flow, while sites located in the region of variable mixing between cold and warm water currents showed intermediate affinities. The apparent relationship between the groups established by classification analysis and ordination, the degree of overlap with the cold-temperate central California flora, and our understanding of surface circulation and temperature gradients, provide indirect evidence implicating temperature in the control of the distributions of southern California intertidal macrophytes. Additionally, the changing species composition along the coast south of Point Conception clearly demonstrates the transitional nature of the southern California shallow-water biota and underscores the importance of this unique region to eastern North Pacific biogeography.

Introduction

The 1000 km California coastline is of great importance to the understanding of eastern North Pacific biogeography. Historically, the area near Point Conception (34° 26' N) has been recognized (Dall, 1899; Bartsch, 1912) as a distributional barrier for nearshore marine biota, and has been reported (e.g. Newell, 1948; Hedgpeth, 1957; Briggs, 1974; Brusca & Wallerstein, 1979) to serve as the boundary between cold and warm temperate biogeographical provinces. Although much of our understanding of California coastal biogeography has been based on faunal distributions (e.g. Newell, 1948; Garth, 1955; Valentine,

1966; Hayden & Dolan, 1976; Horn & Allen, 1978), phycologists have long been aware (see Setchell & Gardner, 1903) of the large number of seaweeds that terminate their ranges at or near Point Conception. Recently, assessments of the geographical ranges of eastern North Pacific algae (Pielou, 1978; Murray, Littler & Abbott, 1980) have provided quantitative evidence in support of the importance of Point Conception to benthic algal distributions.

Distributions of shallow-water marine organisms have been considered to be strongly influenced by patterns of oceanic circulation and coastal water temperatures. Circulation of nearshore waters in the eastern North Pacific is complex (Fig. 1), particularly south of

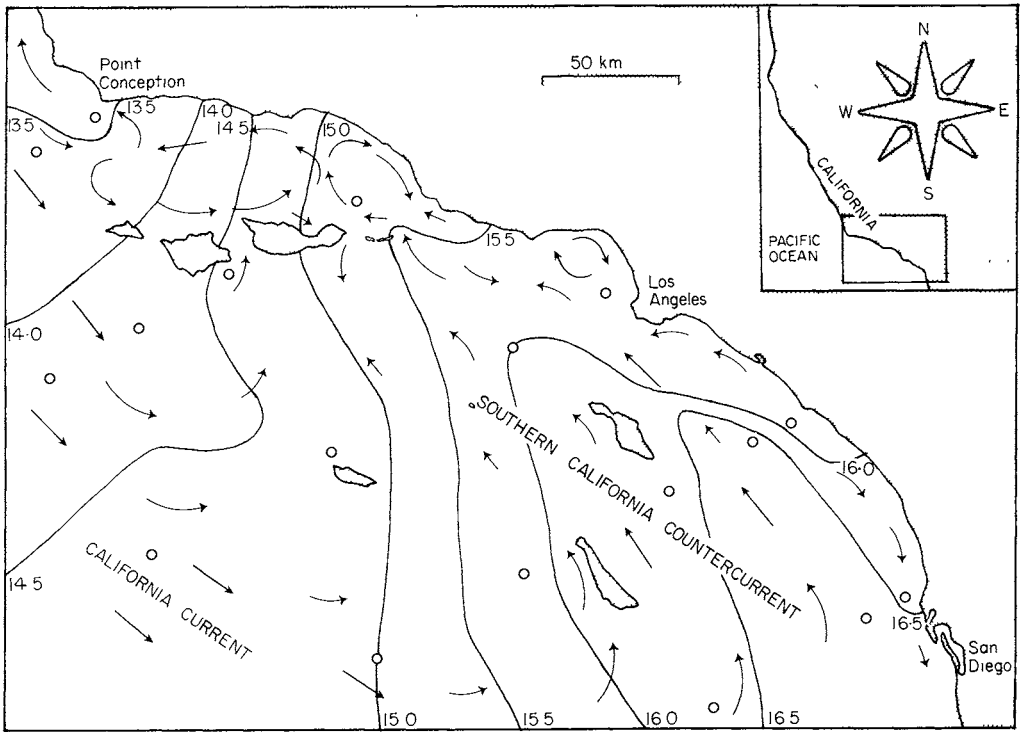


FIG. 1. The general patterns of surface circulation and surface water temperature in Southern California. Surface circulation patterns have been interpreted from Jones (1971) and Pirie *et al.* (1975), while water temperature isotherms have been based on averages of the 1949–59 10-m depth monthly means (January, April, July and October) for the indicated (○) CalCOFI stations (Anon., 1963).

