Biogeographic Patterns in Mussel Community Distribution from the Southern California Bight

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INTRODUCTION

The diverse assemblage of organisms associated with *Mytilus californianus* Conrad (Mollusca: Bivalvia) populations is a useful tool for examining biogeographic patterns of intertidal species distributions in the Southern California Bight. Mussels, as members of the genus *Mytilus* are often called, are attached to the underlying substrate and to other mussels by strong byssal threads. This mode of attachment enables mussels to form layered beds up to 20 cm thick (Paine 1976). Sediment, detritus, and debris are trapped in the spaces between mussels, providing food and shelter for a variety of other invertebrates (Reish 1964, Paine 1966, Kanter 1977, Suchanek 1979). This complex association of organisms is referred to as the *Mytilus californianus* community.

The mussel community is extremely rich, often supporting several hundred species (Kanter 1977, Suchanek 1979); its species richness is rivaled only by that of the *Balanus-Endocladia* association described by Glynn (1965). Past studies of mussel beds have dealt only with specific questions concerning succession (Hewatt 1937, Reish 1964, Cimberg 1975) and trophic structure (Paine 1966, Kanter 1977). Questions concerning community distribution patterns over major geographic areas have not been addressed. Large-scale investigations of other intertidal communities have concentrated on macroinvertebrates, macrophytes, or both (Dawson 1959, 1965, Nicholson and Cimberg 1971, Littler 1980); the microbiota occupying interstices in algal turf and mussel beds were generally not considered.

The Southern California Bight contains intertidal mussel beds at mainland and offshore island localities. Prior to the Bureau of Land Management's (BLM) Outer Continental Shelf studies initiated in 1975, no detailed investigations into mussel community structure or distribution had been performed in the bight. This paper discusses some of the findings of the third-year (1977-1978) BLM program, including: (1) mussel community composition, (2) mussel community species richness, and (3) biogeographic patterns and similarities among mussel communities of the bight.

METHODS

This section describes in general terms the methods of data acquisition and analysis employed in the BLM study. A more detailed description and presentation of data is in my BLM report (Kanter 1979).

The *Mytilus californianus* community was sampled at 20 rocky intertidal sites along the southern California coast (Fig. 1). Two study sites were located on each of the following Channel Islands: San Miguel, Santa Rosa, Santa Cruz, Anacapa, Santa Catalina, San Nicolas, and San Clemente. In addition, six mainland localities were sampled: Government Point, Goleta Point, Ventura, Corona del Mar, Carlsbad, and San Diego. Descriptive site references and collection dates are listed in Table 1.

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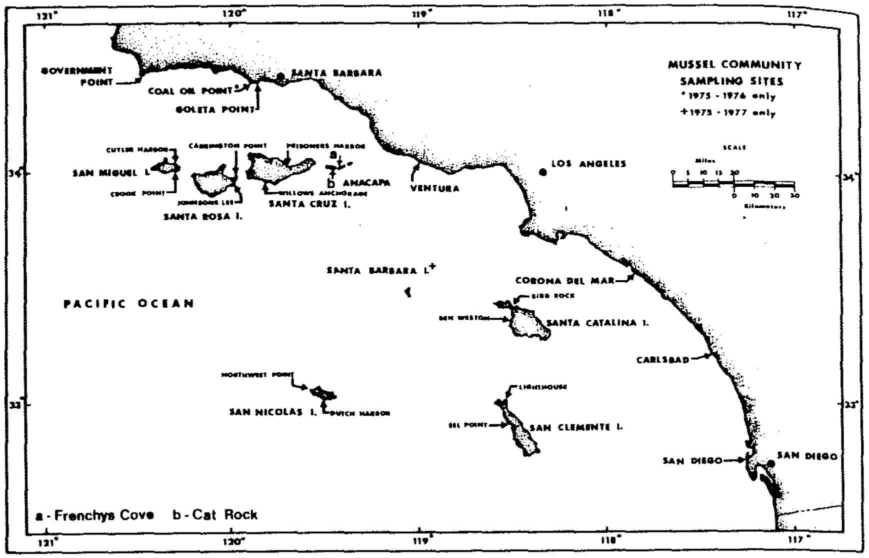

