



Relationship Between Depth, Latitude and Sediment and the Structure of Benthic Infaunal Assemblages on the Mainland Shelf of Southern California

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ABSTRACT

Understanding the distribution of biological populations along habitat gradients is a necessary component of defining reference conditions for ecological assessments. Data from a regional benthic survey conducted in 1994 were used to define the relative role of three habitat factors (depth, sediment grain size, and latitude) in structuring the distribution of benthic infaunal assemblages on the southern California coastal shelf. Benthic samples were collected with a 0.1 m² Van Veen grab from 251 sites on the continental shelf (10 to 200 m deep) from Point Conception, California, to the United States-Mexico international border. The relationship between habitat and assemblages was investigated by conducting Q-mode cluster analysis to define groups of stations with similar species composition and then examining whether differences were present in physical habitat attributes among those groups of stations. The analysis yielded four habitat-related benthic infaunal assemblages along the southern Califor-

nia coastal shelf: a shallow-water assemblage from 10-32 m, a mid-depth assemblage between 32-115 m, and two deep-water (115-200 m) assemblages, one in fine and one in coarse sediments. Within the 500 km of coastline examined, latitude was not an important factor in defining assemblages.

INTRODUCTION

Biological populations are typically distributed along habitat gradients in a complex set of continuums that often lead to zonation of communities. Classification of communities along gradients had its early roots in plant ecology, where moisture and elevation gradients were found to organize forest communities (Orloci 1975, Whittaker 1978). Gradient analysis and community classification were later extended to marine communities, where depth and sediment type have been found to serve as aquatic analogs to elevation and soil moisture (Boesch 1973, 1977; Smith *et al.* 1988).

More recently, the study of zonation along habitat gradients has taken on an applied significance as biocriteria have become a central focus of ecological assessments (Jackson and Davis 1994). Biocriteria require definition of reference condition, which typically varies as a function of habitat (Weisberg *et al.* 1997, Van Dolah *et al.* in press). Determining which habitat factors are most important in organizing biological assemblages, and which thresholds along the defined gradients represent natural breaks in biological assemblages, are necessary components of defining reference conditions (Hughes *et al.* 1986).

In southern California, most benthic sampling is stratified by depth (Thompson *et al.* 1987, Thompson and Jones 1987, Thompson *et al.* 1993, Zmarzly *et al.* 1994, Diener *et al.* 1995, Dorsey *et al.* 1995, Stull 1995) because of its perceived importance in determin-

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ing the structure of benthic infaunal assemblages. Available data support this assumption. Qualitative descriptions of assemblages based upon large dominant organisms collected in a regional survey in the late 1950s (Allan Hancock Foundation 1959, 1965) indicated that the assemblages were separated by depth, sediment grain size, and geography (Barnard and Hartman 1959, Barnard and Zieshenne 1960). Recurrent group analysis by Jones (1964, 1969) also suggested that depth and sediment grain size are important factors. Analysis of data collected between 1975 and 1978 from 11 mainland shelf areas between Point Conception and San Diego (Fauchald and Jones 1978, 1979a, 1979b) supported earlier findings. These studies, while not designed to assess the relationship between physical factors and the structure of assemblages, provide important information about the structure of benthic assemblages and serve as a benchmark for conditions in southern California 20 to 40 years ago. More recent studies have been conducted over more limited geographic areas, often within a limited depth range (Smith *et al.* 1988, Zmarzly *et al.* 1994, Dorsey *et al.* 1995, Diener *et al.* 1995). Here we present the analysis from a regional benthic survey conducted in 1994 with the goal of defining the relative role of three habitat factors in structuring the distribution of benthic infaunal assemblages on the southern California coastal shelf.

METHODS

Between July 13 and August 22, 1994, benthic samples were collected from 251 sites on the continental shelf (10 to 200 m deep) from Point Conception, California, to the United States-Mexico international border. Sites were selected randomly, stratified by depth zone (inner shelf from 10-25 m, middle shelf from 26-100 m, and outer shelf from 101-200 m). Details of site selection are described in Bergen (1996) and Stevens (1997).

