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Biogeography of Rocky Intertidal Macroinvertebrates of the Southern California Islands

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INTRODUCTION

The macroinvertebrate fauna of the rocky intertidal zone on the Southern California Islands is incompletely known; consequently, it has not been possible to determine zoogeographical relationships among the various islands or between the islands and the mainland. Three studies (Hewatt 1946, Caplan and Boolootian 1967, Littler and Murray 1975) have been published on the rocky intertidal biotas for three of the islands, although only one of these (Hewatt 1946) is a comprehensive faunistic study. Based on extensive collections from rocky and sandy beaches at six stations around Santa Cruz Island, Hewatt (1946) recorded a total of 297 invertebrate species. It is noteworthy that, of this total, many were small, inconspicuous forms that dwell among and beneath macrophytes (*e.g.*, articulated corallines) and macroinvertebrates (*e.g.*, mussels). After assembling the latitudinal distribution records for the various species, Hewatt concluded that Santa Cruz Island was located in a transitional area between northern and southern faunas. This conclusion was based, in part, on the determination that nearly equal percentages of the island's rocky intertidal species occurred mainly to the north (30 per cent) or south (27 per cent) of Point Conception, while the remaining species (43 per cent) were broadly distributed along the mainland. The vertical distribution of the 19 predominant rocky intertidal macroinvertebrates at two sites on the southeastern portion of San Nicolas Island was assessed by Caplan and Boolootian (1967). Their analyses are of little biogeographical value, however, since they were concerned with only those species whose densities exceeded 100/m^2 from any quadrat sampled. Rocky shore species on the leeward, east-facing side of San Clemente Island near Wilson Cove were reported by Littler and Murray (1975). However, since the inception of the intensive Bureau of Land Management intertidal baseline studies (Littler 1977, 1978, 1979, 1980), our knowledge of the fauna there has greatly expanded.

Historically, Point Conception has been considered an important marine biogeographical boundary along the Pacific coast of North America (reviewed by Hedgpeth 1957 and Valentine 1966), with the cold-temperate Oregonian Province lying to the north and the warm-temperate Californian Province to the south (Fig. 1). The Oregonian Province and the Aleutian Province are included in the East Pacific Boreal Region (Fig. 1), while the Californian Province describes a warm-temperate region separate from the East Pacific Tropical Region, which includes the Mexican and Panamanian Provinces. The Cortezian Province in the Gulf of California probably should not be considered warm-temperate (as Briggs [1974] has suggested), but rather as having tropical affinities (W. Newman, pers. comm.). The biogeographical boundary at Point Conception does not appear to be sharp. Instead, it can be considered to represent an overlap area, with cold-temperate species ranging two to three degrees in latitude to the south and warm-temperate species ranging two to three degrees to the north. The existence of this overlap zone was clearly described by Newell (1948) using the molluscan range data of Schenck and Keen (1936) and Keen (1937). The area of overlap, termed the Californian Transition Zone, delineates the latitudinal range of a number of short-range endemic species (Newman in press).

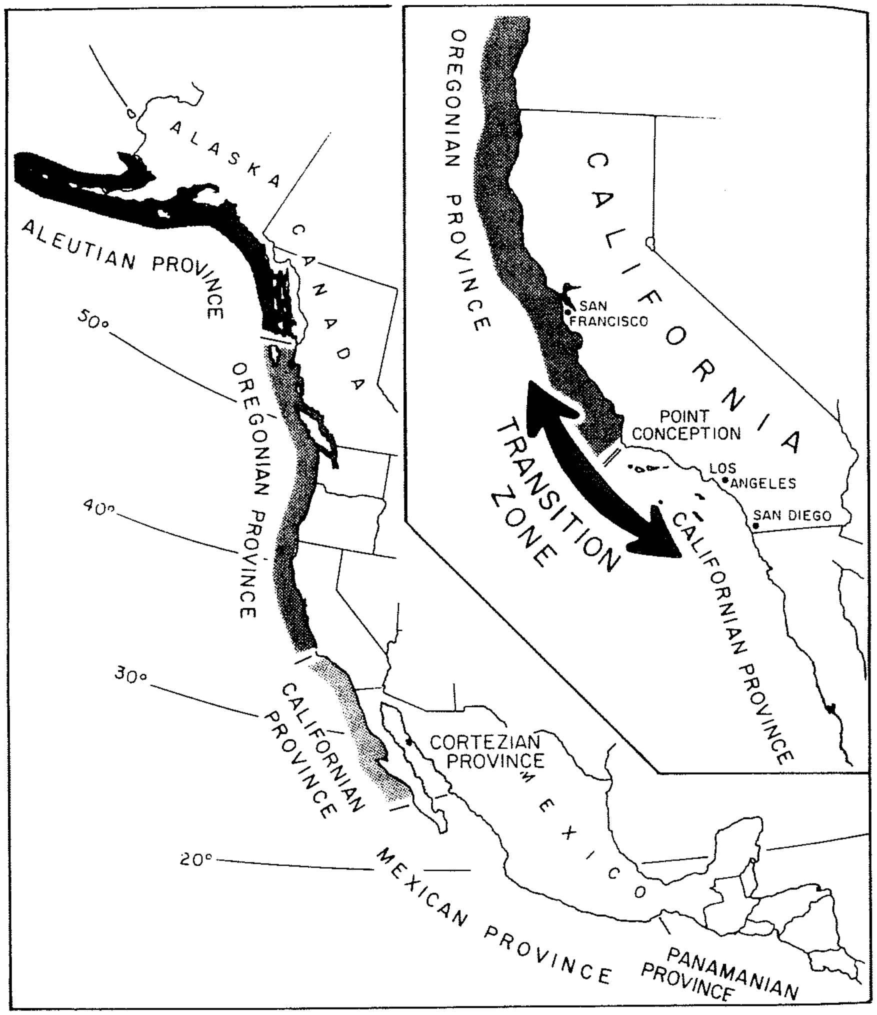

FIGURE 1. *Zoogeographical provinces of the Pacific coast of North America (modified from Briggs 1974).*

