

Biogeography of the California Marine Algae with Emphasis on the Southern California Islands

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INTRODUCTION

The biogeographical patterns of the marine algal flora of California have received little attention since the classical studies by Setchell (1893, 1917, 1935). This has been due in part to a lack of adequate floristic records, a long-standing obstacle (see Svedelius 1924) to advances in understanding worldwide distributions of marine algae. In the past, as indicated by Hayden and Dolan (1976), coastal marine faunistic patterns have served to delineate biogeographical provinces. Unfortunately, most of the previous distributional analyses have considered only the biota and quantitative attempts to define the physical factors controlling biological patterns have been unsuccessful. Of the physical parameters hypothesized to determine or strongly influence species distributions, temperature has been proposed most frequently as being of greatest importance (*e.g.*, Ekman 1953, Hedgpeth 1957, Briggs 1974). Setchell (1893, 1915, 1917, 1920a, 1920b, 1935), in a series of papers, attempted to explain the global distributions of marine algae, particularly the Laminariaceae, on the basis of temperature. More recently, Abbott and North (1972) discussed temperature influences on the California coastal flora in an effort to advance our understanding of the effects of thermal discharges. However, attempts to statistically correlate temperature with biogeographical patterns have been unsuccessful due to difficulties in selecting an appropriate single "temperature factor" (see Valentine 1966).

Two major distributional boundaries in the eastern north Pacific, the first near Point Conception (34°27'N) and the second near Monterey Bay (36°35' to 36°57'N), have been identified along the California coastline in recent biogeographical studies (*e.g.*, Valentine 1966, Hayden and Dolan 1976, Horn and Allen 1978). The region near Point Conception has historically been recognized as an important distributional boundary (Dall 1899, 1909, Bartsch 1912) and has commonly been reported as separating northern cold-temperate (Oregonian) from southern warm-temperate (Californian) biogeographical provinces (*e.g.*, Newell 1948, Hall 1960, Valentine 1966). Monterey Bay, however, has not been consistently recognized as a distributional barrier, although recent studies have established its biogeographical significance (Hall 1964, Valentine 1966, Hayden and Dolan 1976, Horn and Allen 1978).

Biogeographical studies have always been plagued by the necessity of interpreting distributional data which may be incomplete or affected by different levels of taxonomic study. For the California algae, further work is required before a complete understanding of species distributions is obtained. This is particularly crucial for portions of the California coastline that have received little scientific attention (*e.g.*, 35-36° and 39-42°N) and for southern California, where significant changes in species composition have occurred during this century (Widdowson 1971, Thom and Widdowson 1978). Yet, it is important to construct models, where sufficient data exist, so that advances can be made in interpreting complex distributional patterns. The

newly published comprehensive treatment of the marine algae of California (Abbott and Hollenberg 1976) has at last provided the necessary distributional data, thus enabling preliminary biogeographical assessment. The present study was undertaken to analyze these distributional records and to examine the degree to which they correlate with the previously recognized faunal boundaries near Point Conception and Monterey Bay. This research complements a recent study of patterns of latitudinal overlap of congeneric seaweed species of the Pacific coasts of the Americas (Pielou 1978) through an intensive analysis of algal distributions along the biogeographically important California coastline.

The Southern California Islands begin just to the south of the major distributional boundary at Point Conception and are of central importance to the understanding of the eastern north Pacific biogeography (Neushul *et al.* 1967). Until lately, the islands have received little scientific attention despite their biogeographical importance and the fact that they contain most of the pristine coastal habitats remaining in southern California. The biological significance of the complex surface currents in the vicinity of the Southern California Islands (see Seapy and Littler 1980) was recognized by Neushul *et al.* (1967) in their studies of the shallow-water benthic biota of Anacapa Island. The islands are in a region of variable mixing between cold California Current water from the north and west and the warm Southern California Counter-current water from the south (Schwartzlose 1963, Reid *et al.* 1958). Neushul *et al.* (1967), although providing no supportive data, indicated that the shallow-water benthos of the islands reflected prevailing oceanographic conditions and hypothesized that the affinities of each of the Southern California Islands could be characterized by its proportion of northern and southern biotic elements. Anacapa, Santa Barbara, and Santa Cruz Islands and the eastern portion of Santa Rosa Island were believed to be subject to variable mixing of cold and warm surface waters and to have both northern and southern biotic elements. Greater northern (San Miguel, San Nicolas, western Santa Rosa Island) or southern (San Clemente, Santa Catalina Islands) affinities were expected for the other islands based on their more consistent exposure to colder or warmer water, respectively.

Previous algal research on the Southern California Islands has been reviewed by Murray (1974); with the exception of the extensive studies directed by Littler (1977, 1978, 1979), additional work has been limited to ecological research on San Clemente Island (Littler and Murray 1974, 1975, 1978, Murray and Littler 1978) and Santa Cruz Island (Foster 1975a, 1975b). Littler (1977, 1978) has reported the seasonal distribution and abundance of marine macrophytes and macroinvertebrates for intertidal sites on all but Anacapa Island; the biota of Anacapa Island has recently been assessed, however (Littler 1979). These studies have greatly increased our knowledge of the island marine algal floras and have provided the data necessary for distributional analysis. A major contribution of this paper is the first thorough quantitative algal biogeographical analysis of the Southern California Islands. Additionally, the floristic affinities of each of the islands are interpreted with respect to the biogeographical boundary at Point Conception.

