Megabenthic Invertebrate Assemblages of the Mainland Shelf of Southern California in 1994

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ABSTRACT

Here we present results of the first synoptic trawl survey of the mainland shelf of southern Califor nia in July and August 1994. We collected trawl samples at 114 stations selected at random from Point Conception, California, to the United States-Mexico international border at depths of 10 to 200 m. A total of 66,333 invertebrates representing 204 species was collected. Site and species assemblages were described using cluster analysis. Five primary site clusters and three primary species clusters of invertebrates, with minor subgroupings, were delineated. Primary site clusters were the following: (1) Inner Shelf, (2) Inner/Middle Shelf, (3) Middle Shelf, (4) Middle/Outer Shelf, and (5) Outer Shelf. Primary species clusters were (1) Pacific Spiny Brittlestar-Mosaic Sand Star, (2) White Sea Urchin-Brokenspine Brittlestar, and (3) Fragile Sea Urchin-California Heart Urchin. Overall, depth was more important than geographical area or sediment type in determining invertebrate assemblages.

INTRODUCTION

The megabenthic (trawl-caught) invertebrate fauna of the mainland shelf of the Southern California Bight (SCB) is diverse, consisting of several hundred species occupying the soft-bottom habitat at depths of 10 to 200 m (Moore and Mearns 1978, Allen *et al.* 1998). Because these species are relatively sedentary, they have an increased exposure to accumulated contaminants in sediment and low oxygen levels in near-bottom waters. Thus, they respond to changes in the benthic environment and have been monitored for many years to assess impacts resulting from human activities.

Although this fauna has been studied for many years, there has been little focus on megabenthic invertebrate assemblages. Most studies in the area have described assemblages only for local areas (generally near wastewater outfalls) (e.g., CSDLAC 1990, CLAEMD 1994, CSDMWWD 1995, CSDOC 1996). However, interpretation of these local assemblages is difficult without comparison to background assemblages for the SCB as a whole. Thompson *et al.* (1993) used cluster analysis to describe site and species assemblages based upon species-abundance data accumulated from 1971 to 1985 from the southern California mainland shelf, slope, and basins as well as from highly contaminated sites and different (warm and cool) oceanic regimes. However, because this analysis was based upon data collected from different locations in different years, it does not provide a description of the assemblages in the SCB for a single time period. In contrast, Allen and Moore (1997) described recurrent species groups from data collected in 1994 during a synoptic trawl survey of the SCB, but used different analytical methods (based upon presence/absence data on species co-occurrence rather than species-abundance data). Here we present a description of megabenthic invertebrate assemblages (based upon species-abundance data) from the 1994 synoptic survey of the southern California coastal shelf.

The objectives of this study were (1) to describe synoptic site and species assemblages of megabenthic

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invertebrates for the southern California mainland shelf; (2) to describe their distribution with regard to depth, region, and sediment type; and (3) to compare them to previously described assemblages using a different database but similar analytical methods (Thompson *et al.* 1993) and the same database but different analytical methods (Allen and Moore 1997).

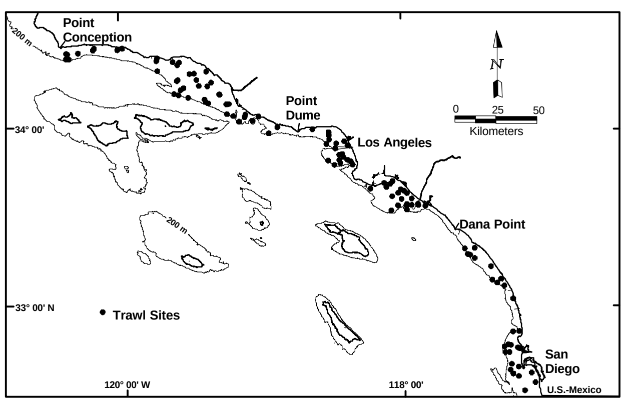
METHODS

Trawl samples were collected at 114 randomly selected stations from Point Conception, California, to the United States-Mexico international border at depths of 9 to 215 m (rounded to 10 to 200 m for the purposes of this report) (Figure 1). A stratified random design was used, with the following depth strata: (1) inner shelf —10 to 25 m; (2) middle shelf — 25 to 100 m; and (3) outer shelf —100 to 200 m (Bergen 1996, Stevens 1997). These strata were not sampled equally, with 53 samples collected from the middle shelf zone, 31 from the outer shelf zone, and 30 from the inner shelf zone.

Samples were collected from July 12 to August 22, 1994, with 7.6-m head-rope semiballoon otter trawls with 1.25-cm cod-end mesh. Trawls were towed for 10 min at 1 m/sec (2 kn) along isobaths. Invertebrates were identified to species, counted, examined for anomalies, and weighed by species to the nearest 0.1 kg.

At each site, sediment for grain size characterization was collected using a 0.1 m^2 modified Van Veen grab. Sediment grain size was determined using a Horiba Model LA-900 laser scattering particle size distribution analyzer in conjunction with Horiba Data Systems software (Schiff and Gossett 1998).

FIGURE 1. Stations sampled by trawl on the mainland shelf of southern California at depths of 10-200 m, July to August 1994.



Data Analysis

Abundance-based site and species groups were defined using cluster analysis. Prior to analysis, the data were screened to reduce the confounding effect of rare species by including only those with an overall survey abundance of at least 10 individuals which occurred in at least 5 stations. Five stations were dropped from the data since they had fewer than five individuals of any species. Ultimately, 45 invertebrate species from 109 stations were selected for the cluster analysis.

After selecting the species for the analysis, the abundance data were square-root transformed and standardized to mean species abundance. The square-root transformation was applied to moderate the influence of the most abundant taxa (Sokal and Rohlf 1981, Clark and Green 1988). The data were standardized by dividing species abundance at a given station by the mean abundance of that species over all stations. The benefit of standardization is that it effectively equalizes extreme abundance values and facilitates relative comparisons among species (Clark 1993).