The reason Point Conception is important biogeographically is clearly related to patterns of oceanic circulation. Off central California, the broad and sluggish California Current generally flows southeastward along the coast (Wyllie 1966) and near-shore waters are maintained at cold temperatures through spring and summer due largely to the extended upwelling period between about April and August (Bolin and Abbott 1963). At Point Conception, the coastline turns sharply to the east. California Current flow does not follow the shoreline, however, but continues southeastward (Reid *et al.* 1958) to the west of the Santa Rosa-Cortez Ridge, the submerged peninsula that extends from Point Conception to Cortez Bank and includes Santa Rosa and San Nicolas Islands. South of Cortez Bank, the California Current turns eastward in a

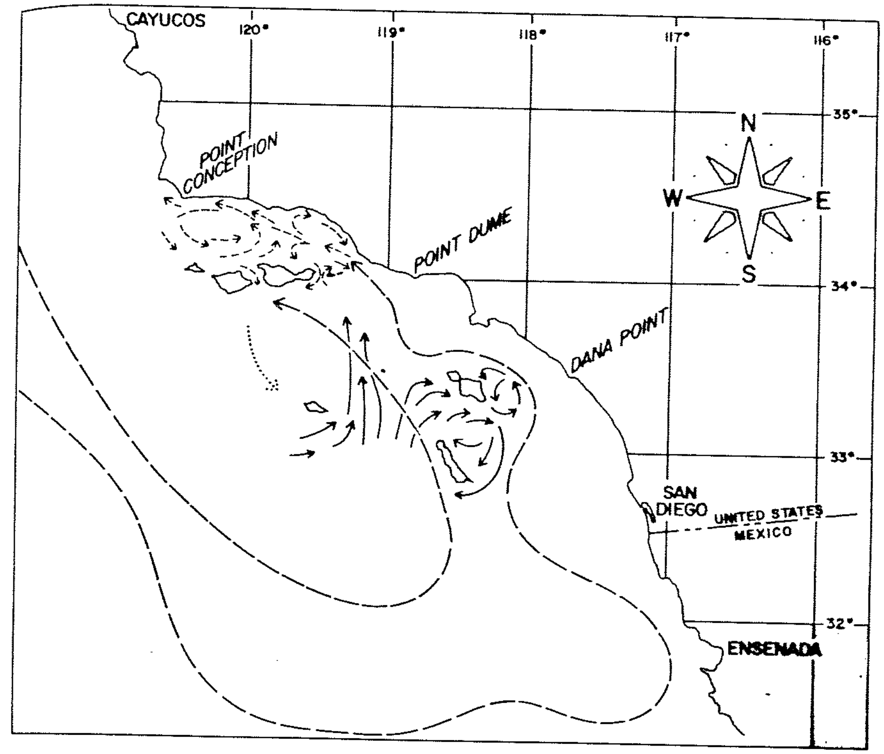

FIGURE 2. *Surface current patterns off southern California (after Seapy 1974). Long dashed lines represent mean geostrophic flow contours for the month of August, averaged for a 16-year period between 1950 and 1965 (Wyllie 1966). Short dashed lines indicate surface current flow during August 1969 based on drift bottle studies (Kolpack 1971). The solid lines are surface currents derived from 10-m drogue releases during October 1958 (Scripps Inst. Oceanogr. 1962), while the single dotted line between Santa Rosa and San Nicolas Islands is based on Neushul* et al. *(1967).*

broad arc (Fig. 2), forming the Southern California Eddy or Countercurrent (Sverdrup and Fleming 1941). This eddy is most strongly developed during the summer months (Wyllie 1966), a finding supported by the recent drift card studies of Squire (1977). For this reason, the 16-year mean geostrophic flow contours of Wyllie (1966) for the month of August were used to illustrate this general flow (Fig. 2). This pattern of flow, including several of the counterclockwise-flowing eddies, has been substantiated by recent satellite thermal imagery done in late June 1976 (Hendricks 1977). The northwesterly-flowing arm of the Southern California Eddy is generally a weak flow (Reid *et al.* 1958). Consequently, the near-shore waters remain along the coast for an extended period and become much warmer than the offshore waters which are continuously replaced by cold California Current water (Reid *et al.* 1958). The warm, northwesterly-flowing coastal waters move along the southern California mainland as far north as Point Conception, where they encounter the cold, southeasterly-flowing waters of the California Current. Such markedly different hydrographic histories and physical-chemical properties of the coastal waters to the northwest and southeast of Point Conception lead to the prediction of a biogeographical break between cold-temperate and warm-temperate faunas at Point Conception.

In light of the above hydrographic patterns, the Southern California Islands should, hypothetically, exhibit intermediate biogeographical affinities with biotas on the mainland to the north and south of Point Conception. This was indeed the conclusion of Hewatt (1946) concerning Santa Cruz Island. Because San Miguel Island lies on the eastern edge of the southeasterly-flowing California Current, we predict that it should show the strongest northern affinity of all the islands. San Nicolas Island should also have strong northern affinities since it is bathed directly by the California Current; however, because it is located to the southeast of San Miguel Island, it receives waters that should be somewhat warmer. San Clemente and Santa Catalina Islands, located in the pathway of the warm, northerly-flowing Southern California Eddy (Fig. 2), are hypothesized to show the strongest affinities of all the islands with the southern mainland biota. Santa Barbara Island should show intermediate affinities, as should Anacapa Island and the southern sides of Santa Cruz and Santa Rosa Islands, because the waters impinging on them should represent a mixture of cold and warm waters from the California Current and Southern California Eddy, respectively (Fig. 2). The northern sides of Santa Rosa and Santa Cruz Islands are bathed by colder, eastward-flowing waters of the counterclockwise gyre in the Santa Barbara Channel. This gyre is fed by California Current water (Fig. 2) deflected into the Channel by San Miguel Island (Kolpack 1971, Hendricks 1977), and the northern sides of these two islands are generally colder than the southern sides (Neushul *et al.* 1967). The biogeographical relationships hypothesized above for the islands are basically similar to those proposed by Neushul *et al.* (1967), who also utilized oceanographic data from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program in developing a biogeographical model for the islands.