METHODS AND MATERIALS

Abbott and Hollenberg (1976) was used to provide the distributional data for the biogeographical analyses of the California algal flora. Records for 668 algal species were examined and ranges along the 1,287-km California coastline were determined. Distributional data for a subspecies, variety, or form were considered as part of the records for the species concerned, while entries reported as alternate life history phases (*e.g.*, *Falkenbergia hillebrandii*) were excluded from analyses. Treatments were restricted to the Chlorophyta (72 species), Phaeophyta (137 species), and Rhodophyta (459 species). Distributions were recorded according to presence or absence for each one-degree latitudinal interval. A species was said to occur

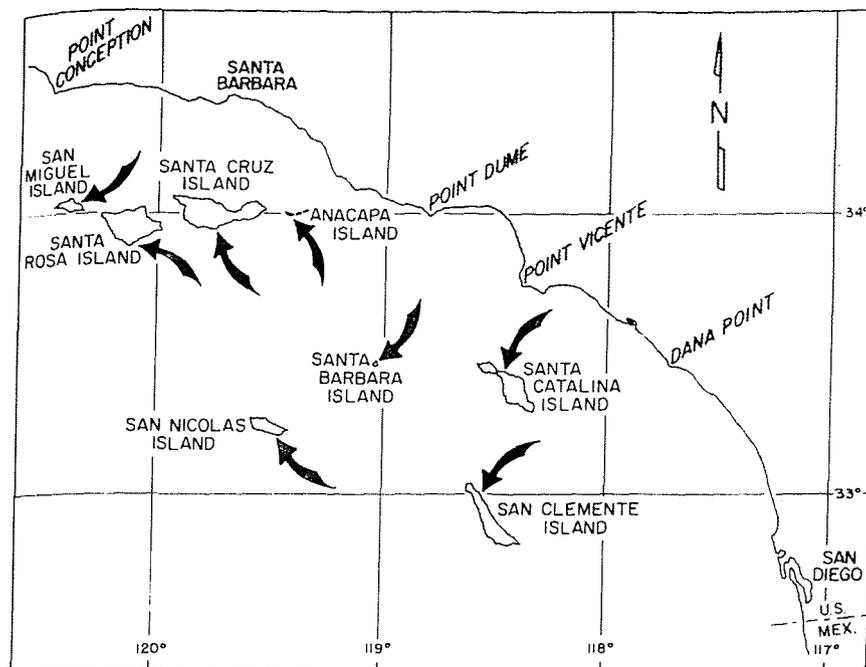


FIGURE 1. Location of the rocky intertidal sites on the Southern California Islands used for the distributional analyses.

within an interval if collection records were listed for any geographical location within that one-degree section of coastline, or if the species' range included that interval (*e.g.*, any report between 32°00'N and 32°59'N was assigned to the 32°N interval). We began with latitude 32°00'N and proceeded in one-degree increments through 42°00'N, the range of latitudes for California. Species with seemingly disjunctive ranges, presumably owing to incomplete collection data (about 10 per cent), were assumed to exhibit continuous distributions.

Species restricted to single latitudinal intervals (one-degree endemics) were also identified and eliminated from our distributional analyses to partially offset bias due to disproportionate intensity of taxonomic study. Floral richness was determined by plotting numbers of species as a function of latitudinal interval. Species with northern or southern range terminations (exclusive of one-degree endemics) were also distinguished and their range end-points plotted by latitudinal interval to reveal major biogeographical barriers. For the latitudinal interval 41-42°N, species with southern range terminations were distinguished from one-degree endemics using Phinney's (1977) records for the Oregon coast; Dawson (1961) was similarly employed to estimate the number of species with northern range terminations in the 32-33°N interval.

Distributional data for the Southern California Islands were obtained for Chlorophyta, Phaeophyta, and Rhodophyta from the sites (Fig. 1) studied by Littler (1977, 1978, 1979). Generic and familial categories including more than one species were not utilized in the analyses. The data obtained by Littler (*op. cit.*) comprise approximately 70 per cent of the island records (see Murray 1974 for previous records) and were used exclusively in our distributional analyses because they represent relatively comparable levels of study for each