FIGURE 1. *Location of mussel community sampling sites.*

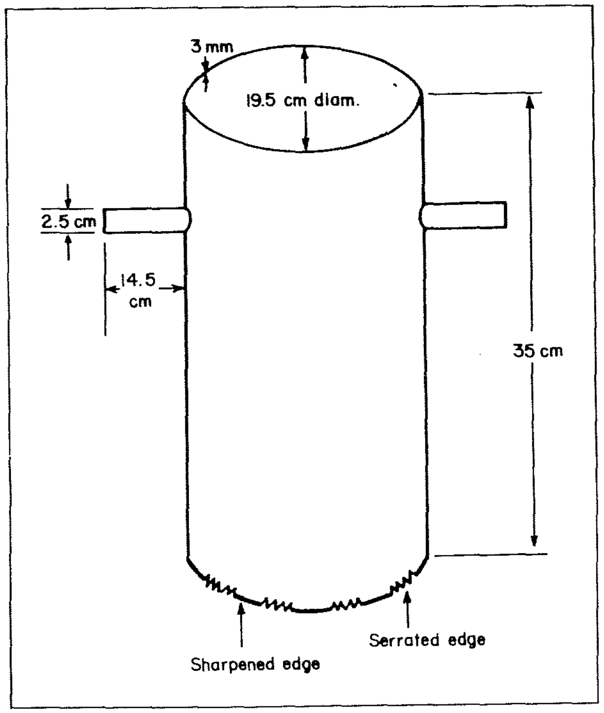

FIGURE 2. *Corer used for sampling.*

TABLE 1. Dates of collection and specific site reference abbreviations.

Collection sites	Abbreviation	Dates
Islands:		
Outer San Miguel Island, Crook Point	SMO	October 26, 1977
Inner San Miguel Island, Cuyler Harbor	MIG	October 27, 1977
Outer Santa Rosa Island, Johnsons Lee	ROS	October 12, 1977
Inner Santa Rosa Island, Carrington Point	SRO	October 11, 1977
Outer Santa Cruz Island, Willows Anchorage	CRU	November 11, 1977
Inner Santa Cruz Island, Prisoners Harbor	SCO	October 13, 1977
Outer Anacapa Island, Cat Rock	ANA	February 23, 1978
Inner Anacapa Island, Frenchys Cove	ANI	November 13, 1978
Outer Santa Catalina Island, Ben Weston	CAO	December 13, 1977
Inner Santa Catalina Island, Bird Rock	BIR	November 25, 1977
Outer San Nicolas Island, Dutch Harbor	SNI	December 9, 1977
Inner San Nicolas Island, Northwest Point	SNO	December 8, 1977
Outer San Clemente Island, Eel Point	CLM	November 9, 1977
Inner San Clemente Island, Lighthouse Point	CLI	November 10, 1977
Mainland:		
Government Point	GPT	December 7, 1977
Goleta Point	GOL	October 14, 1977
Ventura	VEN	October 13, 1977
Corona del Mar	COR	December 12, 1977
Carlsbad	CAR	November 12, 1977
San Diego	SD	November 11, 1977

The accessible extremes of beds at selected sites were sampled to examine the difference between mussel communities occupying different intertidal heights. These sites included Cuyler Harbor (San Miguel Island), Eel Point (San Clemente Island), and Goleta Point. The different intertidal height samples are labeled A and B for reference. The actual vertical height and community differences are discussed in following sections.

An area 1,500 cm^2 was sampled by collecting five 300-cm^2 core replicates (Fig. 2). The 1,500 cm^2 sample size was previously determined to be an optimal size based on species-area curve graphical analysis (Cain 1938) and information loss computations (Smith 1976). The core sample was removed intact, where possible, to include organisms, sediment, detritus, and debris. The sample was preserved in 15 per cent buffered formalin and returned to the laboratory for processing of biotic and abiotic components.

In the laboratory, samples were washed with fresh water and the mussels separated from the rest of the sample. The entire sample was hand sorted to recover all organisms (greater than 0.5 mm) from the sediment, debris, and detritus. All invertebrates and attached algae were identified. The numbers of each animal species were recorded. Algae were not quantified beyond presence or absence. Data were reduced and analyzed to quantitatively describe mussel bed composition, diversity, and community similarity.

Species richness (number of species) was used to refer to the variety of organisms in the mussel community. The number of species represents a cumulative number for a consistent sample size of 1,500 cm^2 (five 300-cm^2 replicates). Indices including Shannon-Weaver (H')

Table 2. Diversity of biota at each mussel community sampling locality (1977-1978) ranked by faunal richness. (The letters A and B designate separate collections from different intertidal heights.)