MATERIALS AND METHODS

Rocky intertidal macroinvertebrates were collected from nine sites on the eight Southern California Islands (Fig. 3) between August 1975 and February 1978 as part of the Bureau of Land Management's Outer Continental Shelf research program in the Southern California Bight (Littler 1980). These species records are included in technical reports (Littler 1977, 1978, 1979) for the Bureau of Land Management. In these studies, quarterly standing stock assessments were made for six of the island sites (San Miguel, southeast end of San Nicolas, Santa Cruz, Santa Barbara, Santa Catalina, and San Clemente) over a two-year period; Santa Rosa Island was assessed over a one-year period, while the sites on Anacapa Island and the west end of San Nicolas Island were sampled during single visits. However, the level of actual faunistic sampling and taxonomic effort was comparable at each site.

For comparative zoogeographical purposes, macrofaunal records from mainland sites that could be considered northern and southern were desired. For a southern site, we chose the Bureau of Land Management study area at Ocean Beach, which has been sampled quarterly over a two-year period (Seapy and Littler 1977, 1978a). For a northern site, we used Cayucos Point in central California, which we sampled intensively in 1973 (Seapy and Littler 1978b) and on two subsequent occasions in 1976 and 1977.

Species records for each of the eleven sites were compiled as a presence-absence data matrix. Records for two taxonomic groups were excluded: the bryozoans, because our tentative identifications and unknowns have not been resolved, and the hydroids, because identification below the generic level is not presently reliable for the common forms (Rees and Hand 1975). For the remaining taxa, a literature search was conducted to determine the latitudinal ranges for as many of the species as possible, with the result that ranges were assigned to all of the

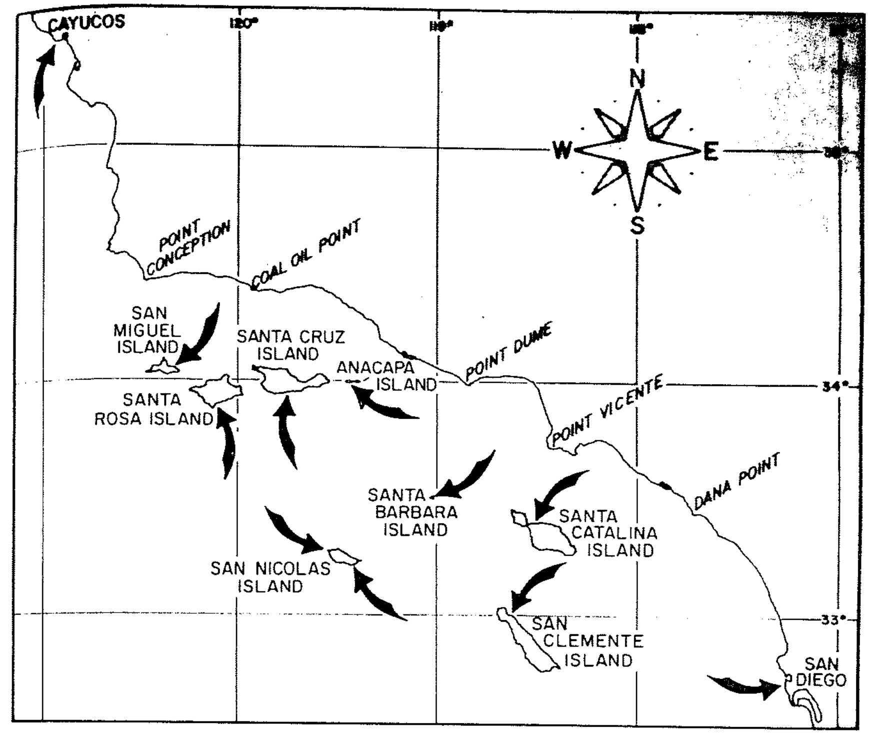

FIGURE 3. *Location of the sampling sites on the Southern California Islands and on the mainland at Ocean Beach (near San Diego) and Cayucos Point.*

represented species of anthozoans, polychaetes, molluscs, crustaceans, and echinoderms, but were only partially completed in the cases of the ascidians (10 of 13 species) and poriferans (8 of 23 species). In determining the latitudinal ranges, the most recent authority was accepted and a variety of sources were used: Porifera (de Laubenfels 1932); Anthozoa (Ricketts, Calvin, and Hedgpeth 1968); Polychaeta (Hartman 1969); Gastropoda (Dall 1921, Oldroyd 1925-1927, Morris 1966, McLean 1978, Keen 1971, Abbott 1974, D. Lindberg, pers. comm., G. MacDonald, pers. comm.); Polyplacophora (Burghardt and Burghardt 1969, McLean 1978); Bivalvia (Dall 1921, Oldroyd 1925-1927, McLean 1978, Keen 1971); Crustacea (Schmitt 1921, Menzies 1948, Garth 1958, Haig 1960, Ricketts, Calvin, and Hedgpeth 1968, McLaughlin 1974, Haig and Wicksten 1975, Nations 1975, Newman 1975); Echinodermata (Fisher 1911, Ricketts, Calvin, and Hedgpeth 1968); and Ascidiacea (Van Name 1945). Perusal of the range data suggested that the species could be grouped into four categories: northern, southern, widespread, and transitional. Species classified as northern range northward from Point Conception through the Oregonian Province, and often through the Aleutian Province, as well. However, the southern limit for most of these species was not Point Conception but San Diego or northern Baja California. Southern species are those that range southward from Point Conception through the Californian Province and possibly into the Cortezian, Mexican, and, in a number of cases, the Panamanian Provinces. As with the southerly limits of the northern

TABLE 1. Macroinvertebrate species present at all eleven study sites.