Samples were collected with a 0.1 m² Van Veen grab. Only samples with a penetration depth of at least 5 cm and no evidence of disturbance (i.e., by washing) were accepted for processing. Sediment for infaunal analysis was sieved through a 1-mm mesh screen. The residue was placed in a relaxant solution of 1 kg of MgSO₄ per 20 L of seawater for 30 min and then preserved[†] in 10% sodium borate buffered formalin. Samples were rinsed and transferred from formalin to 70% ethanol after approximately one week. Samples for total organic carbon (TOC), sediment grain size, trace metals, dichloro-diphenyl-trichloroethane (DDT), polychlorinated biphenyls (PCBs), and polycyclic

aromatic hydrocarbons (PAHs) were taken from the top 2 cm of a second grab sample.

Samples were sorted into six major taxonomic categories (annelids, arthropods, mollusks, ophiuroids, other echinoderms, and other phyla), and the wet weight of each group was measured. Specimens were then identified to the lowest practicable taxon, using nomenclature presented in SCAMIT (1994), and enumerated.

The relationship between habitat and assemblages was investigated by conducting Q-mode cluster analysis on infaunal data to define groups of stations with similar species composition and then examining any differences in physical habitat attributes among those groups of stations. Three physical habitat attributes were examined: depth, percent fines in the sediment (<63 μ), and latitude.

Cluster analysis was conducted using flexible sorting of Bray-Curtis dissimilarity values, with $b = -0.25$ (Bray and Curtis, 1957, Lance and Williams 1967, Clifford and Stephenson 1975). Data were square-root transformed and standardized by the species mean of abundance values higher than zero (Smith 1976, Smith *et al.* 1988). The step-across distance re-estimation procedure (Williamson 1978, Bradfield and Kenkel 1987) was applied to dissimilarity values higher than 0.80. Prior to cluster analysis, species occurring at fewer than 15 sites were eliminated, except when total abundance of the species was ≥ 50 individuals. Since the objective was to define natural groupings of stations with similar species composition, potentially contaminated sites were eliminated from the analysis. A site was considered potentially contaminated if: (1) three or more chemicals exceeded Long *et al.* (1995) effects range low (ERL) values, (2) one or more chemicals exceeded Long *et al.* (1995) effects range median (ERM) values, and/or (3) TOC was greater than 2% or the sample was in designated discharge areas surrounding stormwater/municipal wastewater outfalls or was in Santa Monica Bay (Bergen 1996). After these exclusions, 175 stations remained for analysis (Figure 1).

The number of habitat-defined assemblages was determined by sequentially examining each split of the cluster analysis dendrogram, starting at the top, to assess whether each split reflected habitat differentiation. Habitat differentiation was defined as: (1) a significant (Mann-Whitney U-test) difference in any of three habitat variables (depth, latitude, percent fines) between the two groupings defined by the dendrogram split, and (2) segregation of more than 95% of the sites in the split according to the significant habitat variable. When more than one habitat variable was significant in the U-test,

FIGURE 1. Map of sample sites used in the cluster analysis.

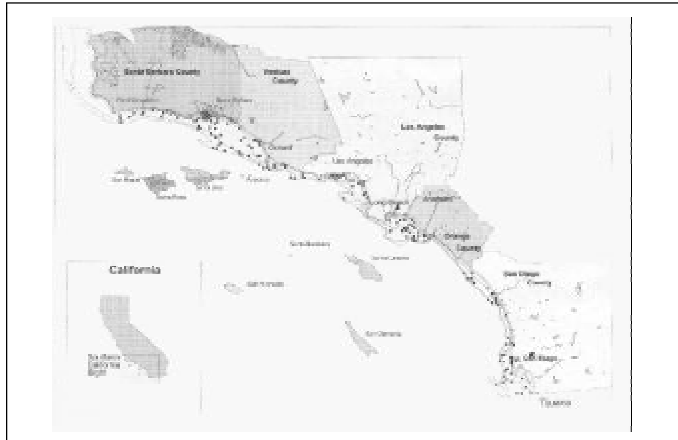
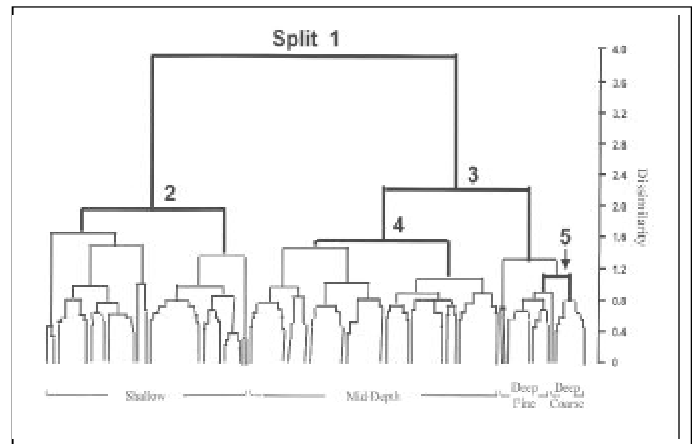