The Bray-Curtis measure was used to convert the species composition and abundance data into a dissimilarity matrix (Bray and Curtis 1957, Clifford and Stephenson 1975). Clustering was conducted using an agglomerative, hierarchical, flexible sorting method (SAS PROC CLUSTER [SAS Institute 1989]), with *beta* set at -0.25 (Tetra Tech 1985). Both Q-mode cluster analysis (to identify groups of stations that exhibit similar species abundance patterns) and R-mode cluster analysis (to identify complementary groups of species that occur in similar habitats) were conducted and used to produce a two-way coincidence table (Kikkawa 1968, Clifford and Stephenson 1975).

The relative proportional contribution of species clusters in site clusters was determined by (1) calculating for each species at each site the proportion of its total abundance across all 109 sites, (2) summing these proportions for all species in a given species cluster (e.g., Species Cluster A) within a given site cluster (e.g., Site Cluster 1) to give a species cluster/site cluster total (e.g., sum of Species Cluster A proportions in Site Cluster 1), and (3) dividing each species cluster/site cluster total by the sum of all species cluster/site cluster totals within a site group.

Site clusters were named after shelf-zone distribution. Primary species clusters were named after their two most abundant species in their secondary site clusters. Secondary species clusters were named after their single most abundant species.

RESULTS

At least 204 species of invertebrates, representing 8 phyla, 20 classes, and 110 families, were collected during the trawl surveys (see Allen *et al.* 1998 for list of species). The surveys sampled 67 species of mollusks, 56 species of arthropods, 41 species of echinoderms, 24 species of cnidarians, 6 species of annelids, 5 species of chordates, 5 species of poriferans, and 3 species of brachiopods. The most diverse classes were Malacostraca (52 species), Gastropoda (51 species), and Anthozoa (20 species). The most diverse families were Paguridae (right-hand hermit crabs), Majidae (spider crabs), and Crangonidae (bay shrimp) with 10, 9, and 7 species, respectively.

Ten species accounted for 95% of the total invertebrate abundance in the survey (Table 1). The three most abundant invertebrates were white sea urchin (*Lytechinus pictus*), brokenspine brittlestar (*Ophiura luetkeni*), and ridgeback rock shrimp (*Sicyonia ingentis*); these species accounted for 77% of the total invertebrate abundance. In the reduced data set (consisting of 45 species from 109 stations) selected for cluster analysis, the most frequently occurring species were California sand star (*Astropecten verrilli*), ridgeback rock shrimp, white sea urchin, and gray sand star (*Luidia foliolata*) (Table 2). The three most abundant species in these selected stations were the same as those for the survey (Tables 1 and 3).

Site Clusters

Five primary site clusters were delineated after analysis (Figure 2). Stations were roughly clustered according to water depth (Figure 3) and to a lesser degree by sediment grain size measures (Figure 4). Site Cluster 1 generally included the shallowest stations sampled while Site Cluster 5 included the deepest stations sampled (Figure 3). All five clusters were broadly distributed throughout the study area except for Site Cluster 1, which was found only on the inner shelf of the central region (Figure 5).

Site Cluster 1 (Inner Shelf Cluster) included eight of the shallowest stations, ranging in depth from 13 to 23 m (mean = 17.3 m). This site cluster delineates a shallow, sandy (mean = 73.6% sand) inner shelf habitat (Figures 3 and 4). Site Cluster 1 included all members (i.e., a complete set) of Species Cluster A1 (Tables 2 and 3). Only two species, spiny sand star (*Astropecten armatus*) and California sand star, occurred in more than 50% of the stations in this cluster (Table 2). Spiny sand star, the most abundant species, was found at all of the stations (Table 3).

Site Cluster 2 (Inner/Middle Shelf Cluster) included 30 stations ranging in depth from 9 to 72 m (mean = 28.9 m), characterizing an inner and middle shelf habitat with predominantly sandy sediments (mean = 71% sand) (Figures 3 and 4). This site cluster included complete Species Clusters A2, A3, and B2 (Tables 2 and 3). California sand star, occurring at 83% of the stations, was the only species in this group that was found at more than 50% of the stations (Table 2). This species was nearly 30 times more abundant in this cluster than in Site Cluster 1 (Table 3).

Site Cluster 3 (Middle Shelf Cluster) contained 23 stations ranging in depth from 25 to 91 m (mean = 57.5 m), characterizing a middle shelf habitat with fine silt-sand sediments (mean = 58.3% silt/clay) (Figures 3 and 4). This site cluster included all members of Species Clusters A4, B1, B2, and B3 (Tables 2 and 3). Seven species occurred in more than 50% of the stations (Table 2). California sand star, ridgeback rock shrimp, and brokenspine brittlestar were found in more than 75% of the stations, with California sand star occurring at 91%

TABLE 1. Invertebrate species comprising 95% of the total invertebrate abundance in a regional trawl survey of the mainland shelf of southern California at depths of 10-200 m, July to August 1994.

Scientific Name	Common Name	Abundance (n=66,333)	Percent Total	Percent Cumulative
Lytechinus pictus	white sea urchin	28,378	42.8	42.8
Ophiura luetkeni	brokenspine brittlestar	12,385	18.7	61.5
Sicyonia ingentis	ridgeback rock shrimp	10,078	15.2	76.6
Allocentrotus fragilis	fragile sea urchin	3,825	5.8	82.4
Spatangus californicus	California heart urchin	2,825	4.3	86.7
Acanthoptilum sp.	trailtip sea pen, unid.	1,613	2.4	89.1
Brisaster latifrons	northern heart urchin	1,296	2.0	91.1
Neocrangon zacae	shortkeel bay shrimp	937	1.4	92.5
Astropecten verrilli	California sand star	918	1.4	93.9
Parastichopus californicus	California sea cucumber	742	1.1	95.0

TABLE 2. Frequency of occurrence of invertebrate species in species clusters and site clusters on the mainland shelf of southern California at depths of 10-200 m, July to August 1994. (Spp. Clus. = species cluster).