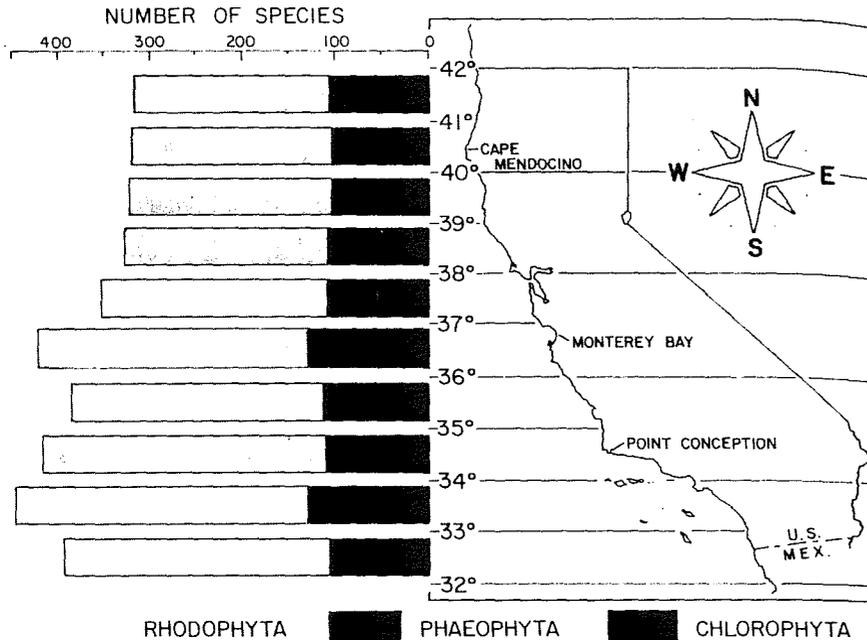


FIGURE 2. Latitudinal richness of the California marine algal flora.

island. The available historical data (Murray 1974) have been characterized by disproportionate research; consequently, Anacapa, Santa Catalina, and Santa Cruz Islands have larger known algal floras than the other five islands.

The Jaccard coefficient (Jaccard 1908, Sokal and Sneath 1963), the most widely-used measure in bio-associational studies (Cheetham and Hazel 1969), was used to measure the degree of similarity between the island floras. We then employed single-level similarity comparisons of all possible island pairs, separate computer-mediated classification, and principal coordinates ordination analysis. Computer analyses were performed using the programs described by Smith (1976).

The insular algal floras were also compared with the mainland distributional patterns derived from Abbott and Hollenberg (1976). The degree of overlap with the floras for the California mainland north and south of Point Conception was established for each island.

RESULTS

Maximal floral richness was obtained at 33-34°N (446 species), while the fewest species (318) occurred at 40-41°N (Fig. 2). Floral diversity increased southward and was significantly correlated ($r = -0.87$, $P < 0.01$) with latitude. This increase was due to the greater numbers of red (Rhodophyta) and brown (Phaeophyta) algal species reported for the southerly California latitudes; both Rhodophyta ($r = -0.93$, $P < 0.01$) and Phaeophyta ($r = -0.63$, $P < 0.05$) exhibited significant correlations between floral richness and latitude. In contrast, the green algae (Chlorophyta) showed little latitudinal variability in species number (Fig. 2); hence, a significant correlation between richness and latitude was not obtained.

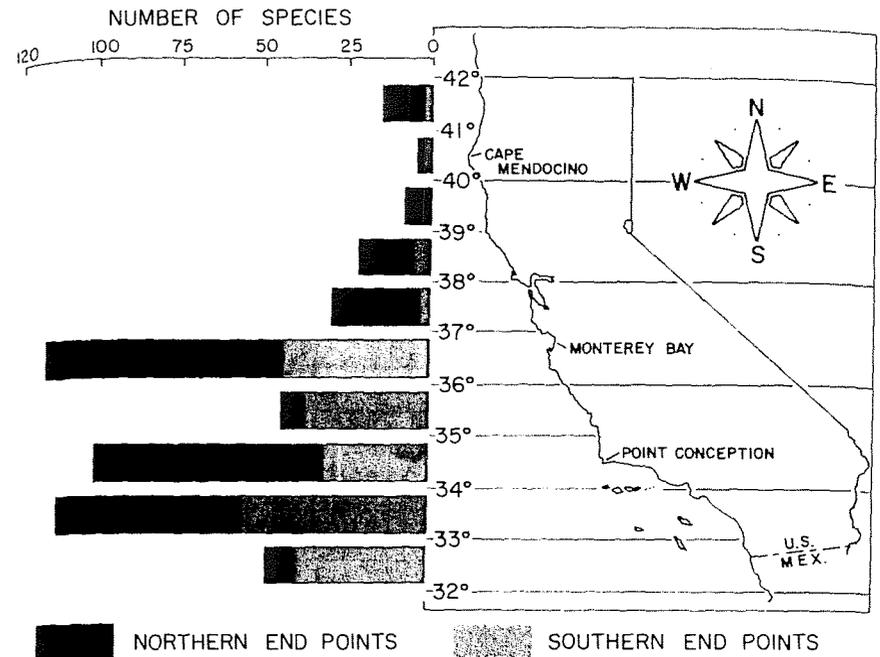


FIGURE 3. Range terminations of California marine algae as a function of latitude.