Mollusca: Gastropoda (10 species)	Mollusca: Polyplacophora (2 species)
Acmaea (Collisella) digitalis	*Cyanoplax hartwegii*
Acmaea (Collisella) limatula	*Mopalia muscosa*
Acmaea (Collisella) pelta	Cnidaria: Anthozoa (1 species)
Acmaea (Collisella) scabra	*Anthopleura elegantissima*
Acmaea (Collisella) strigatella	Arthropoda: Crustacea (6 species)
Fissurella volcano	*Balanus glandula*
Littorina planaxis	*Chthamalus dalli*
Littorina scutulata	*Chthamalus fissus*
Lottia gigantea	*Pollicipes polymerus*
Ocenebra circumtexta	*Pugettia producta*
Mollusca: Bivalvia (2 species)	*Tetraclita squamosa rubescens*
Mytilus californianus	Echinodermata: Echinoidea (1 species)
Septifer bifurcatus	*Strongylocentrotus purpuratus*

category, the northerly limit of the southern species was not usually Point Conception but some area in central California, most commonly near Monterey. Species classified as widespread range broadly through at least the Californian and Oregonian Provinces. Many of the species in this category occur farther northward and/or southward of the Oregonian and Californian Provinces, respectively. Finally, a special category, termed transitional, was required to account for the ranges of about 15 per cent of the species that ranged narrowly through the area of latitudinal overlap for the northern and southern categories—approximately through central and southern California. The existence of such a transitional species grouping, extending over an approximate four-degree latitudinal range, has been recognized for benthic barnacles by Newman (in press), who termed the area the Californian Transition Zone. Recently, a "coastal-trend-grid coding system" was developed by Hayden and Dolan (1976) to analyze zoogeographical patterns for the coasts of North and South America. These authors identified several co-range termini along the Pacific coast, including a major one separating the Oregonian and Californian Provinces approximately between San Diego and Monterey. This result is consistent with the present interpretation and with those of Newell (1948) and Newman (in press).

The second analytical approach was to subject the presence-absence data matrix to computer-mediated classification analyses. To emphasize site differences, the 22 species present at all of the sites (Table 1) were deleted from the raw data matrix. A matrix of dissimilarity values for all possible site pairs was first generated, using the Canberra metric dissimilarity measure: $D = \frac{1}{n}\sum_{1}^{n} \mid X_{1j} - X_{2j} \mid / (X_{1j} + X_{2j})$, where n is the number of species present at sites 1 and 2, X_{1j} is the presence (1) or absence (0) of the *jth* species at site 1, and X_{2j} is the presence or absence of the *jth* species at site 2. The matrix of Canberra metric dissimilarity values was then analyzed in two ways. First, the matrix was subjected to cluster analysis and a dendrogram was generated. The weakness of this approach is that the dendrogram is built by the progressive fusion of sites into site groupings, and misclassifications can occur at higher levels of the clustering (or fusion) process. To counteract this problem, the dendrograms were interpreted in light of results obtained from principal coordinates (PCOORD) ordination analysis. This type of ordination analysis is recommended (Clifford and Stephenson 1975)

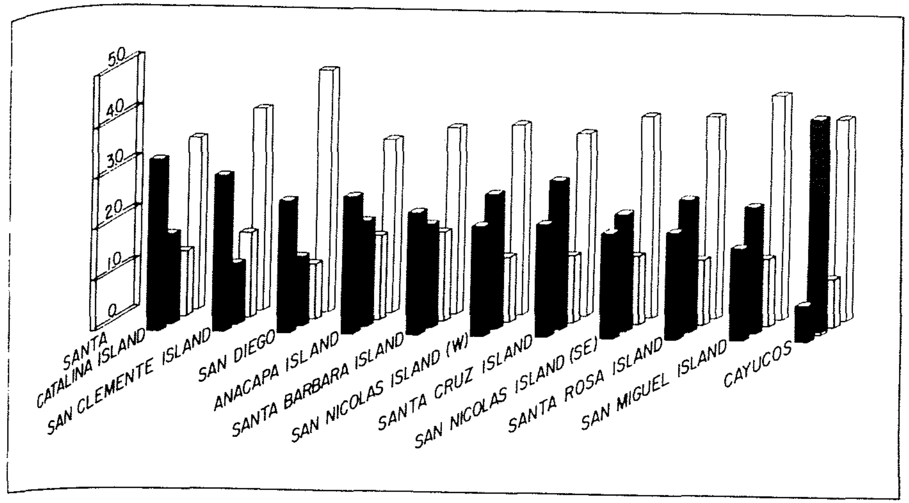

FIGURE 4. *Composition of the macroinvertebrate fauna at each site expressed as per cent of the fauna represented by northern (black bars), southern (dark bars), transitional (light bars), and widespread (clear bars) species.*

when the starting point is a dissimilarity matrix. Cluster and ordination analyses were performed using (1) all of the species (except those 22 species listed in Table 1 as common to all sites), (2) the Gastropoda separately, and (3) a reduced matrix that included only those species whose abundances exceeded one per square meter, averaged over all tidal intervals sampled at a given site. The analysis using the Gastropoda was performed to see whether or not the patterns shown by the total complement of species were supported by the gastropods (the largest major group) alone. The analysis using only those species whose abundances exceeded one per square meter was performed to determine the effect of excluding species that were not relatively common components of the fauna. This analysis was also useful because possible site differences in collection intensity could be eliminated by excluding the rarer species. Such a bias in sampling could have been the case for Anacapa Island and the west end of San Nicolas Island, each of which was visited only once. However, sampling differences would not appear to be likely because the collecting efforts were intensive and resulted in the identification of a comparably large number of species at both sites (98 at Anacapa Island and 82 at the west end of San Nicolas Island).