Collection sites		Number of species Fauna	Flora	Diversity H'	Evenness J'
Islands:					
Outer Anacapa Island, Cat Rock		174	15	3.218	0.642
Inner Santa Catalina Island, Bird Rock		163	16	3.482	0.694
Inner San Clemente Island, Lighthouse Point		157	14	3.231	0.660
Outer Santa Cruz Island, Willows Anchorage		148	1	2.892	0.579
Inner Santa Cruz Island, Prisoners Harbor		130	17	3.024	0.624
Inner San Nicolas Island, Northwest Point		130	14	2.613	0.560
Inner Santa Rosa Island, Carrington Point		120	15	2.615	0.550
Outer Santa Rosa Island, Johnsons Lee		109	11	2.728	0.583
Outer San Miguel Island, Crook Point	(B)	104	14	1.596	0.344
Outer San Miguel Island, Crook Point	(A)	103	12	1.911	0.412
Outer San Clemente Island, Eel Point	(B)	102	10	2.426	0.526
Outer San Nicolas Island, Dutch Harbor		101	2	3.426	0.745
Outer San Clemente Island, Eel Point	(A)	95	4	2.356	0.521
Inner Anacapa Island, Frenchys Cove		79	7	1.867	0.430
Inner San Miguel Island, Cuyler Harbor	(A)	79	7	1.915	0.454
Inner San Miguel Island, Cuyler Harbor	(B)	72	9	1.517	0.357
Outer Santa Catalina Island, Ben Weston		46	21	1.845	0.508
Mean		112.47	11.12	2.510	0.541
Mainland:					
San Diego		120	23	2.706	0.579
Ventura		107	7	2.487	0.537
Carlsbad		102	13	2.272	0.505
Goleta Point (B)		91	11	1.862	0.422
Goleta Point (A)		90	22	1.644	0.369
Corona del Mar		90	6	2.687	0.602
Government Point		77	12	2.472	0.580
Mean		96.7	13.4	2.304	0.513

diversity (Pielou 1966) and Pielou's evenness (J') were provided for comparative purposes only, since their applicability to this study is severely limited.

Intersite and intertidal height comparisons of community similarity were accomplished by classificatory analysis (Clifford and Stephenson 1975). The intersite comparison included only species which occurred in more than 25 per cent of the geographic areas. The Bray-Curtis index (Clifford and Stephenson 1975) was used to compute inter-entity distances. Flexible sorting strategy was employed in the construction of hierarchical dendrograms (Lance and Williams 1966). Species counts were transformed by square root and species mean prior to normal analysis, and by square root and species maximum prior to inverse analysis (Smith 1976). Intrasite intertidal height comparison results were displayed in dendrogram form. The intersite comparison results were displayed in the form of a two-way coincidence table with symbols representing species' relative abundance (Clifford and Stephenson 1975, Smith 1976).

Table 3. Mussel community faunal richness and intertidal height separation of collections from the same locality. (The letters A and B designate separate collections from different intertidal heights.)

Locality	Number of species A	B	Differences in intertidal height (m)	(ft)
Goleta Point	90	91	1.45	4.73
Cuyler Harbor, San Miguel Island	79	72	2.41	7.89
Crooks Point, San Miguel Island	103	104	0.03	0.11
Eel Point, San Clemente Island	95	102	0.33	1.05

RESULTS AND DISCUSSION

Mussel Community Composition and Species Richness

The mussel bed communities in the Southern California Bight are extremely rich. The assemblages examined contained, conservatively, 610 species of invertebrates and 141 species of algae (Table 2). Three invertebrate phyla, the Annelida, Mollusca, and Arthropoda, contributed over two-thirds of all the species recorded.

Sampled mussel beds displayed a large range in faunal richness. The community at Cat Rock on the outer side of Anacapa Island was the most diverse, supporting 174 species. Richness was lowest in the mussel beds at Ben Weston (Santa Catalina Island), which contained only 46 species (Table 2).

The species found in the mussel beds are too numerous to list here (see Kanter 1979). The most common species, however, included the limpets (Mollusca: Gastropoda) *Collisella scabra*, *C. limatula*, *C. pelta*, and *C. strigatella*; the barnacles (Arthropoda: Cirripedia) *Chthamalus dalli*, *C. fissus*, *Balanus glandula*, *Tetraclita squamosa*, and *Pollicipes polymerus*; the marine worms (Annelida: Polychaeta) *Arabella semimaculata*, *Nereis mediator* (= *grubei*), *Typosyllis "fasciata"* sp. D, and *Typosyllis hyalina*; and the nemerteans (Nemertea) *Emplectonema gracile* and *Paranemertes peregrina*.

Algae attached to the surface of the mussels totaled 141 species for all collections combined. The number of algal taxa recorded from a single collection ranged from a low of one at Prisoners Harbor (Santa Cruz Island) to a high of 23 from San Diego (Table 2). The most common attached algal taxa included *Gelidium* spp., *Ulva* spp., *Carpopeltis* spp., *Haliptylon* spp., *Porphyra* spp., *Gigartina* spp., and *Polysiphonia* spp. These groups were represented in several of the mussel beds; in general, more species were found at island than at mainland localities.