Major California distributional barriers were identified by plotting species' range terminations by latitude (Fig. 3). These data revealed two probable floral disjunctions—the first near Monterey Bay (36-37°N) and the second near Point Conception in southern California (33-35°N)—however, the latter was less sharp and stretched over 2° latitude. The California distributions of 115 species were reported to terminate at 36-37°N, with 71 species reaching their northern limits and 44 their southern limits at this latitude. A total of 211 species recorded range terminations between 33 and 35°N, a zone containing Point Conception and the Southern California Islands. The majority of these range end-points (123) were also northern limits, suggesting that this region of the coastline, like Monterey Bay, presents a more significant barrier to species with distributional centers south of these biogeographical boundaries.

Biogeographical relationships of the Southern California Islands were interpreted from quantitative comparisons of species composition. These included individual similarity determinations of all possible island pairs, hierarchical classification (cluster) analysis, and ordination analysis by principal coordinates. These assessments revealed a consistent pattern of three distinct island groups:

- Group I: Anacapa, San Clemente, and Santa Catalina Islands
- Group II: Santa Barbara and Santa Cruz Islands
- Group III: San Miguel, San Nicolas, and Santa Rosa Islands

The trellis diagram (Fig. 4) presents the similarity comparisons for all possible island pairs. Inter-island similarity averaged 45.4 per cent, with highest floral affinities for Santa Catalina and San Clemente Islands (64.2 per cent) and Santa Barbara and Santa Cruz Islands (62.3 per cent). Least similarity (32.6 per cent) was determined between Santa Catalina and San Miguel

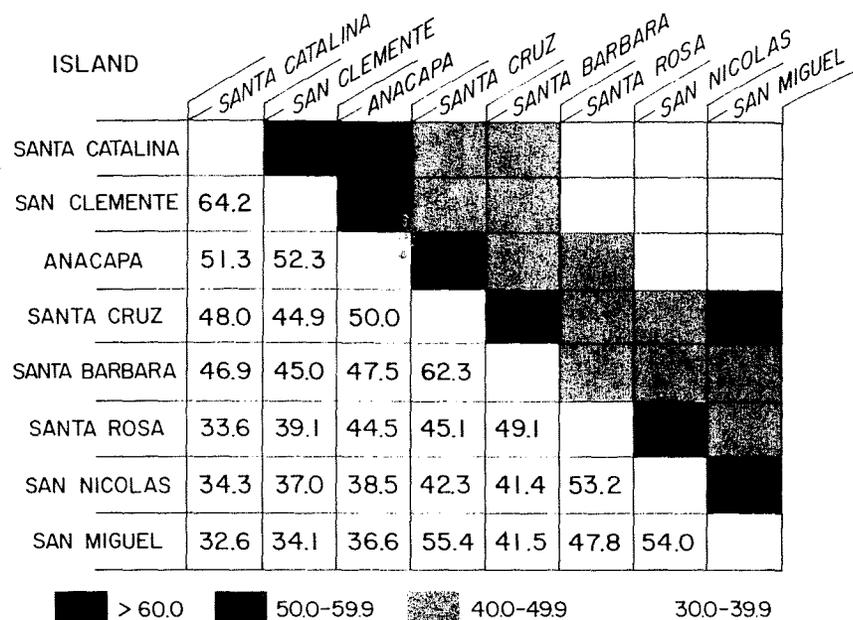


FIGURE 4. Similarity (per cent) comparisons of algal floras for all possible island pairs.

Islands. Anacapa, San Clemente, and Santa Catalina Islands (55.9 per cent) averaged slightly greater floral association than did San Miguel, San Nicolas, and Santa Rosa Islands (51.7 per cent). Members of Group II showed close floral affinities with both Groups I (47.0 per cent) and III (45.8 per cent), while the last two groups had the least overall similarity (36.7 per cent).

The associations of the insular algal floras determined by hierarchical classification and principal coordinates analyses substantiated the trends established by the individual site-pair comparisons and more clearly established the relationships of the three island groups. Based on the classification analysis (Fig. 5), floral similarity was again greatest between Santa Catalina and San Clemente Islands and between Santa Barbara and Santa Cruz Islands. Anacapa Island clearly exhibited greatest association with Santa Catalina and San Clemente Islands (Group I), while San Miguel, San Nicolas, and Santa Rosa Islands (Group III) formed a distinct unit. The floristic affinities of Santa Barbara and Santa Cruz Islands (Group II) were more clearly defined by classification analysis, because greater association occurred with Anacapa, San Clemente, and Santa Catalina Islands (Group I) than with members of Group III. Principal coordinates analysis provided further support for the composition of the three island groups (Fig. 6) since identical site assemblages were obtained in the two-dimensional space resulting from the first two ordination axes. Santa Barbara and Santa Cruz Islands (Group II) again occupied an intermediate position with respect to Groups I and III.

The percentage of algal species in common with the California mainland was determined for each of the islands to compare the relative affinities of island floras with the coastal algal floras north and south of Point Conception. Overall, the algal floras of all eight islands were more closely associated with the mainland California algae south of Point Conception, averaging 95.4 per cent overlap compared with only 80.1 per cent for the central California flora (Table 1).