Point Conception. Here, the southern California coastline swings abruptly eastward, away from the principal flow of the cold California Current which remains some 250 km seaward. The resulting broad embayment, which extends southward to Mexico, is characterized (Reid, Roden & Wyllie, 1958; Jones, 1971; Pirie, Murphy & Edmisten, 1975) by variable surface circulation patterns that mostly bathe the mainland coast with warm water brought from the south by the northwesterly flowing Southern California Countercurrent. Thus, mean coastal surface water temperatures along the mainland east and south of Point Conception are significantly higher than to the north, where there is closer proximity to the colder California Current (Fig. 1).

The eight Southern California Islands (Fig. 1) are located in this region of variable mixing between the cold waters of the California Current and the warm nearshore waters of the Southern California Countercurrent (Reid *et al.*, 1958; Schwartzlose, 1963; Pirie

et al., 1975). The biogeographical significance of the exposure of the offshore islands to different oceanographic temperature regimes was recognized by Neushul, Clarke & Brown (1967) in their examination of insular subtidal algal communities. Earlier, Hewatt (1946) had suggested that the coastal invertebrates of the islands exhibited intermediate biogeographical affinities with the faunal elements characteristic of mainland habitats north and south of Point Conception. The absence of sufficient floristic and faunistic data, however, has resulted in a lack of definitive studies concerning the biogeographical relationships of the Southern California Islands. Recently, separate analyses of the distribution of intertidal seaweeds (Murray *et al.*, 1980) and macro-invertebrates (Seapy & Littler, 1980) have confirmed the transitional nature of the islands. The intertidal floras along the southern California mainland have received much attention during the past 25 years (Dawson, 1959, 1965; Nicholson & Cimberg, 1971; Widdow-

son, 1971; Thom & Widdowson, 1978), mostly concerning the documentation of human-induced changes in species composition. Only recently, however, have the geographical patterns of mainland seaweed distributions been assessed. Thom (1980) analysed the distributions of frequently occurring species at fifty-one stations located along the 450 km of mainland coastline south of Point Conception and reported substantial floristic differences between sites at the extreme north and south of this range, but that the compositional changes were gradual and continuous. Although Thom (1980) was unable to eliminate factors such as human disturbance, sand movement and wave action, he did suggest that water temperature is the overriding factor causing changes in algal species composition along the southern California mainland.

The purpose of our research is to determine if the distributional patterns of southern California intertidal macrophytes are related to patterns of ocean circulation and seawater temperature as previous research suggests. An

emphasis has been placed on understanding the biogeographical affinities of the floras of the eight Southern California Islands and on more completely defining the relationships of the island floras to the mainland macrophyte assemblages north and south of Point Conception.

Methods and Materials

The rocky intertidal macrophyte floras were determined for twenty-one southern California sites located between Point Conception and the United States–Mexico border (Fig. 2, Table 1). Seven stations were established on the mainland and fourteen were located on the offshore islands. Sites were visited one to several times from July 1975 to July 1978 and all algal species lists were based on a minimum of 3 days of intensive collection. Any bias in the species composition between sites due to the season of collection was considered insignificant, because of the small variation in species presence–absence data obtained for