RESULTS AND DISCUSSION

Analysis of the latitudinal range data for the macroinvertebrate species at the various sites (Fig. 4) indicates that a high percentage of the fauna, averaging 39 per cent and ranging from 34 to 48 per cent, consisted of species displaying widespread distributional ranges. For these species, there were no apparent trends shown between sites. The percentage of the fauna classified as transitional (short-range endemics) averaged 14 per cent and ranged from 10 to 18 per cent, being lowest at the two mainland sites. Among the island sites, the southerly and near-shore islands (San Clemente, Santa Catalina, Santa Barbara, and Anacapa) displayed somewhat higher percentages of transitional species than did the northerly and offshore islands (San Nicolas, San Miguel, Santa Rosa, and Santa Cruz). However, these differences are so

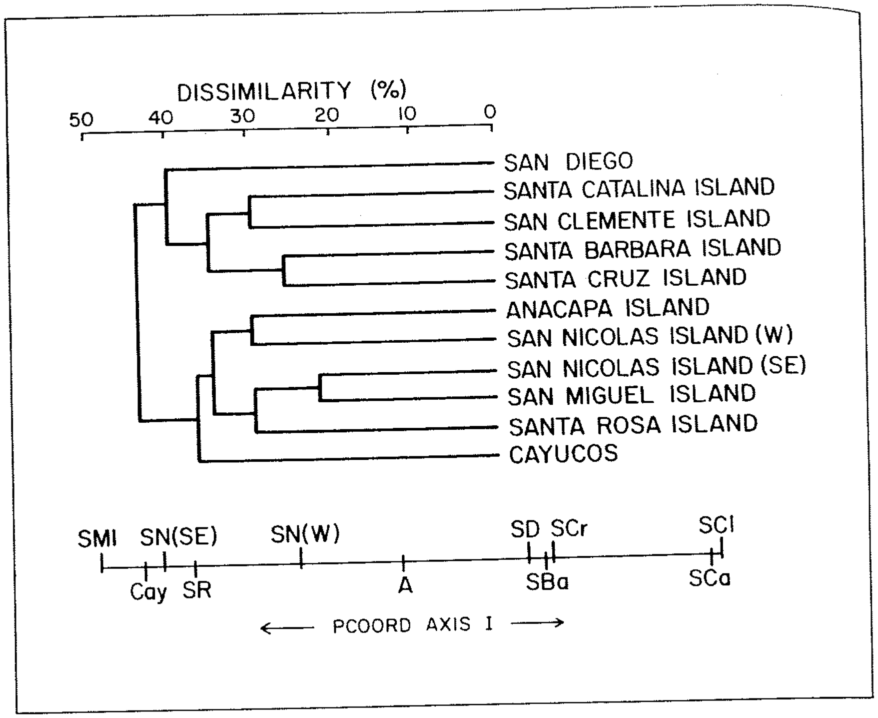

FIGURE 5. *Classification analyses using all species except those common to all sites. Cluster analysis results of per cent dissimilarity between sites and site groupings are displayed as a dendrogram (above). Principal coordinates (PCOORD) ordination results are shown for axis I (below).*

slight as to be of questionable significance and only suggest a possible trend. In combination, the species that were widespread and transitional comprised an average of 53 per cent of the fauna at each site, and ranged from 48 to 60 per cent.

The percentages of the fauna represented by northern and southern species (Fig. 4) are essentially in agreement with the hypothesized inter-island affinities based on hydrographic considerations. The two island sites having the highest proportions of southern species were Santa Catalina (34 per cent) and San Clemente (31 per cent). Both sites had somewhat higher percentages of southern species than the southern mainland site at San Diego (26 per cent), perhaps because such a high proportion of the species at San Diego (48 per cent) was classified as widespread. Anacapa and Santa Barbara Islands had the next highest percentages of southern species (27 and 24 per cent, respectively), although the percentages of northern species at these two sites were only somewhat less (22 per cent at Anacapa and 21 per cent at Santa Barbara). At the remaining sites, the percentage of northern species was greater than the percentage of southern species, ranging from 24 per cent at the southeast end of San Nicolas Island to 29 per cent at Santa Cruz Island. The only historical data against which the present results can be directly contrasted are those of Hewatt (1946) for Santa Cruz Island. The comparison provides quite good agreement, with Hewatt having 1 per cent more northern species, 5 per cent more

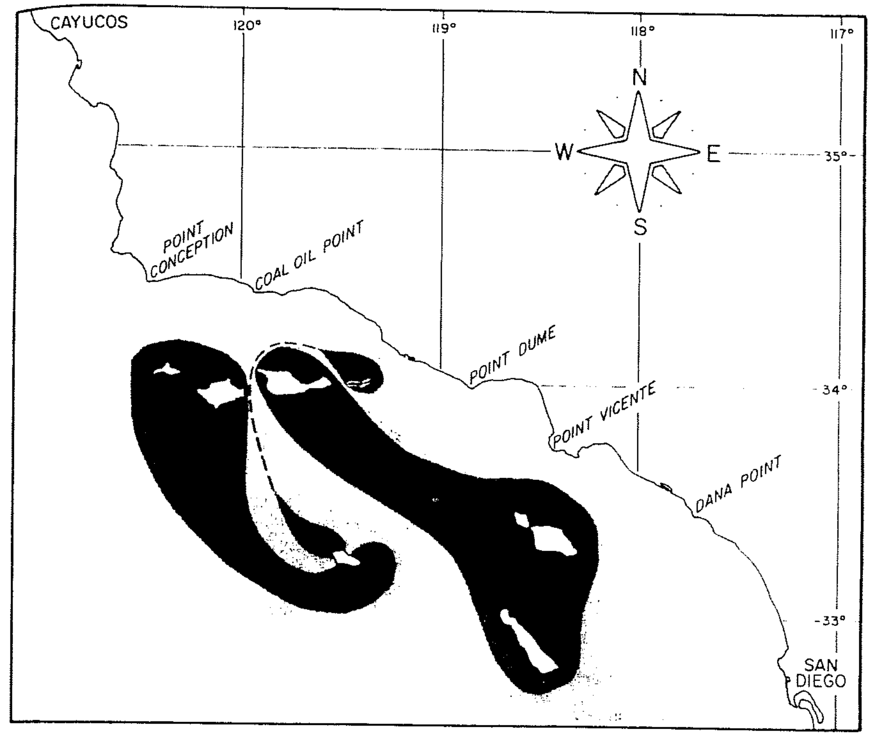

FIGURE 6. *Map overlay of cluster analysis results (Figure 5) using all of the species except those common to all sites.*

southern species, and 6 per cent fewer widespread and transitional species than we recorded at our Santa Cruz Island site.