There was no apparent relationship between the numbers of floral and faunal species collected at different sites. For example, 15 algal species were recorded at outer Anacapa Island, while 174 animal species were observed in the same samples. However, only one algal species was recorded at Willows Anchorage (Santa Cruz Island), where 148 animal species were observed.

Collections from different intertidal heights at the same locality were very similar with regard to the total number of faunal species (Table 3). The two collections from Goleta Point contained 90 and 91 species, while those from Crooks Point (San Miguel Island) contained 103 and 104 species. A difference of seven species between upper and lower intertidal samples was recorded from mussel beds at Cuyler Harbor (San Miguel Island) and Eel Point (San Clemente

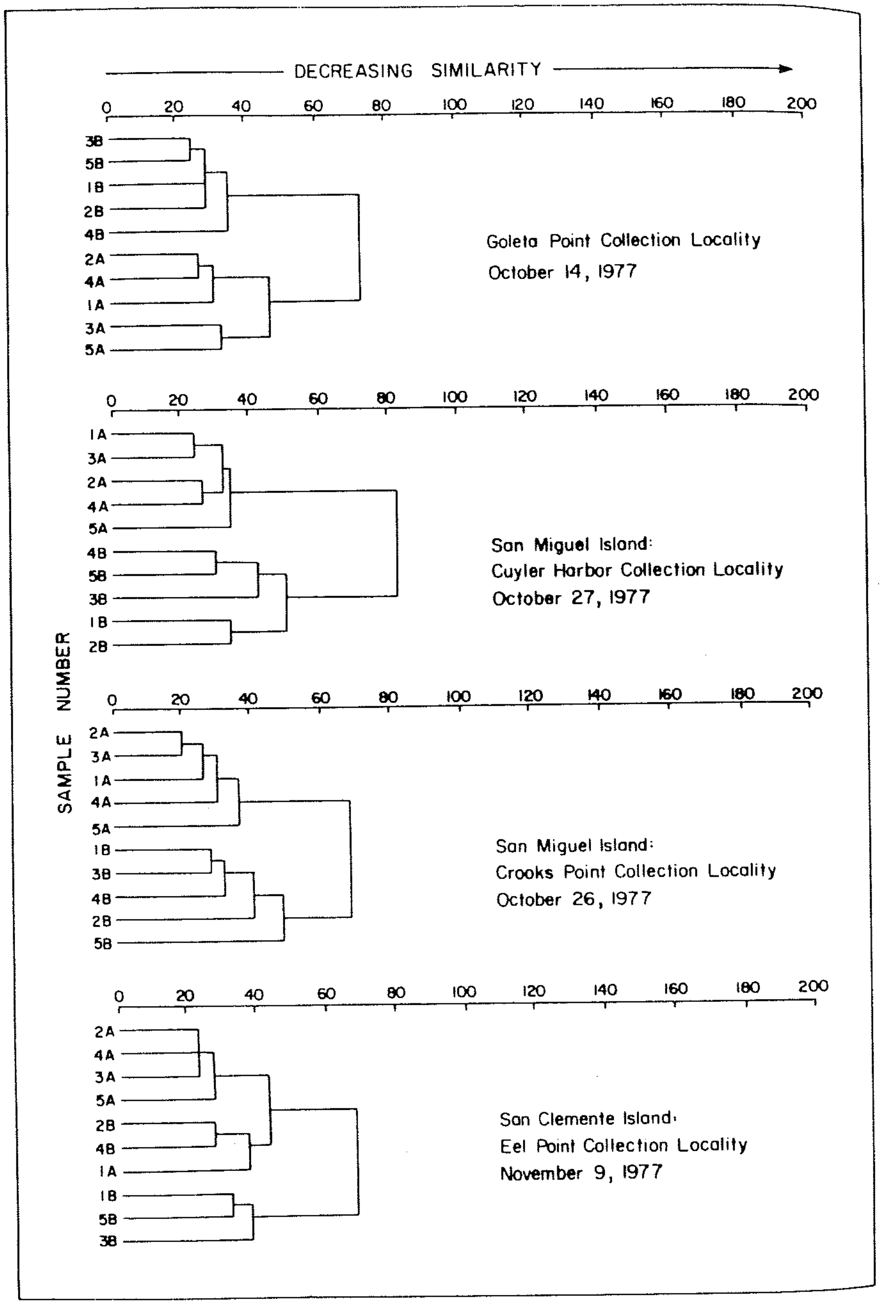

FIGURE 3. *Dendrograms of mussel community samples from different intertidal heights within a locality. Upper intertidal sample replicates labeled* A, *lower samples labeled* B.

Island). Those collections separated by large intertidal height differences did not display a proportionate difference in species richness. For example, Goleta Point samples separated by a distance of 1.45 m (4.73 ft) differed by one species, whereas the Eel Point (San Clemente Island) beds were only 0.33 m (1.05 ft) apart but differed by seven in species count.