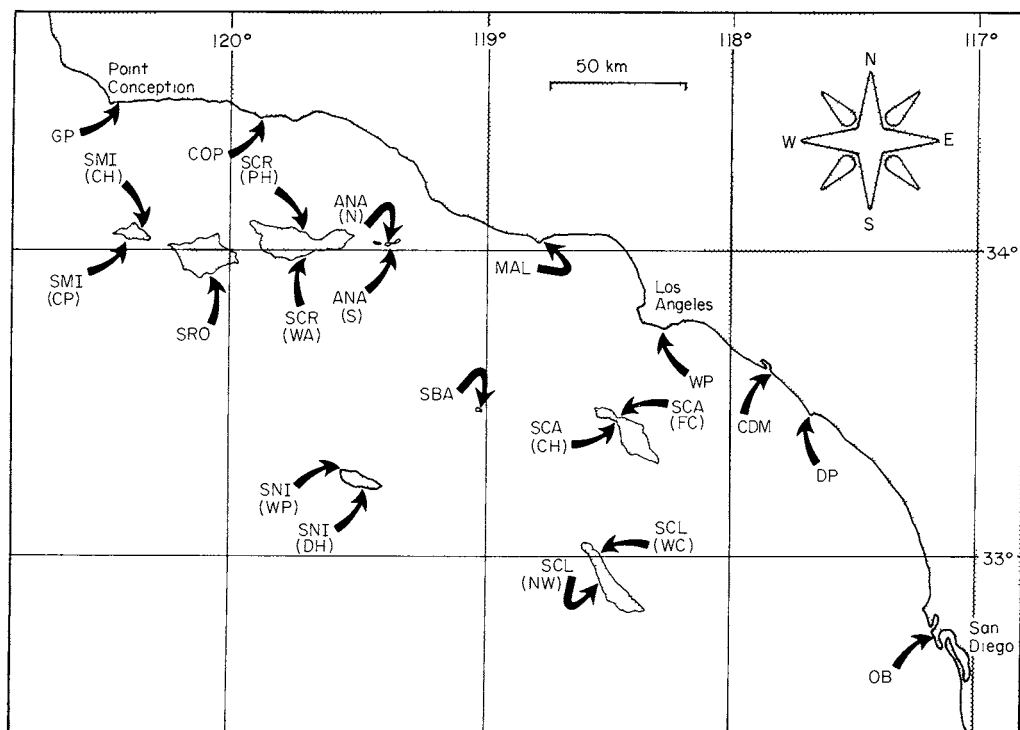


FIG. 2. Locations of the twenty-one rocky intertidal stations (station identities are given in Table 1).

TABLE 1. The twenty-one intertidal stations (grouped by cluster analysis) and the percentage of macrophytes in common with the central California flora north of Point Conception

Site group	Abbreviations	Per cent overlap
Group I		
Santa Catalina Island, Fisherman Cove	SCA (FC)	71.3
Santa Catalina Island, Catalina Harbor	SCA (CH)	73.9
San Clemente Island, Wilson Cove	SCL (WC)	71.3
San Clemente Island, Northwest Coast	SCL (NW)	75.0
Anacapa Island, South Coast	ANA (S)	83.1
Anacapa Island, North Coast	ANA (N)	81.4
Group II		
Corona Del Mar	CDM	84.4
Dana Point	DP	74.6
Whites Point, Los Angeles	WP	87.7
Ocean Beach, San Diego	OB	81.0
Group III		
Santa Barbara Island, Cave Canyon	SBA	80.4
Santa Cruz Island, Willows Anchorage	SCR (WA)	80.9
Coal Oil Point	COP	89.2
Paradise Cove, Malibu	MAL	89.7
Santa Cruz Island, Prisoners Harbor	SCR (PH)	91.8
Group IV		
San Nicolas Island, Dutch Harbor	SNI (DH)	93.8
Santa Rosa Island, South Point	SRO	92.3
Government Point	GP	96.4
San Miguel Island, Cuyler Harbor	SMI (CH)	95.4
San Miguel Island, Crook Point	SMI (CP)	98.4
Group V		
San Nicolas Island, West Point	SNI (WP)	90.2

any one site over numerous seasonal visits (see Littler, 1977, 1978, 1979, 1980a, b). Our floristic data are listed in Littler (1979) and are available upon request from the authors. These comprise distributional records for 222 taxa (220 algae and two spermatophytes) and constitute greater than 70% of the reported algal records (Murray, 1974) for the Southern California Islands. Additionally, these records provide comparable data sets for the analyses of island and mainland intertidal algal floras.

To determine if the southern California intertidal sites (including the eight offshore islands) could be partitioned into distinct subunits based on between-site differences in floristic composition, a similarity matrix was compiled. The elements were similarity coefficients for all possible pairs of sites based on the presence or absence of macrophyte species. Similarity was measured by the Jaccard Coefficient (Jaccard, 1908; Clifford & Stephenson, 1975), which has been used

frequently (Cheetham & Hazel, 1969; Pielou, 1979) in bio-associational studies. The Jaccard Coefficient, as a percentage is:

$$J(\%) = a / (a + b + c) \times 100,$$

where a is the number of species common to both sites, and b and c are the numbers of species occurring at only one or the other of the sites. As indicated by Pielou (1979), a similarity matrix provides an objective means to judge whether natural discontinuities exist among the intertidal floristic collections.

Additionally, the binary (presence-absence) data for the twenty-one sites were subjected to computer-mediated hierarchical classification (cluster) analysis and principal coordinates ordination to gain a clearer understanding of the distributional patterns; principal coordinates ordination is a useful technique for analysing data from a matrix of dissimilarities (Clifford & Stephenson, 1975). The Canberra metric dissimilarity measure (Lance & Williams,

1967; Clifford & Stephenson, 1975) was employed in the classification analysis and ordination. It is:

$$D = \frac{1}{n} \sum_1^n |X_{1j} - X_{2j}| / (X_{1j} + X_{2j}),$$

where *n* is the number of taxonomic units present at sites 1 and 2, and *X*_{1*j*} and *X*_{2*j*} represent the presence (=1) or absence (=0) of the *j*th species at sites 1 and 2. Programs written by Smith (1976) were used for the computer analyses.