FIGURE 2. Dendrogram illustrating the primary station groups identified in the cluster analysis.



the habitat segregation test was applied using a habitat definition comprised of multiple variables. This testing procedure was conducted down each branch of the dendrogram until a split yielded no significant difference in habitat or until a split contained fewer than 10 sites.

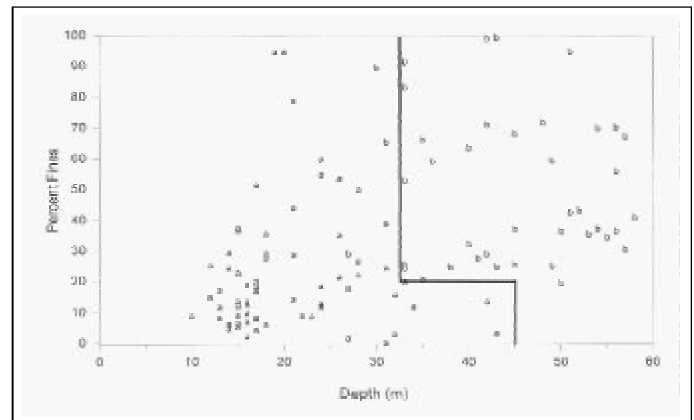
RESULTS

Sequential analysis of the dendrogram splits yielded four habitat-related benthic infaunal assemblages along the southern California coastal shelf (Figure 2). The first split was primarily associated with depth; 96% of the sites separated along the 32 m depth contour (Figure 3, Tables 1 and 2). Percent fines differed significantly between the two station groups (Table 1), but primarily as a modifier of the depth variable. Between 32 and 45 m, all sandy (<20% fines) sites had an infaunal composition consistent with the shallow group, whereas all sites with more than 20% fines had an infaunal composition consistent with deeper sites (Figure 3). Presumably, the shallow water biota can extend into deeper waters under high-energy conditions.

Additional splits of the shallow station group did not yield consistent habitat differentiation, but the deeper group split based upon depth, with 96% of the sites segregating at 115 m (Table 1). Grain size was not significant in this split, although all of the muddy sites between 87 and 115 m had biological characteristics of the deeper group (Figure 4).

The 35-115 m group did not split further, but 96% of the deeper group segregated based upon a grain size threshold of 45% fines (Figure 5). This was the first

FIGURE 3. Distribution of cluster groups from dendrogram split 1 relative to depth and sediment type. All stations deeper than 60 m were from the “b” side of the split.



dendrogram split for which depth was not a significant factor. Sample size was too small to investigate additional dendrogram splits beyond the grain size separation.

Biological Characterization

Fauna found in the shallow habitat was the most distinctive. Nearly 70% of the common and abundant species (i.e., those occurring in more than 60% of the samples with average abundance greater than 20/m²) were common and abundant only in the shallow habitat (Table 3). These species were found in other habitats, but were relatively rare (Table 4). Of the remaining species, all except one were common and abundant in all habitats.

The two most abundant distinctive species in the shallow assemblage were the amphipod *Amphideutopus oculus*

TABLE 1. Range of values for depth, percent fines and latitude for stations in each division of the cluster dendrogram. Bolded pairs indicate significant difference in mean.