Only at Cayucos Point was the percentage of the fauna represented by widespread species (40 per cent) exceeded by another category, northern species (43 per cent). It is also noteworthy that Cayucos Point had the lowest percentage (7) of southern species (Fig. 4). One might expect to observe the reverse faunal relationship at the southern mainland site, San Diego. While the percentage of southern species (26) was higher than the percentage of northern species (14) at San Diego (Fig. 4), the difference was not as pronounced as that recorded at Cayucos Point. These data suggest that Point Conception represents a stronger zoogeographical barrier to southern species ranging northward than to northern species ranging southward. Interestingly, this was the conclusion of Van Name (1945) regarding the distribution of ascidians on the Pacific coast of North America, and of Horn and Allen (1978) for California coastal fishes. However, Newell (1948) found that the "nodal point" (where there are equal numbers of species from both the Oregonian and Californian Provinces) was near Point Conception for molluscs, with similar decreases in numbers of Californian and Oregonian species to the north and south of Point Conception. The "nodal point" for barnacle and copepod species from the two provinces (Newman in press) occurred between one and two degrees north of Point

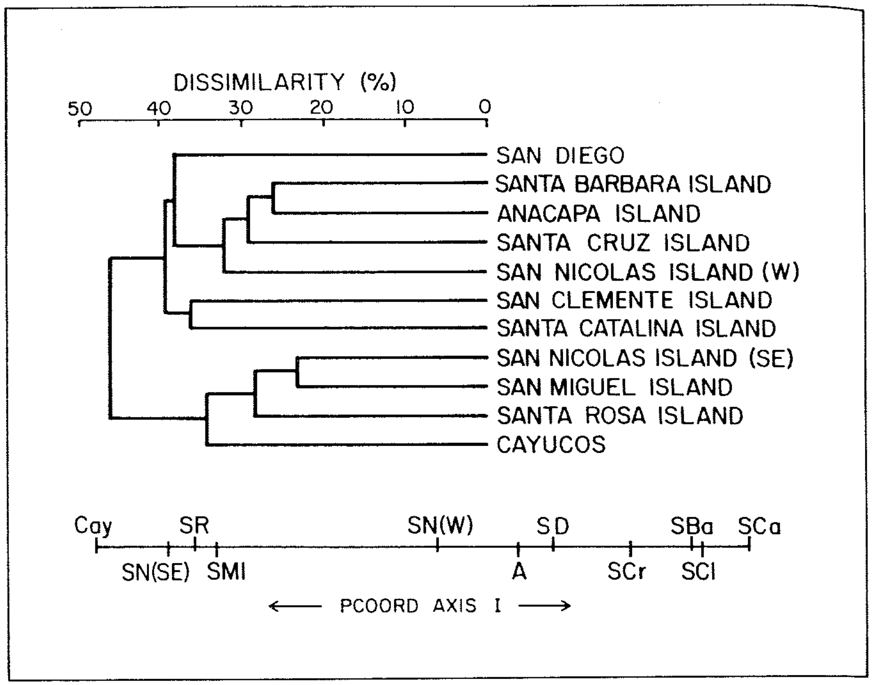

FIGURE 7. *Classification analyses using only the Gastropoda. Cluster analysis results of per cent dissimilarity between sites and site groupings are displayed as a dendrogram (above). Principal coordinates (PCOORD) ordination results are shown for axis I (below).*

Conception. Thus, different taxonomic groups appear to respond somewhat differently to the transition zone.

While the preceding analysis enabled a division of the sites into two groups with predominantly southern and northern affinities, between-site relationships were more clearly revealed by the classification techniques. The cluster analysis using all of the 252 species showed two major groupings (Fig. 5). One group linked San Diego to San Clemente, Santa Catalina, Santa Barbara, and Santa Cruz Islands, and a second group linked Cayucos Point to San Miguel, Santa Rosa, San Nicolas, and Anacapa Islands. Within these two larger groupings, Santa Catalina and San Clemente Islands were paired, as were Santa Barbara and Santa Cruz, and San Miguel and the southeast end of San Nicolas Island. These results are more clearly displayed by overlaying the cluster groupings on a map of the Southern California Islands (Fig. 6). The linkage of Anacapa and the west end of San Nicolas Island by the cluster analysis would appear to represent a misclassification as indicated by the principal coordinates analysis (Fig. 5). The latter shows the two sites to be intermediate in position along the ordination axis, with Anacapa closer to the warm-water site grouping and the west end of San Nicolas Island more closely allied with the cold-water grouping. In this and the two subsequent PCOORD analyses, only projections on axis I are shown because use of axis II did not provide additional information for interpreting the cluster analysis results.