Our macrophyte collections were also compared with distributional records compiled by Abbott & Hollenberg (1976) for central California to determine their affinities with the cold-temperate flora north of Point Conception. This was accomplished by calculating for each of the twenty-one sites, the

percentage of species also reported (Abbott & Hollenberg, 1976) to occur between 35° 00' N and 36° 00' N, a ~ 111 km section of California shoreline historically reported (e.g. Valentine, 1966; Briggs, 1974; Brusca & Wallerstein, 1979) to be characterized by cold-temperate biotic elements. The spermatophyte distributions employed in these calculations were obtained from Phillip's (1979) records.

Results

Quantitative analyses of the floristic affinities of the twenty-one rocky intertidal sites provided strong evidence that they could be partitioned into distinct groups. The similarity matrix (Fig. 3), revealed differential relationships of the floras. The greatest similarity (61.4%) occurred between the Santa Catalina

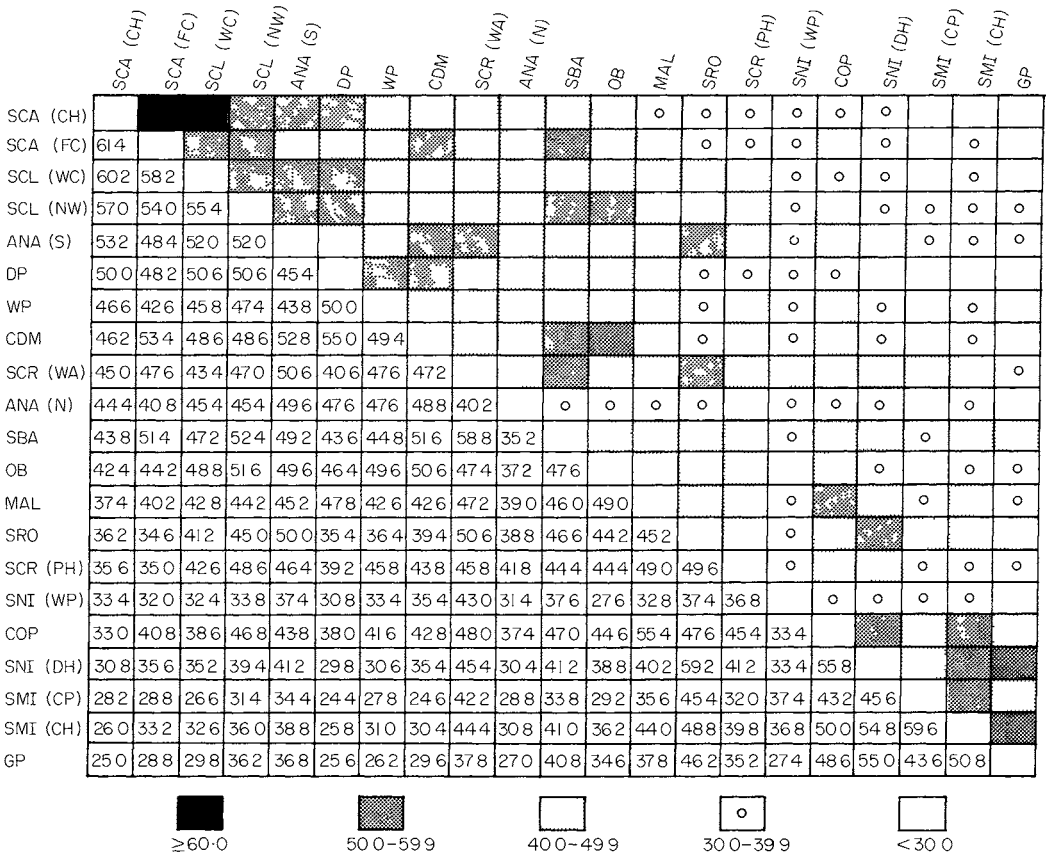


FIG. 3. Similarity (%) comparisons of the macrophyte floras for all possible site pairs based upon the Jaccard Coefficient.

Island sites at Fisherman Cove and Catalina Harbor. These two sites were most closely associated with stations on nearby San Clemente Island and showed least affiliation with sites on San Miguel Island and at Government Point. Least similarity (24.4%) occurred between the mainland flora at Dana Point, and Crook Point, a site located on southern San Miguel Island.

In southern California, shallow-water habitats on the offshore islands have been characterized (Littler, 1980a, b) as relatively pristine compared to the mainland biota which has been subjected to considerable human impact over the past several decades (see Dawson, 1959, 1965; Foster, Neushul & Zingmark, 1971; Nicholson & Cimberg, 1971; Widdowson, 1971; Nicholson, 1972; Thom & Widdowson, 1978). Consequently, we examined the inter-site similarity data to test the hypothesis that independent of geographic location, island-mainland comparisons exhibit significantly less similarity than island-island or mainland-mainland comparisons. The hypothesis was rejected as no significant difference ($P > 0.05$) was determined between the inter-site similarities for these three groups based on single classification analysis of variance.