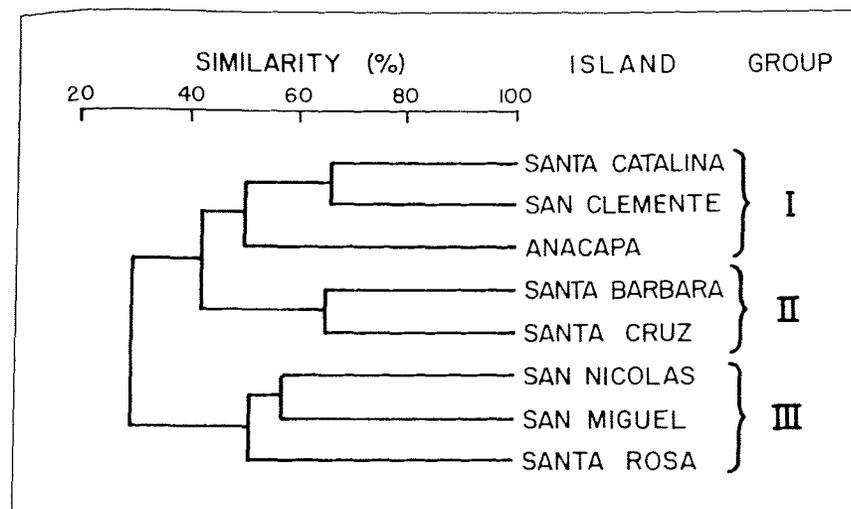


FIGURE 5. Dendrogram (cluster analysis) depicting the percentage of similarity between sites and site groupings of the algal floras for the Southern California Islands.

The percentage of species in common with the northern mainland flora was much more variable among the islands and was generally supportive of the previously established affinities. San Nicolas Island (93.6 per cent) had the greatest number of species in common with the central California flora and San Clemente Island (67.5 per cent) had the least. Group I averaged only 71.1 per cent overlap with the mainland algal flora north of Point Conception, while greater association was evident for Groups II (77.3 per cent) and III (91.0 per cent).

DISCUSSION

Richness of the California algal flora was significantly correlated ($P < 0.05$) with latitude and increased from north to south; maximum diversity was below Point Conception (Fig. 2). Greater species richness south of Point Conception has previously been indicated for the California algal flora (Abbott and Hollenberg 1976) and has similarly been reported for shallow-water benthic molluscs (Valentine 1966) and near-shore fishes (Horn and Allen 1978). Additionally, Horn and Allen (1978) reported a significant correlation between latitude and mean maximum and minimum surface sea-water temperatures, based on data taken from Eber, Saur, and Sette (1968), suggesting a relationship between temperature and richness of coastal fishes. For benthic marine algae, southern California provides more potential habitats per latitudinal degree due to the east-west nature of a large portion of the coastline and the presence of the Southern California Islands. Horn (1974) has suggested that the greater environmental heterogeneity of southern California is expressed by the relative richness of its fish fauna. It has been frequently pointed out (e.g., Schwartzlose 1963, Jones 1971) that the Southern California Bight is a very unusual system, situated within the overlapping boundaries of two major biogeographic regions, containing extremely complex and varied oceanographic and climatological regimes. For the marine algae, this heterogeneity includes the availability of shallow-water habitats subjected to a diversity of temperature ranges due to the complex