				Percent Stations by Site Cluster				
Spp. Clus.		Scientific Name	Common Name	1 (n=8)	2 (n=30)	3 (n=23)	4 (n=30)	5 (n=18)	Total (n=109)
A	**1**	*Astropecten armatus*	spiny sand star	100	-	-	-	-	7
		Pagurus spilocarpus	spotwrist hermit	38	17	-	3	-	8
		Pyromaia tuberculata	tuberculate pear crab	38	47	13	-	6	19
		Crangon nigromaculata	blackspotted bay shrimp	38	23	-	-	-	9
	2	*Pisaster brevispinus*	shortspined sea star	25	37	-	-	-	12
		Heterocrypta occidentalis	sandflat elbow crab	-	47	9	3	-	16
		Randallia ornata	globose sand crab	38	7	9	-	-	6
		Nassarius perpinguis	fat western nassa	-	20	-	-	-	6
	3	*Lovenia cordiformis*	sea porcupine	-	23	4	-	-	7
		Cancer gracilis	graceful rock crab	13	30	-	-	-	9
	4	*Podochela lobifrons*	thinbeak neck crab	-	-	26	-	-	6
		Ophiothrix spiculata	Pacific spiny brittlestar	-	27	61	33	6	30
		Luidia armata	mosaic sand star	-	23	43	3	6	17
		Acanthodoris brunnea	brown spiny doris	-	10	39	-	-	11
B	**1**	*Ptilosarcus gurneyi*	fleshy sea pen	-	-	4	10	11	6
		Delonovolva aequalis vidleri	Vidler simnia	-	3	17	13	-	8
		Acanthoptilum sp.	trailtip sea pen	-	7	30	43	17	23
		Calliostoma turbinum	spindle topsnail	-	3	9	20	-	8
		Stylatula elongata	slender sea pen	-	10	43	13	-	16
	2	*Crangon alaskensis*	Alaska bay shrimp	-	3	61	7	-	16
		Loligo opalescens	California market squid	-	7	35	37	33	25
		Ophiura luetkeni	brokenspine brittlestar	-	17	78	53	28	40
		Astropecten verrilli	California sand star	63	83	91	63	33	70
		Parastichopus californicus	California sea cucumber	-	17	70	73	56	49
		Sicyonia ingentis	ridgeback rock shrimp	-	37	87	70	83	61
		Luidia foliolata	gray sand star	13	30	39	77	67	50
		Pleurobranchaea californica	California sand star	25	13	43	67	44	40
	3	*Philine alba*	white paper bubble	-	-	4	13	-	5
		Lytechinus pictus	white sea urchin	-	37	52	83	39	50
		Octopus rubescens	red octopus	-	10	22	30	22	19
		Metridium "senile"	clonal plumose anemone	-	-	9	30	11	12
C	**1**	*Armina californica*	California armina	-	7	13	-	17	7
		Tritonia diomedea	rosy tritonia	-	7	9	10	28	11
		Amphichondrius granulosus	roughdisk brittlestar	-	3	-	13	22	8
		Metacrangon spinosissima	southern spinyhead	-	-	4	-	50	9
		Neocrangon resima	flagnose bay shrimp	-	-	-	7	72	14
		Neocrangon zacae	shortkeel bay shrimp	-	-	4	20	89	21
		Rossia pacifica	eastern Pacific bobtail	-	7	22	13	67	21
	2	*Megasurcula carpenteriana*	tower snail	-	10	17	13	33	16
		Spatangus californicus	California heart urchin	-	-	-	27	22	11
		Brissopsis pacifica	Pacific heart urchin	-	-	-	13	56	13
		Brisaster latifrons	northern heart urchin	-	-	-	17	67	16
		Allocentrotus fragilis	fragile sea urchin	-	-	4	50	83	28
		Paguristes turgidus	slenderclaw hermit	13	3	-	13	11	7
		Dromalia alexandri	sea strawberry	-	-	-	-	28	5

TABLE 3. Abundance of invertebrate species in species clusters and site clusters on the mainland shelf of southern California at depths of 10-200 m, July to August 1994. (Spp. Clus. = Species cluster).