Inspection of the similarity matrix (Fig. 3), however, revealed patterns of association

among the twenty-one sites. These patterns were clarified further by means of hierarchical classification (cluster) analysis as well as principal coordinates ordination. Five distinct site groups were interpreted from the classification analysis (Fig. 4); these groups could also be distinguished, although less clearly, from the similarity matrix (Fig. 3) and two-dimensional ordination space (Fig. 5). Groups I and V contained island sites alone (Fig. 4; Table 1), Group II mainland sites alone, and Groups III and IV both mainland and island sites. Group I was composed of the island sites most exposed to the warm Southern California Countercurrent (Santa Catalina, San Clemente and Anacapa Islands), while a second related, but clearly distinct group (Group II), included the southernmost mainland sites. Mainland habitats from northern Santa Monica Bay (Malibu) and bordering the central region of the Santa Barbara Channel (Coal Oil Point) together with the island sites subjected to the greatest mixing of cold and warm ocean waters constituted Group III. Group IV was composed of the island (San Miguel, San Nicolas and Santa Rosa Islands) and mainland (Government Point) sites closest to the cold California Current; the site at West Point, San Nicolas Island, was somewhat related to the sites forming Group IV, but was sufficiently distinct to form a separate entity (Group V).

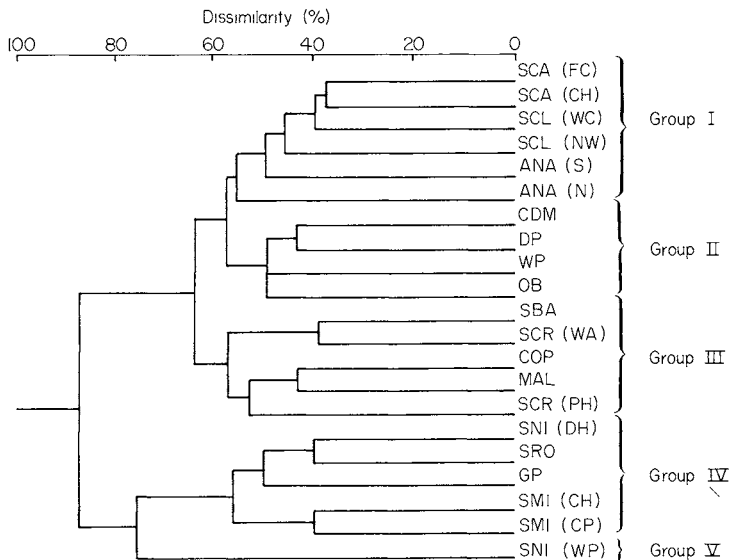


FIG. 4. Dendrogram depicting the percentage dissimilarity between sites and site groupings based on hierarchical cluster analysis.

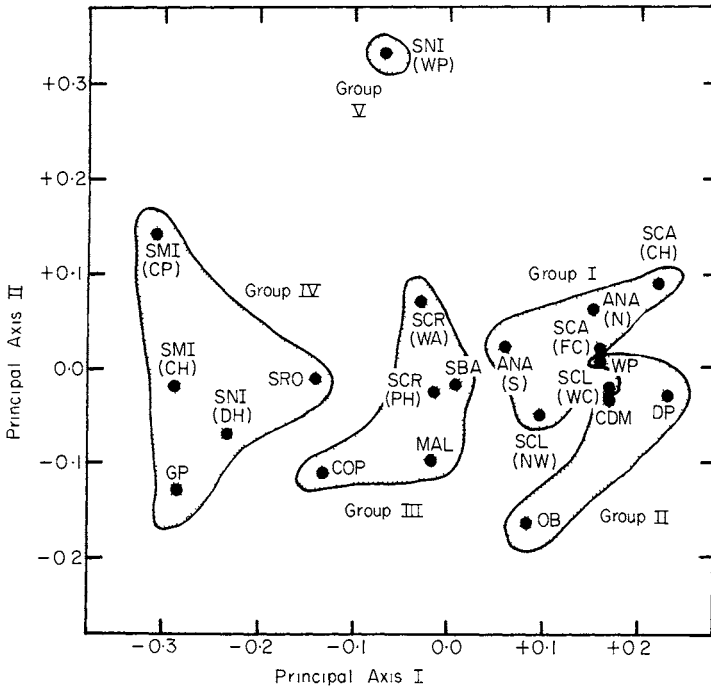


FIG. 5. Diagram depicting the results of principal coordinates ordination of the intertidal sites. Sites are figured in two-dimensional space resultant from their relationships to the first two ordination axes, which account for a cumulative total of 46.4% of the variance (principal axis I = 34.2% and principal axis II = 12.2%). See Table 1 for key to site abbreviations.