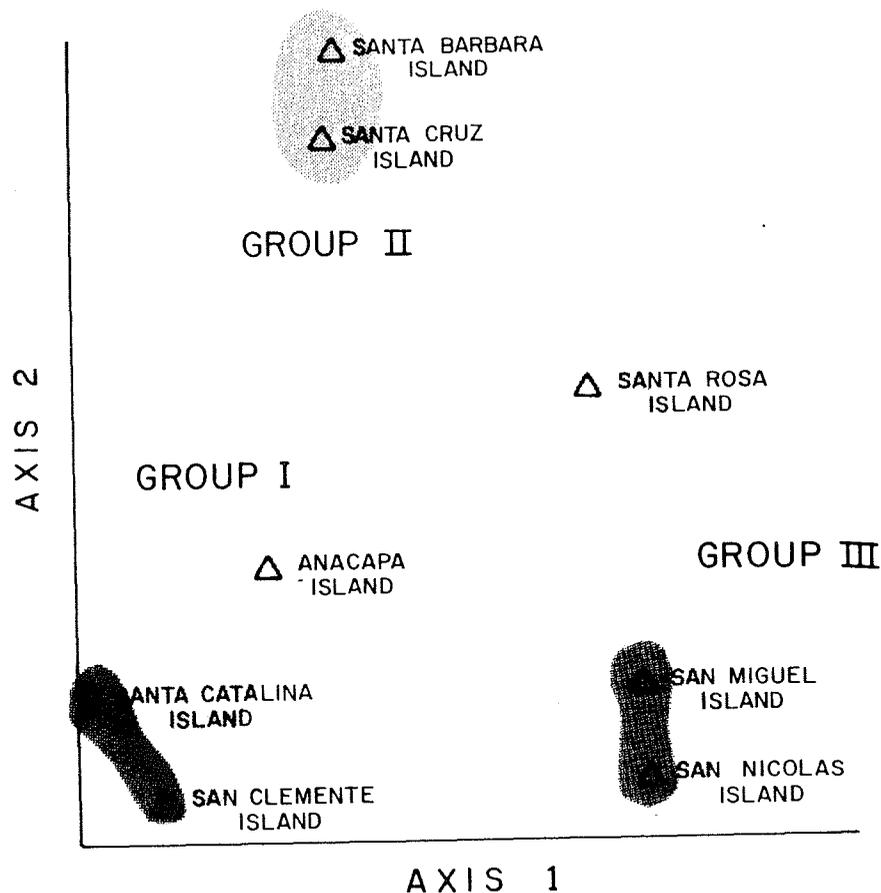


FIGURE 6. Ordination analysis by principal coordinates of the algal floras of the Southern California Islands; sites are depicted in two-dimensional space resulting from relationships with the first two ordination axes.

oceanographic conditions, compounded by the variable exposures of the Southern California Islands to the cold waters of the California Current and the warm waters of the Southern California Countercurrent.

Separate analyses of floral richness for each of the algal divisions indicated that diversity increased from north to south and was significantly correlated with latitude for both the Phaeophyta and the Rhodophyta; however, numbers of Chlorophyta did not change significantly with latitude (Fig. 2). The Chlorophyta generally reach maximal development in warm tropical waters (Dawson 1966) where larger, structurally complex species are conspicuous elements of the flora. For California, the green algae, other than *Codium*, are represented by smaller, generally eurytolerant forms with high surface-to-volume ratios (see Littler and Murray 1974). Additionally, 43 per cent of the California Chlorophyta are reported (Abbott and

TABLE 1. Percentage of Southern California Island algal species in common with mainland distributional records north and south of Point Conception.

Coastline from Point Conception	San Clemente	Santa Catalina	Anacapa	Santa Barbara	
South	97.5	95.7	97.7	94.7	
North	67.5	70.2	75.6	76.6	
	Santa Cruz	Santa Rosa	San Nicolas	San Miguel	Mean
South	96.7	94.5	93.6	92.8	95.4
North	78.0	87.7	93.6	91.8	80.1

Hollenberg 1976) to occur in coastal waters along the entire state, vs. 31 per cent of the Rhodophyta and 18 per cent of the Phaeophyta, suggesting a tendency for broad distributions and wide tolerances to physical factors. Greater species richness in warmer southern California waters was expected for the Rhodophyta. Phaeophyta also showed increased species richness southward, even though maximum brown algal floristic development has typically been described for more northerly latitudes (Dawson 1966). Cheney (1977) proposed that the ratio of green and red algae to brown algae could be used to describe the nature of an algal flora. A ratio of 3.0 or less would indicate a temperate or cold-water flora, while a value of 6.0 or greater would signify a tropical flora; ratios between 3.0 and 6.0 are characteristic of intermediate floras. For California, the Cheney index ranged from 4.2 at 41-42°N to 5.3 at 32-33°N—both values for an intermediate flora; nevertheless, a significant correlation ($r = -0.90$, $P < 0.01$) between the index and latitude was observed, due to the marked southerly increases in Rhodophyta.

Probable distributional barriers for California algae, based on range end-points, occur near Point Conception and Monterey Bay (Fig. 3), regions recognized as biogeographical boundaries for shallow-water benthic molluscs (Valentine 1966), ascidians, crabs, and molluscs (Hayden and Dolan 1976), and coastal fishes (Horn and Allen 1978). The largest percentage (42.5) of algal range terminations occurred near Point Conception and the Southern California Islands (33-35°N), the regions of greatest floral richness. However, the coastline between 33 and 34°N revealed more species range terminations than did the latitudinal interval actually containing Point Conception (34-35°N), thus suggesting that the entire southern California area represents a transitional region. This interpretation is supported by the data of Newell (1948), who previously determined high rates of change (= total end-points/total species) in eastern north Pacific marine Mollusca at both 33°N and 34°N. The biogeographical barriers for the marine algae near Point Conception and Monterey Bay appear to be more significant to species with southern distributional centers; 61.7 per cent of the range terminations near Monterey Bay and 58.3 per cent near Point Conception represented northern range limits. Oceanic currents appear to be of paramount importance in determining this pattern. For example, the coastline runs east-west south of Point Conception, thus removing the southern California mainland from the direct influence of the California Current, whose colder waters flow southeast, extending towards Cabo Colnett in Baja California (see Seapy and Littler 1980). These patterns no doubt permit a considerable extension southward of colder-water species into habitats proximal to California Current waters (*i.e.*, San Miguel, San Nicolas, and Santa Rosa Islands). In addition, southern California locales subjected to persistent upwelling would