Although species richness was similar in samples collected from mussel beds at different intertidal heights within a site, classificatory analysis of the five replicate core samples from each intertidal level revealed that community compositional differences did exist. Analysis of data from Goleta Point and both sides of San Miguel Island produced dendrograms with primary divisions which clearly separated upper and lower collections (Fig. 3).

The separation indicated that upper and lower intertidal samples were dissimilar in species composition and abundance. These results contrasted with those from analysis of Eel Point (San Clemente Island) samples which did not show clear differences between upper and lower intertidal samples (Fig. 3). Thus, the microbiota associated with mussel beds may be vertically stratified, with samples differing in composition depending on bed elevation, but these differences may not be reflected in the community statistical parameters of richness or diversity. Further, samples collected from one intertidal level may not accurately reflect the "total" mussel community at a site unless the entire mussel bed occupies a narrow range in intertidal height.

Mussel Community Similarity Analysis

Classificatory techniques (Clifford and Stephenson 1975) were employed to define similarities and detect biogeographic patterns among mussel communities. The analyses produced normal (site) and inverse (species) dendrograms which were then arranged in a two-way coincidence table. The normal dendrogram clusters localities based on similarity of faunal composition. The inverse dendrogram clusters species with similar distributions. The two-way coincidence table merges the normal and inverse analyses to display species distribution patterns (Fig. 4).

The site groups which resulted from the normal analysis were sequentially numbered for easy reference in subsequent discussions. Species groups were similarly labeled with letters. In order to interpret the species composition of a specific group it was necessary to refer directly to Figure 4. Site abbreviations are listed in Table 1.

The analysis revealed five major patterns which corresponded to characteristic species assemblages occupying the mussel beds of various geographic areas. The observed patterns included: (1) the presence of ubiquitous species groups; (2) clusters of species whose highest abundances characterize particular study sites; (3) clusters of study sites which display a north-south geographic pattern in the similarity of their respective mussel communities; (4) a separation of selected island and mainland communities because of dissimilarities in their species composition; and (5) differences between mussel communities on opposite sides of the same offshore island.

The inverse community similarity analysis yielded six species groups, labeled A through E (Fig. 4). Species group A was a nearly ubiquitous assemblage of organisms found in practically all the mussel beds sampled. Overall abundance of the species in this group was slightly higher in collections from site groups 1, 2, and 3 than in collections from the other site groups. Species group A included the limpets *Collisela scabra*, *C. limatula*, *C. pelta*, and *C. strigatella*, the nemerteans *Emplectonema gracile* and *Paranemertes peregrina*, the crab *Pachygrapsus crassipes*, the barnacles *Chthamalus fissus* and *C. dalli*, the polychaetes *Typosyllis fasciata* sp. D and *Arabella semimaculata*, and the sea anemone *Anthopleura elegantissima*. Other prevalent species were scattered among the remaining species groups including groups C and E. Included among these species were the molluscs *Septifer bifurcatus* and *Lasaea subviridis*, the polychaete *Naineris dendritica*, and the barnacles *Tetraclita squamosa* and *Balanus glandula*.