Further support for the five site-groups was obtained from principal coordinates ordination. Nearly identical assemblages could be distinguished in the two-dimensional space spanned by the first two ordination axes (Fig. 5) except that the southernmost mainland sites (Group II) exhibited greater affinities with the warm-water island sites (Group I); Group III occupied an intermediate position between Group IV and Groups I and II. The site at West Point, San Nicolas Island (Group V) remained distinct from the other sites.

Discussion

The mainland and island shorelines south of Point Conception can be divided into five discrete biogeographic units. The segregation of island sites concurs with the prediction of Neushul *et al.* (1967) and is consistent with earlier, more limited analyses of the distributions of insular macroinvertebrates (Seapy & Littler, 1980) and benthic algae (Murray *et*

al., 1980). Additionally, our distributional patterns closely match those reported by Littler (1980b) during his ecological studies of southern California intertidal communities, suggesting that for this region of the eastern North Pacific, community affinities based on species abundances correlate well with presence/absence biogeographical analyses. Previous research focusing on the distributional patterns of southern California mainland macrophytes has been limited to the study by Thom (1980), who reported gradual and continuous changes in the composition of the most frequently occurring species. We interpret our results to be compatible with those of Thom, only we are able to partition southern California mainland sites into distinct units because we have examined considerably fewer points (7 *v.* 51) along what appears to be a relatively continuous gradient.

Seawater temperature has historically been regarded (Setchell, 1915, 1917, 1920a, b, 1935; Gunter, 1957; Hedgpeth, 1957; Kinne, 1963; Valentine, 1966; Gessner, 1970) as the

most important single factor controlling the ranges of shallow water marine organisms. As indicated by Brusca & Wallerstein (1979), the oceanographically and climatologically complex eastern Pacific Coastal region (see Fig. 1) is characterized by changing temperature and salinity gradients. This complexity is particularly pronounced south of Point Conception where the variability in surface circulation patterns and concomitant temperature gradients long have been recognized (Emery, 1960).

Although variable and complex, the patterns of current flow (Schwartzlose, 1963; Reed *et al.*, 1958; Jones, 1971; Pirie *et al.*, 1975) and coastal water temperatures (Anon., 1963; Wyllie & Lynn, 1971; Hendricks, 1977) appear to correlate well with our distributional data for intertidal macrophytes. Neushul *et al.* (1967) hypothesized that the biotic affinities of the eight offshore islands could be characterized by their proportions of northern and southern species since the islands are located in a region of variable mixing between cold California Current water and the warmer waters of the Southern California Counter-current. Anacapa, Santa Barbara, Santa Cruz, and the eastern portions of Santa Rosa are subjected to both cold and warm surface waters (Anon., 1963; Wyllie & Lynn, 1971; Hendricks, 1977), leading Neushul *et al.* (1967) to suggest that these islands should have both northern (cold water) and southern (warm water) biotic elements. Greater northern (San Nicolas, western Santa Rosa Islands) or southern (San Clemente, Santa Catalina Islands) affinities were expected for the benthos of the other islands based on more consistent exposure to colder and warmer waters respectively. Earlier, Murray *et al.* (1980) reported that, with the exception of Anacapa Island, grouping of the insular intertidal algal assemblages conformed to the model developed by Neushul *et al.* (1967). Similar supportive evidence was obtained for macroinvertebrates by Seapy & Littler (1980), with the exception that the fauna of Anacapa Island more closely affiliated with colder water sites. Because these previous studies were based upon a much more limited data base, one of the major purposes of this study was to expand our knowledge of the distributional patterns of intertidal macrophytes

occupying the offshore islands by increasing the number of stations, and therefore the number of data points along the complex southern California oceanographic gradient. The results of our substantially expanded analyses clearly support earlier findings (Murray *et al.*, 1980; Seapy & Littler, 1980; Littler, 1980b), and essentially the distributional predictions of Neushul *et al.* (1967).

The mainland sites generally exhibited species compositions similar to adjacent insular sites, with the exception of those south of the greater Los Angeles area (Whites Point, Corona Del Mar, Dana Point, Ocean Beach) which formed a group (Group II) distinct from nearby sites on Santa Catalina and San Clemente Islands. Previous researchers (Dawson, 1959, 1965; Nicholson & Cimberg, 1971; Widdowson, 1971; Thom & Widdowson, 1978) have demonstrated that intertidal algal populations near Los Angeles have undergone considerable change over the past 80 years due to human disturbance. Our data support the interpretation that human impact has altered natural distributional patterns as well as abundances (see Littler, 1980a,b) of southern California intertidal macrophytes.