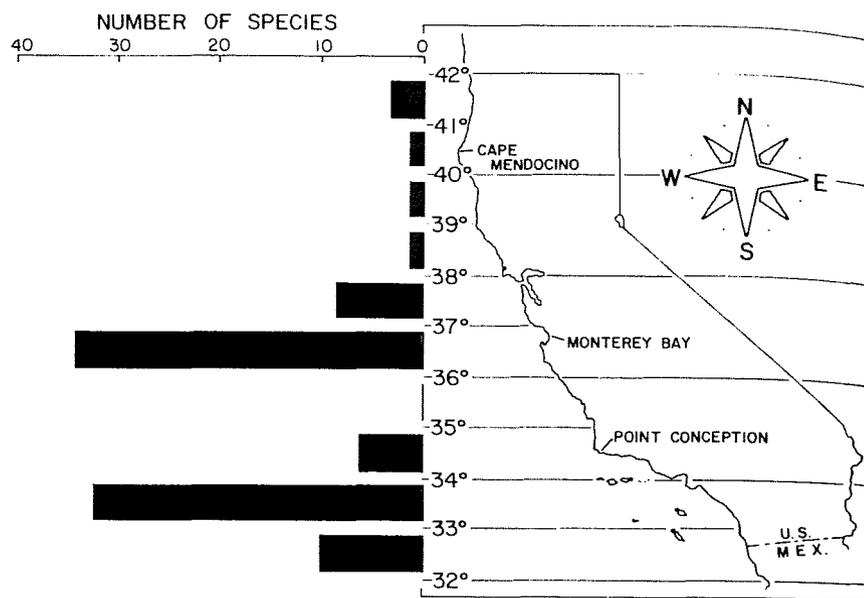


FIGURE 7. Numbers of "one-degree" endemic species as a function of latitude.

provide habitats in southern California for cold-water forms, as suggested by Valentine (1966). The warm Southern California Countercurrent, on the other hand, terminates its northward flow abruptly near Point Conception, thereby severely restricting the northerly extension of warm-water species. This greater influence of the area near Point Conception on southern species has also been noted by Valentine (1966), Neushul *et al.* (1967), and Horn and Allen (1978). Mean minimum surface water temperatures have been determined (Horn and Allen 1978) to decrease most sharply (2°C) at Point Conception, and mean maximum temperatures to drop most significantly (2°C) near both Point Conception and Monterey Bay, possibly providing an explanation as to why these regions seem to function as major biogeographical barriers.

A total of 97 algal species was recorded in only one degree of latitude; these species have been referred to as one-degree endemic forms (Fig. 7). These were far more frequent at 36-37°N and 33-34°N, regions of the coastline most closely investigated by Abbott and Hollenberg (1976), suggesting that the distributional data in other localities are relatively incomplete. Additionally, the numbers of one-degree endemic species correspond well with species disjunction patterns based on range end-point analysis (Fig. 3), thus suggesting the possibility that the different levels of taxonomic effort along the California coastline have contributed somewhat to the biogeographical patterns discussed above. However, previous research on Mollusca (Newell 1948, Valentine 1966) has also demonstrated considerable overlap between the frequency distribution of one-degree endemic forms by latitude and biogeographical boundaries determined by range end-point analysis. The fact that species richness and the Cheney (1977) index show significant correlations with latitude lends credence to the interpretation that factors other than the level of taxonomic effort are operating. Furthermore, studies on benthic invertebrates (Newell 1948, Valentine 1966, Hayden and

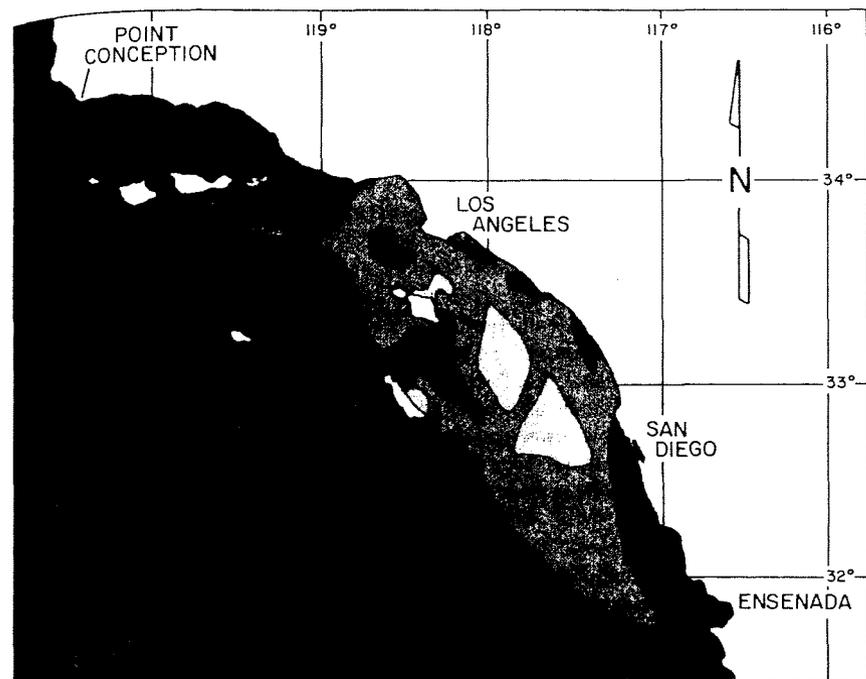


FIGURE 8. Distribution of surface water temperatures within the Southern California Bight based on remote sensing satellite imagery (redrawn from the 23 June 1976 NOAA-3 satellite imagery in Hendricks 1977); darkest tones represent coldest water temperatures with temperature increases of about 1.4 °C with each successively lighter tone.