Cluster Split	Range			N
	Depth (m)	Fines (%)	Latitude	
1a	10 - 43	0.0 - 94.7	32.54 - 34.44	66
1b	27 - 219	0.0 - 99.3	32.60 - 34.46	109
2a	10 - 43	0.0 - 37.3	32.54 - 34.44	32
2b	12 - 42	8.8 - 94.7	32.59 - 34.40	34
3a	27 - 112	12.6 - 99.3	32.54 - 34.44	81
3b	84 - 219	0.0 - 83.4	32.62 - 34.46	28
4a	27 - 78	12.6 - 99.3	32.89 - 34.46	43
4b	50 - 112	23.7 - 70.2	32.62 - 34.44	38
5a	120 - 208	11.6 - 38.8	33.99 - 34.38	10
5b	87 - 219	47.4 - 98.4	32.62 - 34.33	16

TABLE 2. Percent of stations correctly classified by each of the habitat parameters for each split in the dendrogram. Parameters which were used in the combined factors are shown in bold.

Cluster Split	Percent			
	Depth	Fines	Latitude	Combined Factors
1	96.0	81.1	62.3	98.3
2	81.8	77.3	63.6	90.9
3	96.3	77.1	74.3	
4	86.4	63.0	70.4	88.9
5	61.5	96.2	76.9	

Figure 4. Distribution of cluster groups from dendrogram split 3 relative to depth and sediment type.

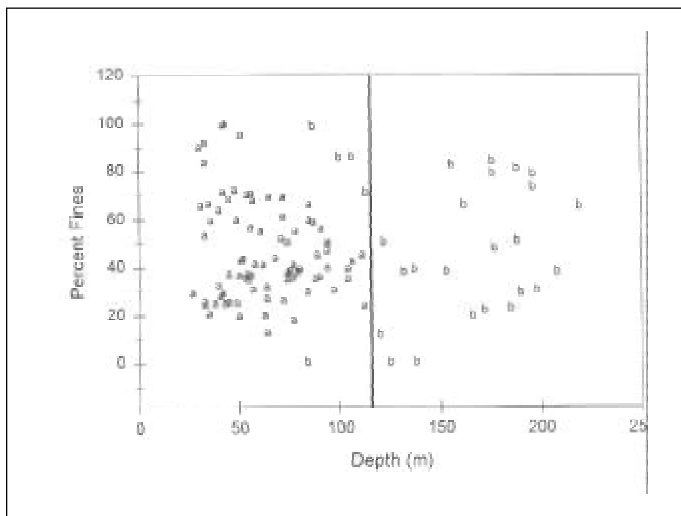


Figure 5. Distribution of cluster groups from dendrogram split 5 relative to depth and sediment type.

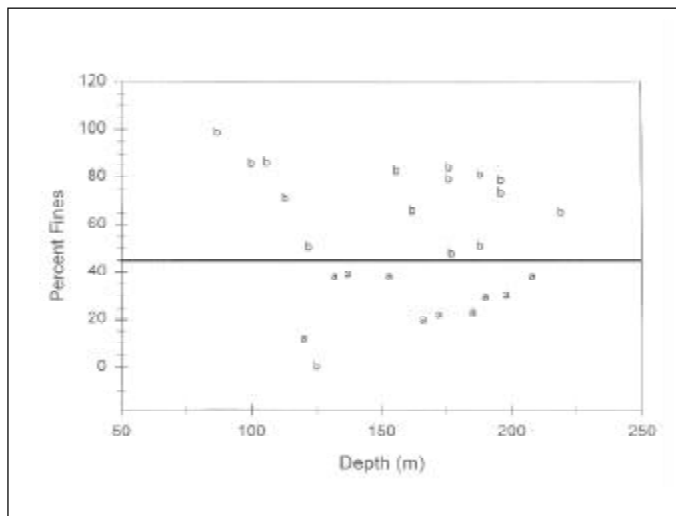


TABLE 3. Average abundance of species with frequency of occurrence greater than 60% and average abundance of at least 20 / m² in each cluster group. AI values are area weighted.