				Number of Individuals by Site Cluster					
Spp. Clus.		Scientific Name	Common Name	1 (n=8)	2 (n=30)	3 (n=23)	4 (n=30)	5 (n=18)	Total (n=109)
A	**1**	*Astropecten armatus*	spiny sand star	17	-	-	-	-	17
		Pagurus spilocarpus	spotwrist hermit	8	8	-	1	-	17
		Pyromaia tuberculata	tuberculate pear crab	33	28	9	-	1	71
		Crangon nigromaculata	blackspotted bay shrimp	18	23	-	-	-	41
	2	*Pisaster brevispinus*	shortspined sea star	2	14	-	-	-	16
		Heterocrypta occidentalis	sandflat elbow crab	-	60	2	1	-	63
		Randallia ornata	globose sand crab	9	2	3	-	-	14
		Nassarius perpinguis	fat western nassa	-	37	-	-	-	37
	3	*Lovenia cordiformis*	sea porcupine	-	17	1	-	-	18
		Cancer gracilis	graceful rock crab	1	24	-	-	-	25
	4	*Podochela lobifrons*	thinbeak neck crab	-	-	19	-	-	19
		Ophiothrix spiculata	Pacific spiny brittlestar	-	16	213	45	1	275
		Luidia armata	mosaic sand star	-	12	58	19	1	90
		Acanthodoris brunnea	brown spiny doris	-	5	16	-	-	21
B	**1**	*Ptilosarcus gurneyi*	fleshy sea pen	-	-	1	16	2	19
		Delonovolva aequalis vidleri	Vidler simnia	-	1	18	5	-	24
		Acanthoptilum sp.	trailtip sea pen	-	2	51	1,555	5	1,613
		Calliostoma turbinum	spindle topsnail	-	1	2	7	-	10
		Stylatula elongata	slender sea pen	-	56	18	11	-	85
	2	*Crangon alaskensis*	Alaska bay shrimp	-	18	90	11	-	119
		Loligo opalescens	California market squid	-	6	69	67	32	174
		Ophiura luetkeni	brokenspine brittlestar	-	39	11,844	94	408	12,385
		Astropecten verrilli	California sand star	13	369	322	129	78	911
		Parastichopus californicus	California sea cucumber	-	66	254	259	163	742
		Sicyonia ingentis	ridgeback rock shrimp	-	172	5,555	1,966	2,385	10,078
		Luidia foliolata	gray sand star	1	32	40	157	46	276
		Pleurobranchaea californica	California sand star	2	23	15	53	28	121
	3	*Philine alba*	white paper bubble	-	-	1	21	-	22
		Lytechinus pictus	white sea urchin	-	1,787	5,068	20,082	1,441	28,378
		Octopus rubescens	red octopus	-	8	5	9	5	27
		Metridium "senile"	clonal plumose anemone	-	-	5	16	7	28
C	**1**	*Armina californica*	California armina	-	4	3	-	4	11
		Tritonia diomedea	rosy tritonia	-	2	2	12	11	27
		Amphichondrius granulosus	roughdisk brittlestar	-	1	-	8	20	29
		Metacrangon spinosissima	southern spinyhead	-	-	1	-	26	27
		Neocrangon resima	flagnose bay shrimp	-	-	-	4	106	110
		Neocrangon zacae	shortkeel bay shrimp	-	-	1	35	901	937
		Rossia pacifica	eastern Pacific bobtail	-	2	7	25	46	80
	2	*Megasurcula carpenteriana*	tower snail	-	3	8	10	15	36
		Spatangus californicus	California heart urchin	-	-	-	486	2,339	2,825
		Brissopsis pacifica	Pacific heart urchin	-	-	-	17	232	249
		Brisaster latifrons	northern heart urchin	-	-	-	14	1,282	1,296
		Allocentrotus fragilis	fragile sea urchin	-	-	1	484	3,340	3,825
		Paguristes turgidus	slenderclaw hermit	27	1	-	5	2	35
		Dromalia alexandri	sea strawberry	-	-	-	-	29	29

of the stations. Brokenspine brittlestar was by far the most abundant species (Table 3).

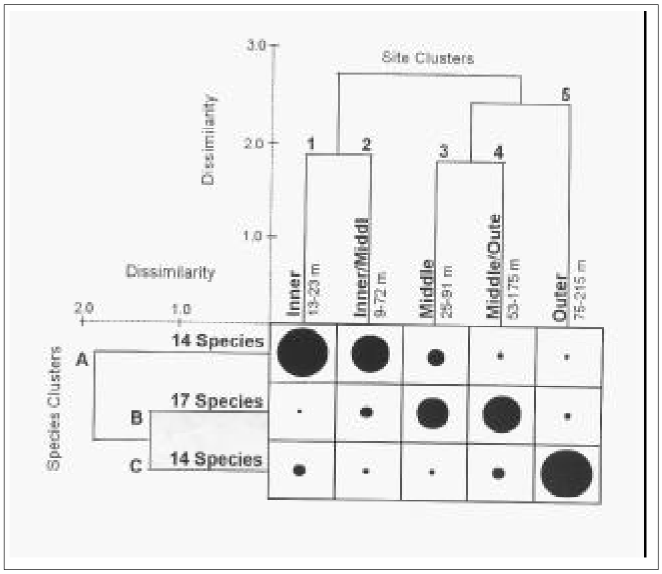
Site Cluster 4 (Middle/Outer Shelf Cluster) included 30 stations ranging in depth from 53 to 175 m (mean = 108.9 m), characterizing a middle/outer shelf habitat with sandy-silt sediments (mean = 58.4% sand) (Figures 3 and 4). These sediments were sandier than the mean sediment values found for Site Clusters 3 and 5. This site cluster included complete Species Clusters B1, B2, and B3 (Tables 2 and 3). Eight species were found in 50% or more of the stations (Table 2). However, only white sea urchin and gray sand star occurred in more than 75% of the stations (83 and 77%, respectively). White sea urchin was 10 times more abundant than ridgeback rock shrimp, the next most abundant species (Table 3).

Site Cluster 5 (Outer Shelf Cluster) included 18 stations ranging in depth from 75 to 215 m (mean = 164.7 m), characterizing an outer shelf cluster habitat with fine sediments (mean = 64.6% silt/clay) (Figures 3 and 4). In addition to water depth, Site Cluster 5 differs from Site Cluster 4 in sediment type. Site Cluster 5 included all members of Species Clusters C1 and C2 (Tables 2 and 3). Ten species occurred in 50% or more of the stations in this cluster (Table 2). Only shortkeel bay shrimp (*Neocrangon zacae*), ridgeback rock shrimp, and fragile sea urchin (*Allocentrotus fragilis*) were found in more than 75% of the samples, with shortkeel bay shrimp occurring in 89% of the samples. However, fragile sea urchin and ridgeback rock shrimp were the most abundant species in this site cluster (Table 3).