An examination of the relationships between warm southern California macrophyte floras and the cold water flora north of Point Conception (Table 1) provides additional evidence implicating temperature as a significant factor influencing species distributions. The strong relationship between the groups established by our analyses and the pattern developed by the degree of overlap with the cold-temperate California flora is clearly evident when these data are considered together (Fig. 6). Further, a correlation with temperature is suggested by the principal coordinates ordination (Fig. 5), as the orientation of the twenty-one southern California sites with respect to principal axis I clearly reveals a comparable pattern to that based on the percentage overlap of the sites with the cold water California flora. Eigen value scores depicting the relationships of the sites to the first ordination axis were significantly correlated (Spearman's rank correlation $r = 0.84$; $P < 0.01$) with the percentage of cold water floristic elements providing quantitative verification of this relationship (Fig. 7).

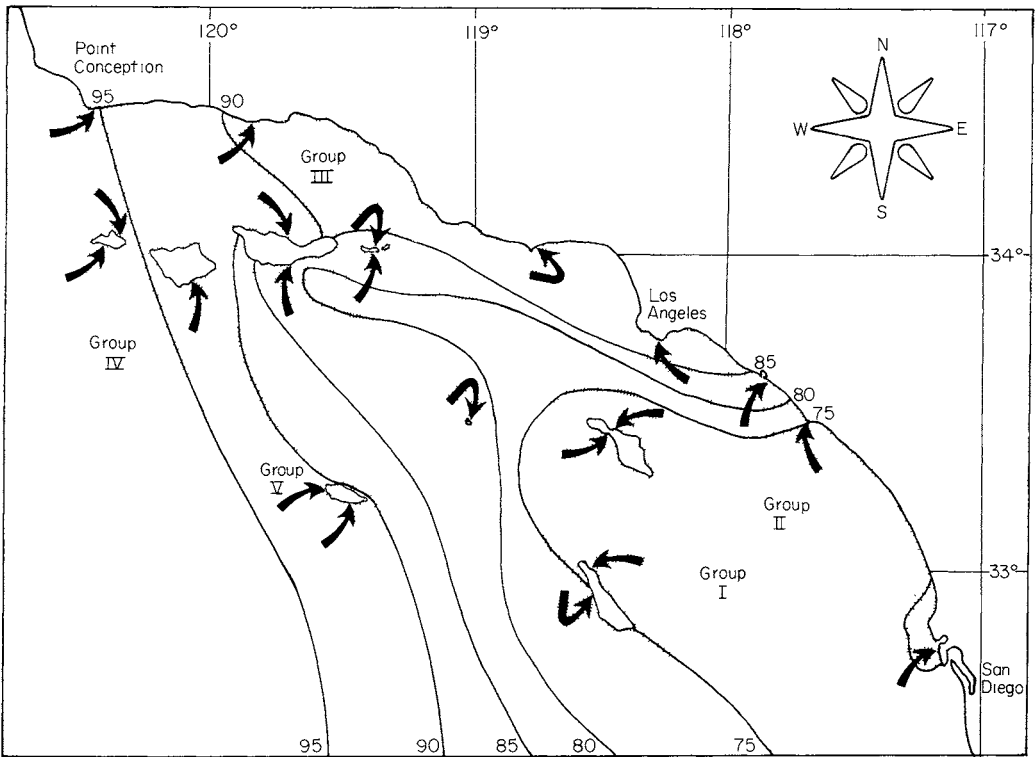


FIG. 6. Relationships of the site groups (I-V) to the patterns of floral overlap with cold-temperate California macrophytes. The percentage of macrophytes in common with the central California flora for the individual sites (Table 1) has been used to generate lines of equal overlap. Site groups are based upon the classification analysis. Individual sites are designated by arrows.

Our analyses also strongly implicate temperature as a factor of great importance in determining the distributions of southern California macrophytes (see Figs. 1 and 6). This finding is certainly in agreement with the statements of previous researchers, but the relationship between temperature and species ranges must be regarded as correlative and not necessarily causative. In this regard, we emphasize the lack of definitive work demonstrating direct numerical correlations of species distributions with temperature data. As pointed out by Brusca & Wallerstein (1979), belief in the prime importance of temperature as a distributional factor for marine organisms along the Pacific Coast of North America is so ingrained that it is not uncommon for workers to draw inferences about ocean temperatures from recorded animal distributions. However, it is widely recognized that many species are capable of

living in much broader temperature regimes than those prevalent where they normally occur. This is especially true for intertidal organisms, particularly upper and mid-intertidal species that daily tolerate wide temperature ranges (Scagel, 1963; Gessner, 1970; Jackson, 1974). Our results, for example, reveal that the Fisherman Cove, Santa Catalina Island flora is most closely affiliated with the floras at Catalina Harbor (Santa Catalina Island) and nearby San Clemente Island (Wilson Cove and Northwest Coast), and has least species overlap (71.3%) with the cold water California flora (Table 1). Based on surface circulation patterns and temperature gradients, we have characterized the Santa Catalina Island and San Clemente Island sites as possessing largely warm water floristic elements. However, the mean annual onshore temperatures at Fisherman Cove range from 12.9°C to 20.9°C (Brusca & Wallerstein,