The predominant taxonomic group was the Gastropoda, which contributed nearly half (113) of the 252 total species. Because of their numerical dominance, it is revealing to examine the degree of correspondence between the classification analysis using all of the species and that using the Gastropoda alone. The cluster analysis for the gastropods (Figs. 7 and 8) is in basic agreement with results obtained using all of the species (Fig. 5), and also provides strong support for the hypothesized inter-island relationships. For example, Santa Catalina and San Clemente Islands are closely allied, as are Santa Barbara, Anacapa, and Santa Cruz Islands, which together are linked to San Diego as warm-water sites. The west end of San Nicolas Island appears to be misclassified because the principal coordinates analysis (Fig. 7) indicates that it is intermediate in position along the ordination axis between the cold-water and warm-water site groupings. The cold-water cluster group, including Cayucos Point, San Miguel Island, west San Nicolas Island, and Santa Rosa Island, is in perfect agreement with the analysis based on all of the species taken together.

Classification results obtained using only those 59 species whose densities exceeded one per square meter (Figs. 9 and 10) are in general agreement with the results for all 252 species. Cayucos Point is linked with San Miguel Island and the southeast end of San Nicolas Island as cold-water sites. Santa Rosa Island, however, is tied to the warm-water site group, and has a peculiar linkage to San Diego. Principal coordinates analysis (Fig. 9) indicates that this represents a misclassification, because Santa Rosa Island is only peripherally linked with the tightly clumped warm-water site grouping. This interpretation was supported further by the

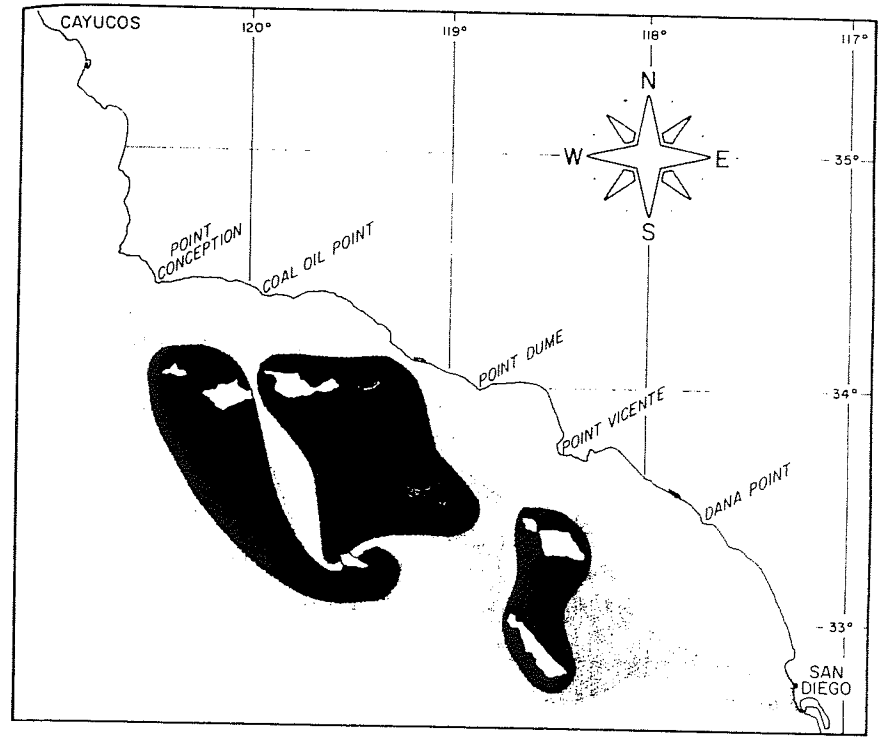

FIGURE 8. *Map overlay of cluster analysis results (Figure 7) using only the Gastropoda.*

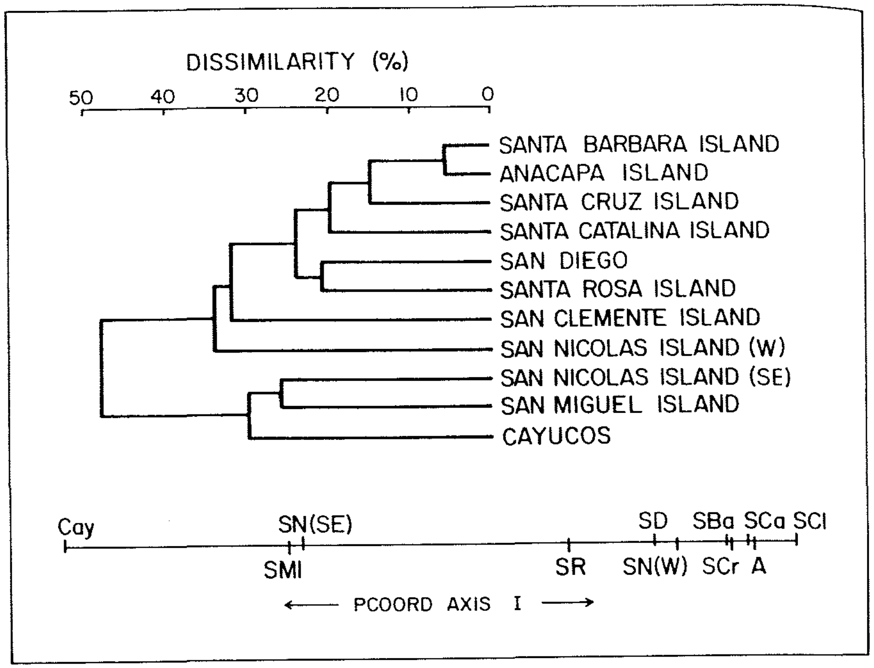

Figure 9. *Classification analyses using only those species whose abundances exceeded one per square meter at each site. Cluster analysis results of per cent dissimilarity between sites and site groupings are displayed as a dendrogram (above). Principal coordinates (PCOORD) ordination results are shown for axis I (below).*

relationship of Santa Rosa Island with the other cold-water sites in the total species (Fig. 6) and gastropod (Fig. 8) analyses.