Species Clusters

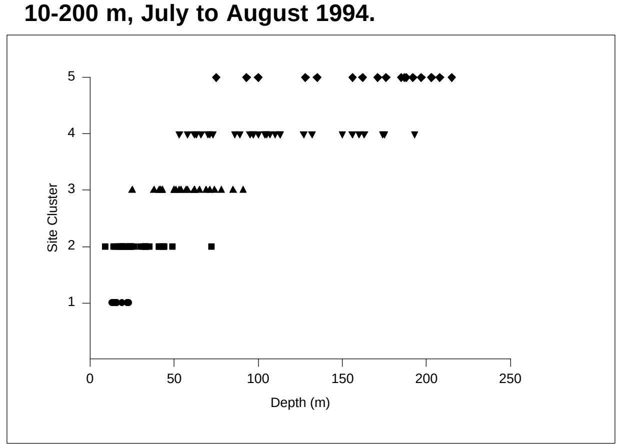
Three primary species clusters with several secondary clusters were delineated after analysis (Figure 2). Species Clusters A through C occupied and were dominant in successively deeper depth zones (Figures 2 and 6). All site clusters included representatives of all three species clusters. Species Cluster A was dominant in Site Clusters 1 and 2, Species Cluster B in Site Clusters 3 and 4, and Species Cluster C in Site Cluster 5.

FIGURE 2. Summary of two-way table and dendrogram for species and site clusters of megabenthic invertebrates on the mainland shelf of southern California at depths of 10-200 m, July to August 1994. Cell dot sizes represent the relative proportional contribution of species clusters within site clusters.



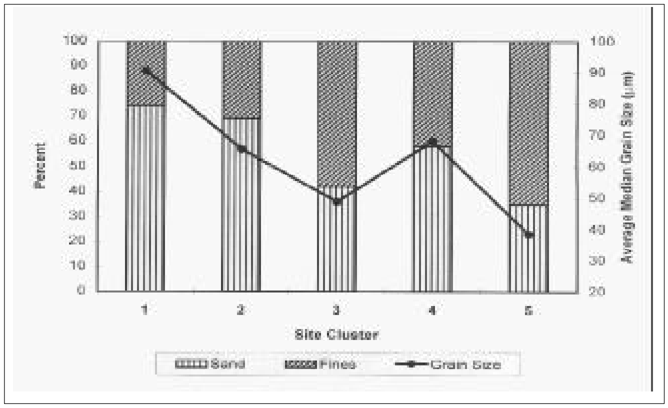
Species Cluster A (Pacific Spiny Brittlestar-Mosaic Sand Star Cluster) included 14 species and 4 secondary clusters (Tables 2 and 3). This species cluster was dominant in Site Clusters 1 and 2 (Figure 6) and hence represents an inner/middle shelf assemblage. No site group included all members of this cluster (Tables 2 and 3); however, 86% of the species were found in Site Cluster 1. The most frequently occurring species were Pacific spiny brittlestar (*Ophiothrix spiculata*), tuberculate pear crab (*Pyromaia tuberculata*), and mosaic sand star (*Luidia armata*) (Table 2). These were also the most abundant species, although mosaic sand star was more abundant than tuberculate pear crab. The first secondary cluster (Species Cluster A1, Tuberculate Pear Crab Cluster) consisted of four species: spiny sand star, spotwrist hermit (*Pagurus spilocarpus*), tuberculate pear crab, and blackspotted bay shrimp (*Crangon nigromaculata*). All species were found together in Site Cluster 1 and hence characterize an inner shelf assemblage. The spiny sand star was found exclusively at stations in Site Cluster 1. The four species of the next secondary cluster (Species

FIGURE 3. Bathymetric distribution of megabenthic invertebrate site clusters on the mainland shelf of southern California at depths of 10-200 m, July to August 1994.



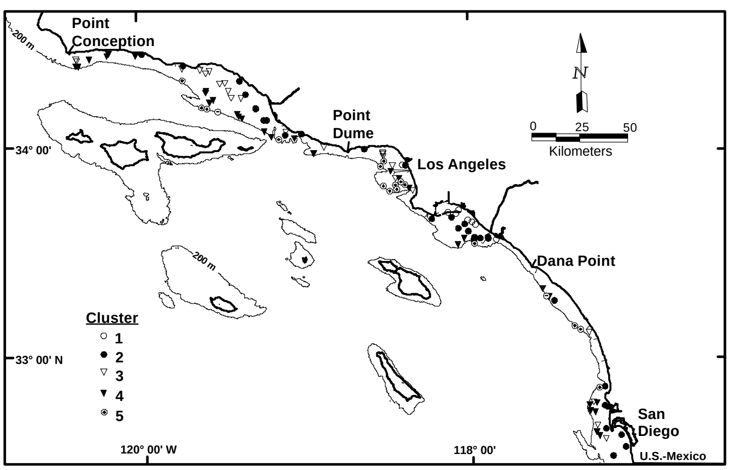
Cluster A2, Sandflat Elbow Crab Cluster) included shortspined sea star (*Pisaster brevispinus*), sandflat elbow crab (*Heterocrypta occidentalis*), globose sand crab (*Randallia ornata*), and fat western nassa (*Nassarius perpinguis*, a snail). These species characterize an inner/middle shelf assemblage and were all found together in Site Cluster 2. The two species of the third secondary cluster (Species Cluster A3, Graceful Rock Crab Cluster), sea porcupine (*Lovenia cordiformis*, a heart urchin), and graceful rock crab (*Cancer gracilis*), were also part of the inner/middle shelf assemblage, occurring together in Site Cluster 2. Four species comprised the final secondary cluster (Species Cluster A4, Pacific Spiny Brittlestar Cluster): thinbeak neck crab (*Podochela lobifrons*), Pacific spiny brittlestar, mosaic sand star, and brown spiny doris (*Acanthodoris brunnea*, a nudibranch). All of these species had broader depth distributions and were found together in Site Cluster 3, thus characterizing a middle shelf assemblage.

FIGURE 4. Relationship of megabenthic invertebrate site clusters to sediment characteristics (percent of sediment type and average median grain size) on the mainland shelf of southern California at depths of 10-200 m, July to August 1994.