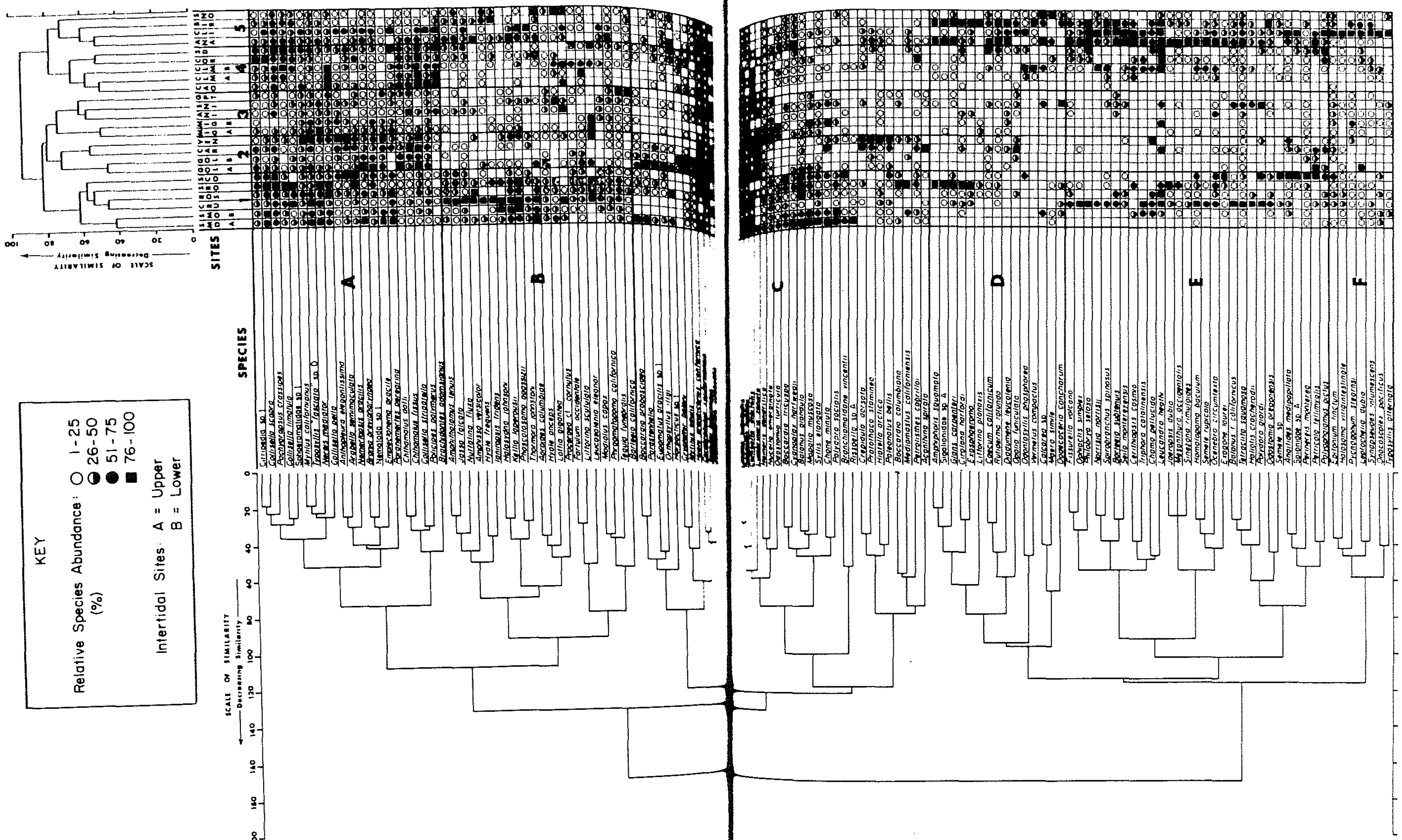

FIGURE 4. *Normal and inverse classification dendrograms with resultant two-way table.*

Species in group B characterized Channel Island study areas (Fig. 4). Most of the species occurred in their highest relative abundance at group 1 sites, although some species occurred at sites in other groups but in low or very low numbers. Among the distinctive species in group 1 were the peanut worm *Phascolosoma agassizii* and the bivalve mollusc *Kellia laperousii*.

Site groups 1 and 2 were characterized by high relative abundance of several members of species group C (*e.g.*, the chitons *Mopalia muscosa* and *Cyanoplax hartwegii*, and the barnacle *Balanus glandula*). Other species were present in all mussel beds, with their highest abundance displayed at group 1 mussel beds (*e.g.*, the bivalve *Lasaea subviridis* and the polychaete *Nereis dendritica*).

Species in groups D, E, and F were frequent, abundant, and characteristic of site group 5 mussel beds. Few members of these species groups were found in site group 2, 3, or 4 mussel beds. However, several of the species from groups D, E, and F were encountered in collections from site group 1. Although absent or in relatively low abundance at other sites, species such as the bivalve *Philobrya setosa* and the gastropod *Cerithiopsis cosmia* were found in very high abundance among beds from site group 5.

Species from group F, although present in some abundance at most sites, were notably absent from site group 2 mussel beds.

The normal classification, which includes sites with upper and lower intertidal collections, shows one primary and three secondary divisions on the dendrogram, resulting in five clusters of sites (Fig. 4, Table 1). The primary dendrogram division separates site groups 1, 2, and 3 from site groups 4 and 5. Secondary dendrogram divisions, in turn, separate site groups 1, 2, and 3 from each other and group 4 from group 5. Site group 1 is composed of northern island localities, including the upper and lower intertidal collections from Crooks Point (San Miguel Island), both sampling areas on Santa Rosa Island, and both sampling areas on Santa Cruz Island. Site group 2 contains mainland collection areas from Goleta Point (both upper and lower intertidal samples), Ventura, and Carlsbad. Site group 3 is composed of northern island collections from Cuyler Harbor (San Miguel Island; both upper and lower intertidal samples), Frenchys Cove (Anacapa Island), a more southern island area at Dutch Harbor (San Nicolas Island), and the northernmost mainland site, Government Point. Site groups 4 and 5 contain mixtures of southern island and mainland collection localities. Site group 4 contains the Ben Weston (Santa Catalina Island) collection area, the upper and lower intertidal sampling areas at Eel Point (San Clemente Island), the Corona del Mar locality, and the San Diego collection area. Site group 5 contains one of the more northern collection areas, Cat Rock (Anacapa Island). However, this study site faces the remainder of the southerly collection sites. Also included in site group 5 are collection sites at the northwest point of San Nicolas Island, Lighthouse Point (San Clemente Island), and the Bird Rock site on Santa Catalina Island.