In all three analyses (Figs. 6, 8, and 10), the northern mainland site at Cayucos was grouped with San Miguel Island and the southeast end of San Nicolas Island. This result is strongly supportive of the hypothesized northerly affinities for these two islands. In the total species and gastropod analyses (Figs. 6 and 8), Santa Rosa Island was also related to the northern grouping, while in the principal coordinates analysis which used only those species whose abundance exceeded one per square meter (Fig. 9) it was more closely aligned with the intermediate and warm-water site group. These results are in agreement with the prediction by Neushul *et al.* (1967) that the southern side of the island would be intermediate between the cold-water site at San Miguel Island and the mixed-water area on the southern side of Santa Cruz Island. In all three analyses, a mixed-water island group including Santa Barbara, Anacapa, and Santa Cruz Islands was identified that was linked with the southern islands (San Clemente and Santa Catalina) and the mainland site at San Diego. These results are consistent with the above hypothesized zoogeographical affinities based on hydrographic patterns (Fig. 2). The only site that did not fit the model well was the west end of San Nicolas Island. In the total species analysis (Fig. 6), this site was aligned with the cold-water grouping, but was not closely related to the southeast end of the island. In the gastropod analysis (Fig. 8), it was grouped with the

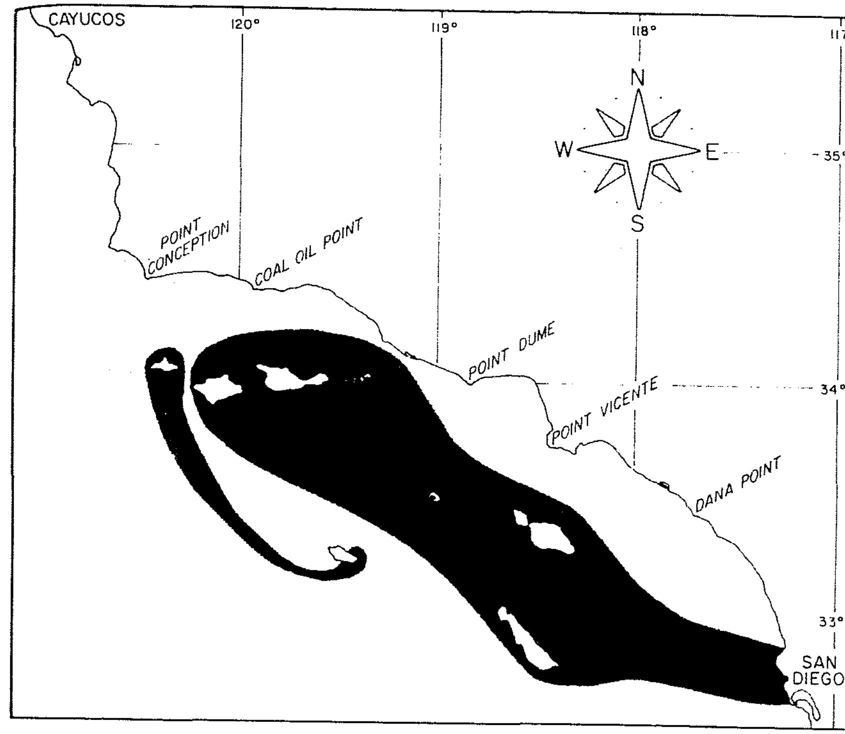

Figure 10. *Map overlay of cluster analysis results (Figure 9) using only those species whose abundances exceeded one per square meter at each site.*

intermediate sites, Santa Barbara, Anacapa, and Santa Cruz Islands. The apparent pattern of water circulation in the vicinity of San Nicolas Island affords a possible explanation for the different zoogeographical affinities of the two sites on the island. The southeast end of the island appears to receive cold, offshore California Current waters from the southwest (Fig. 2); these waters flow past the island and are turned northward by the warm, northwesterly-moving Southern California Eddy, which mixes with them to form a large eddy between San Nicolas Island and Santa Rosa and Santa Cruz Islands (Fig. 2). The warmed waters flow southeastward, eventually meeting the west end of San Nicolas Island. Further studies of current flow, such as the thermal imagery study by Hendricks (1977), are needed to substantiate the magnitude and predictability of this large gyre. Its confirmed existence, in addition to records of actual water temperature differences between the west and southeast portions of San Nicolas Island, would afford a plausible explanation for the zoogeographical differences we obtained for the two sites.

SUMMARY

Comparisons were made between the rocky intertidal macroinvertebrate faunas at sites on the eight Southern California Islands and two mainland locations (San Diego in southern California and Cayucos Point in central California). A high percentage (mean 39, range 34 to 48) of the fauna at all of the sites consisted of species with broad latitudinal ranges. An average

of 14 per cent (range 10 to 18 per cent) of the species at each site was classified as transitional, with the two mainland localities containing the lowest percentages. The percentages of northern and southern species of the fauna at each site were essentially in agreement with hypothesized inter-island affinities based on hydrographic considerations. Santa Catalina and San Clemente Islands had the highest percentage of southern species (34 and 31 per cent, respectively), followed by Anacapa and Santa Barbara Islands (27 and 24 per cent, respectively). Northern species exceeded southern species at the remaining sites.

Cluster and ordination analyses using (1) all 252 species, (2) the 113 gastropod species alone, and (3) the 59 species whose average densities exceeded one per square meter showed two major groupings: San Miguel Island and the southeast end of San Nicolas Island consistently matched with Cayucos Point, and Santa Catalina and San Clemente Islands formed a southern island group. An intermediate island grouping, including Santa Barbara, Anacapa, and Santa Cruz Islands, was linked with the southern islands and San Diego. Santa Rosa Island was also intermediate, but was aligned with San Miguel and San Nicolas Islands. These grouping patterns strongly support hypothetical affinities developed from hydrographic data, which indicate that (1) San Miguel and San Nicolas Islands are primarily bathed by cold California Current waters, (2) Santa Catalina and San Clemente Islands lie mainly in the pathway of the warm Southern California Eddy flow, and (3) the remaining islands receive differing mixtures of the two waters.

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