Species Cluster B (White Sea Urchin-Brokenspine Brittlestar Cluster) included 17 species and 3 secondary clusters (Tables 2 and 3). This species cluster was dominant in Site Clusters 3 and 4 (Figure 6) and hence represents a middle/outer shelf assemblage. All members of this cluster were found together in Site Clusters 3 and 4 (Tables 2 and 3). The most frequently occurring species were California sand star, ridgeback rock shrimp, gray sand star, and white sea urchin. The most abundant species were white sea urchin, brokenspine brittlestar, and ridgeback rock shrimp. The first secondary cluster (Species Cluster B1, Trailtip Sea Pen Cluster) included five species: fleshy sea pen (*Ptilosarcus gurneyi*), Vidler simnia (*Delonovolva aequalis vidleri*, a snail), trailtip sea pen (*Acanthoptilum* sp.), spindle topsnail (*Calliostoma turbinum*), and slender sea pen (*Stylatula elongata*). These species were found together in Site Clusters 3 and 4 and represent a middle/outer shelf assemblage. The next secondary cluster (Species Cluster B2, Brokenspine Brittlestar Cluster) consisted of eight species: Alaska bay shrimp (*Crangon alaskensis*), California market squid (*Loligo opalescens*), brokenspine brittlestar, California sand star, California sea cucumber (*Parastichopus californicus*), ridgeback rock shrimp, gray sand star, and California sea slug (*Pleurobranchaea californica*). These species were all found together in Site Clusters 2 through 4 and hence represent a broad middle shelf assemblage. Without Alaska bay shrimp, which was absent in Site Cluster 5, the remaining species were found together in Site Clusters 2 through 5. Species Cluster B2 contained two of the most abundant species (brokenspine brittlestar and ridgeback rock shrimp) and the most frequently occurring species (California sand star). The third secondary cluster (Species Cluster B3, White Sea Urchin Cluster) consisted of four species: white paperbubble (*Philine alba*, a snail), white sea urchin, red octopus (*Octopus rubescens*), and clonal plumose anemone (*Metridium "senile"*). These species occurred together in Site Clusters 3 and 4 and represent a middle shelf assemblage. This cluster included the most abundant invertebrate species (white sea urchin) in the survey. Species in this secondary cluster were most abundant in Site Cluster 4.

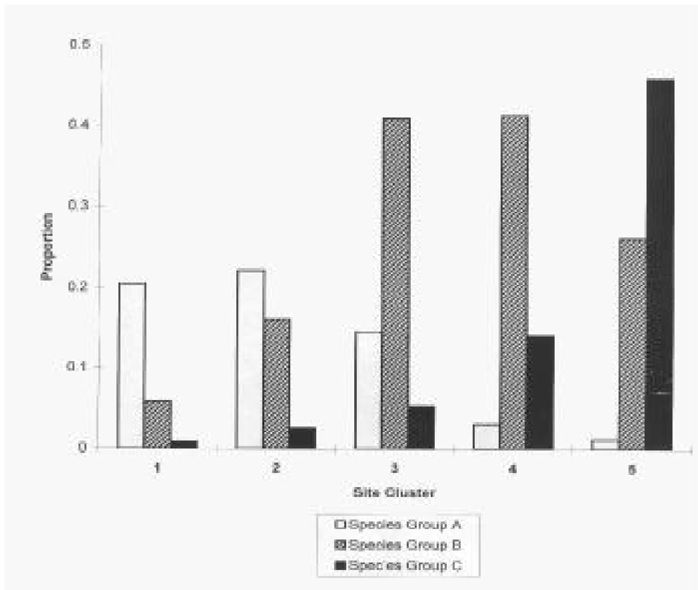
FIGURE 5. Spatial distribution of megabenthic invertebrate clusters on the mainland shelf of southern California at depths of 10-200 m, July to August 1994.



Species Cluster C (Fragile Sea Urchin-California

Heart Urchin Cluster) consisted of 14 species and 2 secondary clusters (Tables 2 and 3). This species cluster was dominant in Site Cluster 5 (Figure 6) and hence represents an outer shelf assemblage. All members of this cluster were found together in Site Cluster 5 (Tables 2 and 3). The first secondary cluster (Species Cluster C1, Shortkeel Bay Shrimp Cluster) included seven species: California armina (*Armina californica*, a nudibranch), southern spinyhead (*Metacrangon spinosissima*, a shrimp), flagnose bay shrimp (*Neocrangon resima*), shortkeel bay shrimp, roughdisk brittlestar (*Amphichondrius granulosus*), rosy tritonia (*Tritonia diomedea*, a nudibranch), and eastern Pacific bobtail (*Rossia pacifica*, a squid). These species occurred together in Site Cluster 5, primarily at stations in Santa Monica Bay. The next secondary cluster (Species Cluster C2, Fragile Sea Urchin Cluster) included seven species: tower snail (*Megasurcula carpenteriana*), California heart urchin (*Spatangus californicus*), northern heart urchin (*Brisopsis latifrons*), Pacific heart urchin (*Brisaster pacifica*), fragile sea urchin, sea strawberry (*Dromalia alexandri*, a benthic siphonophore), and slenderclaw hermit (*Paguristes turgidus*). These species also occurred together in Site Cluster 5, but at stations in the northern and southern regions of the SCB.

FIGURE 6. Relative proportion of possible occurrences of invertebrate species cluster members at site cluster stations on the mainland shelf of southern California at depths of 10-200 m, July to August 1994.



DISCUSSION

All of the site and species clusters appear to be natural groups in that they consist of relatively tight clusters of stations or species. Almost all of the species included in the analysis typically inhabit the soft-bottom habitat although some (i.e., clonal plumose anemone and red octopus) are typically associated with hard substrate or debris. Although most species clusters represent general habitat features, Species Cluster B1 represents a sea pen association.