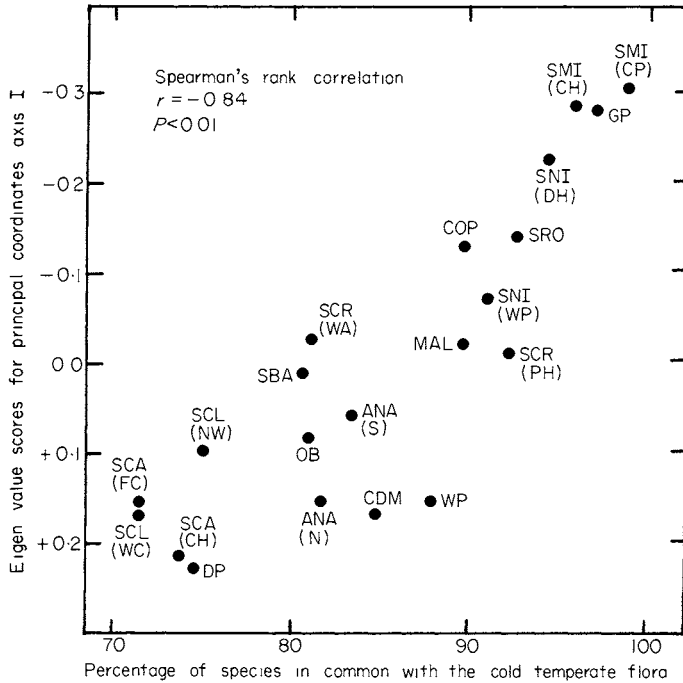


FIG. 7. Scatter diagram revealing the relationship between eigen values for principal coordinates ordination axis I and the percentage of species held in common with the cold-temperate central California flora. See Table 1 for the identification of site abbreviations.

1979), with the former representing a value lower than the annual average temperatures for the cold coastal waters near Point Conception (Anon., 1963). Thus, the difficulties reported by Valentine (1966) in his attempts to correlate numerically a single temperature factor or combinations of factors with the distributions of eastern North Pacific molluscs are readily understandable. Clearly, greater attention should be given to developing an understanding of the causal relationships between temperature and species distributions. As indicated by Connell (1974), 'it is difficult to believe that the absolute boundary of most species ranges is determined directly by temperature'. Brusca & Wallerstein (1979) have obtained sufficient laboratory data on eastern North Pacific idoteid isopods to hypothesize that the southern distributional limit of at least some species is regulated by biotic rather than abiotic factors (e.g. temperature).

Our analyses of intertidal macrophyte assemblages reveal a pattern of changing species composition along the California mainland and island coastlines south of Point

Conception, providing evidence that this region is highly transitional. Most previous biogeographical studies of eastern North Pacific marine organisms have regarded Point Conception as a relatively abrupt boundary between cold and warm temperate provinces. However, there is considerable change in the composition of the flora and fauna not only at Point Conception, but throughout the entire Southern California region. One of the most reliable methods for detecting provincial boundaries (Newell, 1948) is to determine regions where large numbers of species terminate their geographic ranges. Using this technique, several investigators (Newell, 1948; Valentine, 1966; Horn & Allen, 1978; Murray *et al.*, 1980) have independently reported large numbers of range terminations not only for Point Conception, but also for the adjacent, more southerly latitudes. Additionally, it has been recognized (Valentine, 1966; Neushul *et al.*, 1967; Horn & Allen, 1978; Brusca & Wallerstein, 1979; Murray *et al.*, 1980) that Point Conception provides a less effective barrier to northern species than to species

with southern distributional centres. Consequently, the large number of floral and faunal changes for latitudes immediately south of Point Conception are likely due (Valentine, 1966) to the occurrence of more northerly-ranging species in southern California habitats. Most prior biogeographical accounts of California biota have been concerned with larger scale interpretations for the eastern North Pacific, and only very recently have studies focused on distributional patterns in Southern California. Murray *et al.* (1980) for benthic algae and Seapy & Littler (1980) for benthic macroinvertebrates have quantitatively confirmed previous suggestions (Hewatt, 1946; Caplan & Boolootian, 1967; Neushul *et al.*, 1967) that some of the Southern California Islands contain biotic elements characteristic of cold-water locales north of Point Conception. Consequently, our results, which represent the first distributional analysis of southern California mainland and island macrophytes, much more clearly identify the transitional nature of the shallow water marine biota and underscore the importance of this unique region to eastern North Pacific biogeography.

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