Species	Taxonomic Group	Average Abundance (Number / m ²) Cluster Group				
		1		2	3	4
		Deep	Coarse	Deep Fine	Mid-depth	Shallow
<i>Spiophanes missionensis</i>	Annelida	386.0		195.0	563.2	132.2
<i>Amphiodia digitata</i>	Ophiuroidea	236.0				
<i>Euphilomedes producta</i>	Arthropoda	215.0				
<i>Mediomastus</i> spp.	Annelida	168.0		71.6	117.8	76.2
<i>Chloeia pinnata</i>	Annelida	100.0				
<i>Amphiodia urtica</i>	Ophiuroidea	83.0		263.2	422.0	
<i>Spiophanes fimbriata</i>	Annelida	82.0		149.7		
<i>Ampelisca careyi</i>	Arthropoda	69.0		21.0		
<i>Photis lacia</i>	Arthropoda	69.0				
<i>Rhepoxynius bicuspidatus</i>	Arthropoda	59.0			43.0	
Maldanidae*	Annelida	51.0		91.5	105.0	127.9
<i>Pectinaria californiensis</i>	Annelida	50.0		91.1	85.3	
<i>Eudorella pacifica</i>	Arthropoda	35.0				
<i>Lumbrineris</i> spp.	Annelida	35.0		94.0	50.8	57.5
<i>Paraprionospio pinnata</i>	Annelida	33.0		47.8	45.4	108.9
<i>Euclymeninae</i> sp. A	Annelida	31.0			28.2	
<i>Decamastus gracilis</i>	Annelida	21.0				
<i>Terebellides californica</i>	Annelida			23.0	20.2	
<i>Maldane sarsi</i>	Annelida			34.0		
<i>Levinsenia</i> spp.	Annelida			30.3		
<i>Cossura</i> spp.	Annelida			26.9		
<i>Laonice appelloefi</i>	Annelida			21.8		
<i>Sthenelanelia uniformis</i>	Annelida				84.2	
<i>Phoronis</i> sp.	Phoronida				77.9	
<i>Prionospio</i> sp. A	Annelida				76.4	
<i>Ampelisca brevisimulata</i>	Arthropoda				50.2	31.6
<i>Euphilomedes carcharodonta</i>	Arthropoda				47.5	
<i>Paramage scutata</i>	Annelida				46.4	
<i>Parvilucina tenuisculpta</i>	Mollusca				44.0	
<i>Leptocheilia dubia</i>	Arthropoda				42.3	
<i>Heterophoxus oculatus</i>	Arthropoda				37.6	
<i>Pholoe glabra</i>	Annelida				28.0	
<i>Glycera nana</i>	Annelida				26.7	
<i>Tellina carpenteri</i>	Mollusca				24.4	
<i>Gnathia crenulatifrons</i>	Arthropoda				24.2	
<i>Tubulanus polymorphus</i>	Nemertea				23.2	
<i>Ampelisca pugetica</i>	Arthropoda				22.2	
<i>Amphideutopus oculatus</i>	Arthropoda					132.9
<i>Glottidia albida</i>	Brachiopoda					90.3
<i>Spiophanes bombyx</i>	Annelida					82.6
<i>Ampelisca cristata</i>	Arthropoda					65.1
<i>Macoma yoldiformis</i>	Mollusca					54.8
<i>Tellina modesta</i>	Mollusca					50.8
<i>Apoprionospio pygmaea</i>	Annelida					50.0
<i>Owenia collaris</i>	Annelida					44.7
<i>Amphicteis scaphobranchiata</i>	Annelida					24.8
<i>Carinoma mutabilis</i>	Nemertea					24.3
<i>Ampharete labrops</i>	Annelida					23.4
<i>Rhepoxynius menziesi</i>	Arthropoda					22.2
Lineidae	Nemertea					20.3

* All Maldanids except 11 identified species

TABLE 4. Frequency of occurrence and range of abundance (number / m2, excluding 0's) of all species in Table 3.