The primary dendrogram split clearly separated the northern collection areas, site groups 1, 2, and 3, from the southern collection areas, site groups 4 and 5. Remembering that clustering of collection sites implies that the mussel communities sampled in these areas were more similar in species composition and relative abundance to each other than to communities outside the cluster, we can elaborate on the resultant biogeographic patterns.

The northern and southern communities appeared to correspond to the "warm-water" and "cold-water" provinces previously described as occurring north and south of Point Conception, California (Johnson and Snook 1967, Light *et al.* 1970). In addition, the results suggested that the "cold-water" provinces should extend south of Point Conception if one considers the mussel community inhabitants when discussing this phenomenon. This pattern was clearly exhibited by the clustering and close similarity displayed among Northern Channel Island and northern mainland communities. There were, within the northern site groupings, additional patterns. Site group 1, for example, was composed entirely of island collection areas from the northernmost localities, whereas site group 2 was composed almost exclusively of northern mainland localities (with the exception of Carlsbad). Site group 3 contained a notable mixture of study areas. The northernmost mainland collection area at Government Point was very similar to the Northern Channel Island site at San Miguel, the north-facing Frenchys Cove site on Anacapa Island, and the Dutch Harbor collection area of San Nicolas Island. This interesting arrangement was best explained by considering the impinging water regimes in the areas, as discussed later.

The southern localities were also clustered according to the similarities of their respective mussel communities. Site group 5 was composed almost exclusively of southern island localities, whereas site group 4 contained a mixture of mainland and island sites. The inclusion of the Cat Rock (Anacapa Island) locality in site group 5 was notable and is discussed later.

The normal dendrogram results illustrated distinct dissimilarities between many of the pairs of collections from the same islands (Fig. 4). The most dramatic differences were displayed by the collections from San Nicolas Island and Anacapa Island. The Dutch Harbor (San Nicolas Island) and Frenchys Cove (Anacapa Island) collections occurred in site group 3; these clustered with the northern study sites, illustrating that these mussel communities resembled the northern mussel communities more than their intra-island counterparts. Conversely, the Northwest Point (San Nicolas Island) and Cat Rock (Anacapa Island) sites contained communities which more closely resembled the mussel beds found at the southern collection areas. Less dramatic but still notable differences were evident in the communities from opposite sides of San Miguel Island and San Clemente Island. Although each study site maintained fidelity to its overall northern or southern geographic group, faunal differences existed which placed Crook Point (outer San Miguel Island) and Cuyler Harbor (inner San Miguel Island) separately in site groups 1 and 3, respectively, and which placed Eel Point (outer San Clemente Island) and Lighthouse Point (inner San Clemente Island) in site groups 4 and 5, respectively (Fig. 4, Table 1).

Dispersal of planktonic larvae by currents and water masses is a hypothesis often put forth to explain biogeographic patterns of species distribution (Johnson 1939, Seapy 1974). Cleve-Eulser (1928, as cited in Johnson 1939) succinctly expressed the underlying principle: "Regular biological analysis of the oceans and of the coastal waters would no doubt give a more thorough knowledge of the sea currents, their movements and their intermingling, than could be expected from hydrographic observations only." This principle has been applied to individual species and should be applied in community studies.

Most mussel community members reproduce either by releasing gametes into the surrounding waters where external fertilization and larval development occurs, or by releasing larvae after partial development in an egg capsule or within the adults. These planktonic larvae drift with prevailing currents and water masses. Passive drifting ends when the larva has matured enough to actively seek out an appropriate substrate (settlement and metamorphosis, however, can only occur when this substrate is within the behavioral and physiological tolerances of the larva). Larvae may drift a considerable distance from source areas prior to settlement, acting as a biological "tracer" in the water mass they occupy. Broad-scale analysis of the community distribution resulting from this dispersal serves as an independent test of hydrographic studies detailing current structure and water mass movement, and allows prediction of community structure in areas not specifically sampled.