Dolan 1976) have independently offered the same interpretation. *i.e.*, that major biogeographical breaks occur near Point Conception and Monterey Bay; Pielou (1978) has also observed that the number of seaweed species whose distributions span the Point Conception area is small compared with other eastern Pacific regions. However, further studies of species distributions are required before our interpretations merit complete acceptance.

Quantitative comparisons of the floristic composition of the Southern California Islands revealed three distinct assemblages (Figs. 4, 5, and 6): Anacapa—San Clemente—Santa Catalina (Group I); Santa Barbara—Santa Cruz (Group II); and San Miguel—San Nicolas—Santa Rosa (Group III). These groups were comparable to those predicted by Neushul *et al.* (1967), with the exception that our study showed that Anacapa had greatest floristic affinities with San Clemente and Santa Catalina Islands. Based on an understanding of the complicated surface circulation patterns in the vicinity of the Southern California Islands (Schwartzlose 1963, Reid *et al.* 1958), the algal floras appear to be influenced most by temperature (Fig. 8). Neushul *et al.* (1967) emphasized the variability in oceanic circulation near the Northern Channel Islands and reported greater exposure of San Clemente and Santa Catalina Islands to warmer water throughout the greater part of the year. San Miguel, San Nicolas, and the western half of Santa Rosa Island were said to be strongly under the influence of the colder waters of the

California Current, while Anacapa, Santa Barbara, Santa Cruz, and eastern Santa Rosa Island were reported to lie in a region of variable mixing between cold- and warm-water currents. This pattern of surface water circulation has been quantitatively substantiated (Hendricks 1977) using satellite thermal imagery. Hendricks' data (Fig. 8) interestingly reveal a tongue of warm water extending toward Anacapa Island from the south, which may account for its floristic affinities with Santa Catalina and San Clemente Islands.

All of the Southern California Islands had a higher percentage of species in common with the mainland flora south of Point Conception, but a pattern of variable association was determined with the species to the north (Table 1). Greatest affinities with the central California algal flora were determined for the San Miguel, San Nicolas, and Santa Rosa Island sites, reflecting a higher proportion of colder-water species for these islands. San Clemente and Santa Catalina Islands had lowest cold-water floral affinities, and Anacapa, Santa Barbara, and Santa Cruz Islands occupied somewhat intermediate positions. A temperature-based characterization of the Southern California Island algal floras is further suggested by the principal coordinates ordination analysis (Fig. 6), where the orientation of the insular sites, with respect to the first ordination axis, agrees well with interpretations derived from our species overlap comparisons (Table 1), previous studies (Neushul *et al.* 1967), and available temperature data (Fig. 8).

Our results clearly substantiate the previously-held opinions (*e.g.*, Hewatt 1946, Caplan and Boolootian 1967, Neushul *et al.* 1967) that the Southern California Islands contain biotic elements transitional between colder-water locales to the north and warmer-water regions to the south of Point Conception. These data emphasize the importance of the islands to a full understanding of the biogeography of the eastern north Pacific and suggest that environmental heterogeneity increases markedly in California coastal areas south of Point Conception (see Horn 1974).

SUMMARY

Richness of the California algal flora increased southward and was significantly correlated with latitude, mostly due to the Rhodophyta and Phaeophyta. Probable distributional barriers for marine algae, interpreted from range end-point analysis, occurred near Monterey Bay and Point Conception, in agreement with previous studies of coastal faunas. The range distributions of 115 species terminated near Monterey Bay, while 211 algae had northern or southern range end-points near Point Conception and the Southern California Islands. The majority of these terminations represented northern limits, suggesting that the proposed biogeographical boundaries represent greater barriers to species with more southerly distributional centers.

Quantitative assessments of the algal floras of the Southern California Islands using individual similarity comparisons, hierarchical classification analysis, and principal coordinates ordination analysis revealed three distinct island groups: (I) Anacapa, San Clemente, and Santa Catalina Islands; (II) Santa Barbara and Santa Cruz Islands; (III) San Miguel, San Nicolas, and Santa Rosa Islands. The island floras appeared to be influenced mainly by temperature; this assumption is based upon an understanding of the reported oceanic circulation patterns, comparisons of floristic components with the mainland floras north and south of Point Conception, and interpretations of the principal coordinates ordination analysis. All of the island floras had greatest overlap with the mainland algae south of Point Conception; nevertheless, a pattern of variable association (presumably temperature-based) was shown with the central California flora. Our results substantiate the previously-held viewpoint that the Southern California Islands contain biotic elements transitional between colder-water locales to the north and warmer-water regions to the south of Point Conception and emphasize the importance of the islands to understanding eastern north Pacific biogeography.

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