Species	Group 1		Group 2		Group 3		Group 4	
	Frequency Range		Frequency Range		Frequency Range		Frequency Range	
	(Percent)	(Number/m2)	(Percent)	(Number/m2)	(Percent)	(Number/m2)	(Percent)	(Number/m2)
<i>Spiophanes missionensis</i>	100.0	20 - 2210	87.5	10 - 790	100.0	20 - 2470	87.9	10 - 910
<i>Amphiodia digitata</i>	100.0	70 - 470	25.0	20 - 70	50.6	10 - 480	21.2	10 - 140
<i>Euphilomedes producta</i>	90.0	20 - 950	43.8	10 - 20	39.5	10 - 1070	1.5	30
<i>Mediomastus</i> spp.	100.0	10 - 670	68.8	10 - 330	76.5	10 - 1680	62.1	10 - 1110
<i>Chloea pinnata</i>	90.0	10 - 290	62.5	10 - 60	48.1	10 - 650	6.1	10 - 270
<i>Amphiodia urtica</i>	70.0	20 - 350	81.3	20 - 820	96.3	10 - 1420	16.7	10 - 500
<i>Spiophanes fimbriata</i>	90.0	10 - 280	87.5	10 - 420	40.7	10 - 280	1.5	10
<i>Ampelisca careyi</i>	100.0	10 - 310	87.5	10 - 60	67.9	10 - 140	4.5	10
<i>Photis lacia</i>	70.0	10 - 310	-	-	19.8	10 - 180	1.5	10
<i>Rhepoxynius bicuspidatus</i>	80.0	20 - 200	12.5	10 - 30	65.4	10 - 230	4.5	10 - 30
Maldanidae	80.0	20 - 180	93.8	10 - 270	86.4	10 - 570	69.7	10 - 680
<i>Pectinaria californiensis</i>	80.0	10 - 160	100.0	10 - 490	92.6	10 - 490	37.9	10 - 170
<i>Eudorella pacifica</i>	100.0	10 - 60	56.3	10 - 50	37.0	10 - 90	-	-
<i>Lumbrineris</i> spp.	90.0	20 - 60	93.8	20 - 190	79.0	10 - 260	71.2	10 - 210
<i>Paraprionospio pinnata</i>	80.0	10 - 100	100.0	10 - 260	85.2	10 - 270	86.4	10 - 410
<i>Euclymeninae</i> sp. A	70.0	10 - 100	37.5	10 - 50	67.9	10 - 180	31.8	10 - 120
<i>Decamastus gracilis</i>	100.0	10 - 50	25.0	10 - 170	13.6	10 - 20	-	-
<i>Terebellides californica</i>	30.0	10 - 30	75.0	10 - 160	71.6	10 - 80	12.1	10 - 20
<i>Levinsenia</i> spp.	40.0	10	68.8	10 - 110	48.1	10 - 170	6.1	10 - 60
<i>Cossura</i> spp.	20.0	10	68.8	10 - 90	56.8	10 - 570	22.7	10 - 2470
<i>Maldane sarsi</i>	20.0	10	62.5	10 - 130	33.3	10 - 80	-	-
<i>Laonice appelloefi</i>	50.0	10 - 40	62.5	10 - 130	22.2	10 - 60	-	-
<i>Sthenelanelia uniformis</i>	10.0	10	-	-	77.8	10 - 790	33.3	10 - 130
<i>Phoronis</i> sp.	-	-	12.5	10	85.2	10 - 550	59.1	10 - 240
<i>Prionospio</i> sp. A	40.0	30 - 140	68.8	10 - 100	90.1	10 - 340	31.8	10 - 260
<i>Ampelisca brevisimulata</i>	20.0	20 - 60	12.5	10 - 50	88.9	10 - 240	65.2	10 - 110
<i>Euphilomedes carcharodonta</i>	30.0	10 - 590	6.2	10	60.5	10 - 610	50.0	10 - 140
<i>Paramage scutata</i>	10.0	10	18.8	10 - 20	66.7	10 - 260	1.5	10
<i>Parvilucina tenuisculpta</i>	60.0	10 - 130	62.5	10 - 70	69.1	10 - 680	37.9	10 - 170
<i>Leptocheilia dubia</i>	30.0	40 - 80	-	-	64.2	10 - 200	50.0	10 - 330
<i>Heterophoxus oculus</i>	20.0	10	25.0	10 - 90	66.7	10 - 180	3.0	30 - 50
<i>Pholoe glabra</i>	60.0	10 - 40	50.0	10 - 70	65.4	10 - 130	-	-
<i>Glycera nana</i>	70.0	10 - 30	75.0	10 - 60	74.1	10 - 160	7.6	10 - 40
<i>Tellina carpenteri</i>	10.0	10	43.8	10 - 100	60.5	10 - 160	16.7	10 - 100
<i>Gnathia crenulatifrons</i>	50.0	10 - 140	50.0	10 - 60	71.6	10 - 130	22.7	10 - 190
<i>Tubulanus polymorphus</i>	-	-	43.8	10 - 40	65.4	10 - 120	56.1	10 - 260
<i>Ampelisca pugetica</i>	20.0	10 - 30	12.5	10	72.8	10 - 130	22.7	10 - 50
<i>Spiophanes bombyx</i>	10.0	20	-	-	11.1	10 - 60	78.8	10 - 1700
<i>Tellina modesta</i>	10.0	10	12.5	10	2.5	20 - 30	75.8	10 - 350
<i>Glottidia albida</i>	10.0	10	-	-	46.9	10 - 620	74.2	10 - 390
<i>Ampelisca cristata</i>	-	-	-	-	17.3	10 - 60	69.7	10 - 300
<i>Apoprionospio pygmaea</i>	-	-	6.2	10	4.9	10 - 50	69.7	10 - 430
<i>Owenia collaris</i>	10.0	10	-	-	22.2	10 - 100	69.7	10 - 460
<i>Ampharete labrops</i>	10.0	10	-	-	2.5	10 - 40	69.7	10 - 200
<i>Amphideutopus oculus</i>	-	-	12.5	10 - 20	55.6	10 - 280	68.2	10 - 630
Lineidae	40.0	10 - 20	43.8	10 - 30	66.7	10 - 120	66.7	10 - 70
<i>Macoma yoldiformis</i>	-	-	6.3	10	13.6	10 - 140	63.6	10 - 510
<i>Carinoma mutabilis</i>	20.0	10 - 40	18.8	10	44.4	10 - 70	62.1	10 - 170
<i>Rhepoxynius menziesi</i>	-	-	-	-	19.8	10 - 90	62.1	10 - 110
<i>Amphicteis scaphobranchiata</i>	10.0	10	12.5	20	19.8	10 - 40	60.6	10 - 110