Site and species clusters were generally related to water depth, a pattern found for other megabenthic invertebrate population and assemblage attributes (e.g., Thompson *et al.* 1993, CSDOC 1996, Allen and Moore 1997, Allen *et al.* 1998). Although site clusters typically differed by depth, considerable overlap of site clusters often occurs within the predefined depth subpopulations of the survey (Figure 3). Site Cluster 1 was found only in the central region of the inner shelf zone and Site Cluster 5 was almost exclusively associated with the outer shelf depth zone. Similarly, some stations from the intermediate depth site clusters overlapped with these categories and the middle shelf zone. For example, 16 stations from Site Cluster 2 and 1 station from Site Cluster 3 occurred on the inner shelf zone and 16 stations from Site Cluster 4 occurred on the outer shelf zone. The middle shelf zone included stations from Site Clusters 2, 3, 4, and 5. The site clusters suggest that other factors (e.g., grain size) in addition to depth also contribute to the distribution of species (Figure 4).

All site clusters had unique combinations of complete species clusters (Tables 2 and 3). Similarly, complete species clusters were generally found in different combinations of site groups. However, all complete Species Clusters A2 and A3 occurred only at Site Cluster 2 and complete Species Clusters C1 and C2 were found only in Site Cluster 5 (Tables 2 and 3). Species Clusters A2 and A3 differed in habitat; A2 was characteristic of fine sediments and A3 of coarse sediments. Similarly, Species Cluster C1 was typical of fine sediments and Species Cluster C2 was typical of coarse sediments.

No pollution effects were found in the study area. Twenty of the trawl stations were identified as being near potential anthropogenic sources of contamination (e.g., wastewater outfalls, river discharges, oil platforms) (Allen *et al.* 1998). Those stations did not form unique cluster groups.

Historic assemblages of megabenthic invertebrates on the mainland shelf and slope of southern California have been described using ordination and classification analysis to define site groups with similar species composition and abundance (Thompson *et al.* 1993). This previous study defined a number of shelf, slope, and basin assemblages based upon data collected from 1971 to 1985. Three major assemblages occurred in the depth range of the mainland shelf: (1) a pre-1980 Palos Verdes Shelf Assemblage (23-137 m), (2) a post-1981 Storm/El Niño Assemblage (18-37 m), and (3) a Normal Mainland Shelf Assemblage (10-137 m). The latter assemblage corresponds to Site Cluster 3 (Middle Shelf) of the present study. The Outer Shelf/Upper Slope Site Cluster of the earlier study corresponds to Site Cluster 4 (Middle/Outer Shelf) of the present study, although the earlier assemblage is somewhat deeper (45-315 m). The Middle Slope Assemblage (300-490 m) of the early study corresponds to Site Cluster 5 (Outer Shelf) of 1994.

Thompson *et al*. (1993) had an equal number of site and species clusters. Hence, the dominant species in the species clusters were also those of the site clusters. The most frequently occurring species in the Normal Mainland Shelf Assemblage were white sea urchin, ridgeback rock shrimp, and California sand star. In 1994, these species were characteristic of Site Clusters 3 (Middle Shelf) and 4 (Middle/Outer Shelf) and of Species Cluster B (Table 2). In the Outer Shelf/Upper Slope Assemblage, ridgeback rock shrimp, pelagic red crab (*Pleuroncodes planipes*), and white sea urchin were most abundant. With the exception of pelagic red crab, these species were dominant in Site Clusters 3 and 4, and Species Cluster B of 1994. The most abundant species in the Middle Slope Assemblage were Pacific heart urchin, northern heart urchin, and fragile sea urchin — all of which were important members of Site Cluster 5 (Outer Shelf) and Species Cluster C2 of 1994.

A number of obvious changes occurred between the two periods. Pelagic red crab was very abundant and armed box crab (*Platymera* (= *Mursia*) *gaudichaudii*) occurred frequently in Thompson *et al*. (1993); both were rare in 1994. In contrast, California heart urchin, brokenspine brittlestar, and Pacific spiny brittlestar were abundant in 1994 but not in the earlier study. In addition, the inner and middle shelf areas were less well defined in the historic study than in 1994 because of the differences in depth range of the two studies. However, the earlier study describes specific clusters beyond the scope of the 1994 study (e.g., Pre-1980 Palos Verdes Shelf Assemblage, Post-1981 Storm/El Niño Assemblage, and several deeper assemblages).

Comparison of Recurrent Groups and Site/Species Clusters

Invertebrate assemblages have been defined for this region by recurrent group analysis using the same data set (Allen and Moore 1997). Recurrent group analysis differs from cluster analysis in that species groups are defined based upon co-occurrence of species (using presence/absence data) rather than similarities in relative abundance patterns. In addition, site groups are not defined by recurrent group analysis. Nevertheless, the two methods generally, but not always, produce similar results.

A comparison of the invertebrate cluster analysis to recurrent group analysis on the same data (Allen and Moore 1997) found fewer similarities in species associations (Table 4) than in fish associations (see *Demersal Fish Assemblages of the Mainland Shelf of Southern California in 1994* in this annual report). Only three of the seven recurrent groups of invertebrates defined in Allen and Moore (1997) were found in the site clusters. The species selection process for the cluster analysis eliminated all of the species in Recurrent Groups 1, 2, 5, and 7. Each of the remaining groups occurred completely only in a single site cluster, but two occurred together in one site cluster (Table 4). Although no recurrent group occurred completely in Site Clusters 1, 2, or 3, Recurrent Group 3 (Middle/Outer Shelf Group) was found in Site Cluster 4 (Middle/Outer Shelf Cluster) and Recurrent Groups 4 (Submarine Canyon Group) and 5 (Outer Shelf Group) were found together in Site Cluster 5 (Outer Shelf Cluster).