A very generalized composite diagram of circulation patterns (Fig. 5) occurring in the southern California area has been constructed from Jones (1971), Pirie *et al.* (1974), and Bernstein *et al.* (1977). This figure primarily depicts net surface water circulation and does not include the subsurface currents, localized gyres, or seasonal anomalies which are known to exist (Shepard *et al.* 1939, Tibby 1941, Reid 1962, Jones 1971, Bernstein *et al.* 1977). The

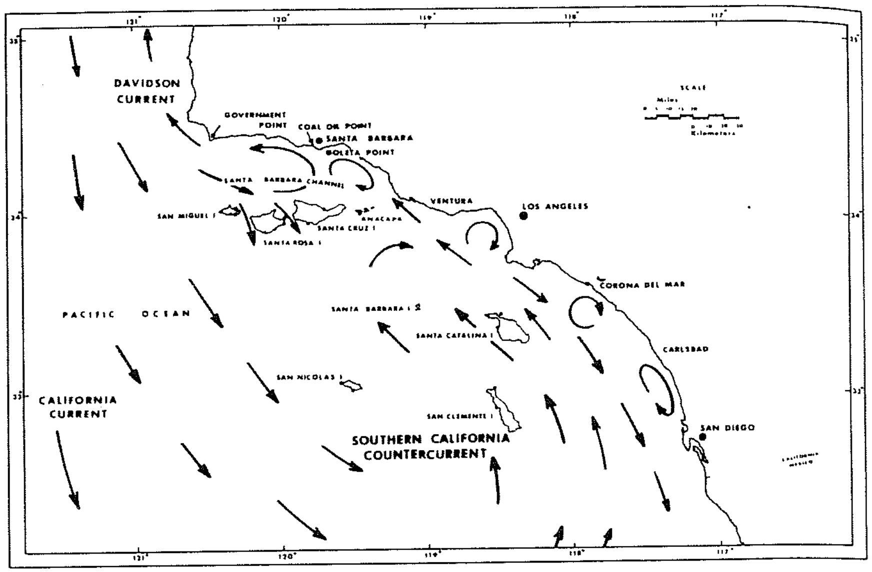

FIGURE 5. *General surface circulation in the Southern California Bight (modified after Jones 1971, Pirie* et al. *1974, and Bernstein* et al. *1977).*

patterns illustrated suggest that cold water arising north of Point Conception flows south and swings in, impinging on the offshore islands in its continued movement down the coast. In addition, movement of warm water arising in lower latitudes flows northward along the mainland coast. Larvae are carried to settlement areas by these two primary current regimes. Mussel community similarities at the various sites suggest that they have received larval recruits from similar source waters (source parental stock). This assumption serves as a basis for delineating and explaining biogeographical patterns among the mussel communities. The similarities of mussel communities illustrated by the classification results (Fig. 4) support the idea of common parental stocks. There is close agreement between the water source to which a site is exposed and the composition of its community. For example, Cat Rock (Anacapa Island) mussel beds closely resemble those communities found on Bird Rock (Santa Catalina Island). The Cat Rock collection area faces due south and is exposed to waters hydrographically similar to those bathing Bird Rock. Conversely, the mussel community at Frenchys Cove (Anacapa Island) is more similar to those found at Cuyler Harbor (San Miguel Island) and Government Point than to species assemblages at Cat Rock, its intra-island counterpart. The Frenchys Cove mussel beds are exposed to almost the same water regimes as mussel beds at Cuyler Harbor and Government Point. Identical arguments could be made in support of the similarities between communities at other sites.

SUMMARY

The community associated with *Mytilus californianus* (mussel) beds from 20 geographic sites in southern California was examined. The study areas included six mainland sites (Government Point, Goleta Point, Ventura, Corona del Mar, Carlsbad, and San Diego) and two sites on opposite sides of seven offshore islands (San Miguel, Santa Rosa, Santa Cruz, Anacapa, San Nicolas, Santa Catalina, and San Clemente). This large community contains, conservatively, 610 species of animals and 141 species of algae. The richest collection came from Cat Rock (Anacapa Island), where the mussel beds supported 174 species of invertebrates. The lowest diversity was recorded for mussel beds from Ben Weston (Santa Catalina Island), which contained 46 species. In general, the island mussel beds supported a greater variety of both animals and plants. Samples were collected from upper and lower intertidal portions of the beds at several sites. Differences in community composition and abundance were associated with position in the intertidal zone.

Community similarity analysis revealed five major patterns which corresponded to characteristic species assemblages occupying the mussel beds in the various geographic areas. The patterns included: (1) presence of some ubiquitous species groups; (2) clusters of species whose highest abundances characterized selected localities; (3) clusters of localities which displayed a north-south geographic pattern in the similarity of their respective mussel communities; (4) a separation of some island and mainland communities because of dissimilarities in their species composition; and (5) differences between mussel communities on opposite sides of the offshore islands. The results of the community analysis suggest that predictions of the probable mussel community inhabitants of areas not sampled can be made. The observed species distribution patterns appear to correspond in part to known patterns of current flow.

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