A comparison of recurrent groups (Allen and Moore 1997) to species clusters of invertebrates (Table 3) reveals a closer relationship than a comparison of the recurrent groups to species clusters of fish (see *Demersal Fish Assemblages of the Mainland Shelf of Southern California in 1994* in this annual report). Although no recurrent group occurred in Species Cluster A, all Recurrent Group 3 species (white sea urchin, ridgeback rock shrimp, California sand star, California sea cucumber, gray sand star, and California sea slug) occurred in Species Cluster B. Of these, all except white sea urchin occurred in Species Cluster B2; white sea urchin occurred in Species Cluster B3. Both Recurrent Group 4 species (eastern Pacific bobtail and southern spinyhead) and all Recurrent Group 5 species (fragile sea urchin, northern heart urchin, shortkeel bay shrimp, and Pacific heart urchin) occurred in Species Cluster C.

Comparison of all three types of associations (recurrent group, site clusters, and species clusters) showed that the middle/outer shelf association is the most distinct

TABLE 4. Distribution of megabenthic invertebrate recurrent groups (Allen and Moore 1997) in site clusters on the mainland shelf of southern California at depths of 10-200 m, July to August 1994. (n = no. stations, listed species occur in at least 50% of stations in site clusters, "0" = relative abundance in site cluster less than 0.5%).

		Relative Abundance (Percent Total in Site Cluster)				
Scientific Name	Common Name	1 (n=8)	2 (n=30)	3 (n=23)	4 (n=30)	5 (n=18)
Astropecten armatus	spiny sand star	12	-	-	-	-
Recurrent Group 3						
Astropecten verrilli	California sand star	9	12	1	0	-
Lytechinus pictus	white sea urchin	-	-	21	77	-
Pleurobranchaea californica	California sea slug	-	-	-	0	-
Luidia foliolata	gray sand star	-	-	-	1	0
Parastichopus californicus	California sea cucumber	-	-	1	1	1
Sicyonia ingentis	ridgeback rock shrimp	-	-	23	8	18
Ophiothrix spiculata	Pacific spiny brittlestar	-	-	1	-	-
Crangon alaskensis	Alaska bay shrimp	-	-	0	-	-
Ophiura luetkeni	brokenspine brittlestar	-	-	50	0	-
Recurrent Group 4						
Rossia pacifica	eastern Pacific bobtail	-	-	-	-	0
Metacrangon spinosissima	southern spinyhead	-	-	-	-	0
Recurrent Group 6						
Allocentrotus fragilis	fragile sea urchin	-	-	-	2	25
Brisaster latifrons	northern heart urchin	-	-	-	-	10
Neocrangon zacae	shortkeel bay shrimp	-	-	-	-	7
Brissopsis pacifica	Pacific heart urchin	-	-	-	-	2
Neocrangon resima	flagnose bay shrimp	-	-	-	-	1
Total Abundance of Species		146	2,984	23,791	26,178	13,224

megabenthic invertebrate assemblage. This result also corresponds to the findings in Thompson *et al*. (1993), with regard to the Normal Mainland Shelf Assemblage. Differences between the studies were due to the different analytical methods utilized and the number of species included in each analysis. However, the fact that many of the species groups were similar between the two analyses when the data were similar supports the premise that these assemblages are natural features of communities within specific habitats rather than artifacts of a particular analytical method.

Recurrent group analysis and site cluster analysis describe assemblages from two perspectives of the community (Allen 1982). If recurrent group analysis is applied to data from a large area, the groups may approximate the biogeographic community (a set of species that live together over a large area and in the same biogeographic province, life zone, and habitat). Members of the biogeographic community often form core elements of the local assemblage (a set of species found at a local site). However, the local assemblage also includes a number of incidental species with centers of distribution in other biogeographic communities found in other biogeographic provinces, life zones, or habitats; hence, this assemblage is best described by site clustering. Because site clustering can describe the assemblage at a given site, this method is appropriate for defining altered sites and ecotone areas (i.e., where different species assemblages overlap).

Species clusters define species groups based upon similar abundance patterns among species, whereas recurrent groups describe species that simply occur together. Species abundance patterns can be influenced by food availability, and if this occurs, species that cluster together may feed in a similar manner. Recurrent groups may consist of co-occurring species with different abundance patterns and feeding habits (Allen 1982). Species clusters may differ from recurrent groups if the abundance patterns of species that occur together differ.

In general, the megabenthic invertebrate assemblages are dominated by echinoderms (mostly urchins, sea stars, and brittlestars) and decapod crustaceans (mostly shrimp), with different species occurring in different assemblages. No matter what analytical method is used, the megabenthic invertebrate assemblage studies that have been conducted to date for the SCB converge on each other where study areas overlap, and complement each other where they do not. Combining the results of this study with those of the two previous studies (Thompson *et al*. 1993, Allen and Moore 1997) provides the following overview of the megabenthic invertebrate assemblages. In the mainland shelf, there are inner (10-

25 m), middle (25-90 m), and outer (90-300 m) shelf assemblages, with ecotone assemblages where species comprising these assemblages overlap in depth range (Figure 2, Tables 2 and 3) (Thompson *et al*. 1993, Allen and Moore 1997). The historical study indicates that the outer shelf assemblage extends deeper (to 300 m, Thompson *et al*. 1993) than the 200 m depth limit of the 1994 survey (Allen and Moore 1997, present study). Historically, the inner shelf assemblage changed in species composition following the 1981-1983 El Niño period (due to oceanic warming); inner and mainland shelf assemblages changed on the Palos Verdes Shelf after 1979 (due to reduced discharges of contaminants in the area) (Thompson *et al*. 1993). Below the shelf assemblages are mid-slope (300-500 m, mesobenthal zone in Allen and Smith 1988), and lower slope (500-750 m) and basins (750-900 m) (both within the bathybenthal zone, which extends from 500 to 1,000 m; Allen and Smith 1988). With minor differences, these assemblages correspond to characteristic life zones of mainland shelf and slopes of the northeastern Pacific (Allen and Smith 1988).

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