and the polychaete *Spiophanes bombyx* (Table 3). The brachiopod *Glottidia albida*, the amphipod *Ampelisca cristata*, and the bivalve mollusk *Tellina modesta* were also characteristic of shallow habitats.

Fifty-six percent of the species in the mid-depth assemblage were distinctive (Table 3). The most abundant were the polychaete *Sthenelanelia uniformis* and phoronids in the genus *Phoronis*. The polychaetes *Sthenelanelia uniformis* and *Paramage scutata*, and the ostracod *Euphilomedes carcharodonta*, were also common. Of the remaining species, five were universal, two were shared with both deep habitats, two were shared with the deep coarse habitat, and one was shared with the deep fine habitat.

Twenty-nine and 35% of the species in the deep fine and deep coarse habitats, respectively, were distinctive (Table 3). In the deep fine sediment assemblage, four species were distinctive: the polychaetes *Levinsenia* spp., *Maldane sarsi*, *Cossura* spp. and *Laonice appelloefi* (Table 3). In the deep coarse sediment assemblage, six species were distinctive: the brittlestar *Amphiodia digitata*, the ostracod *Euphilomedes producta*, the polychaete *Decamastus gracilis*, the amphipod *Photis lacia*, and the cumacean *Eudorella pacifica*.

Of the remaining species, two (the polychaete *Spiophanes fimbriata* and the amphipod *Ampelisca careyi*) were common in deep habitats, regardless of sediment type. The ophiuroid *Amphiodia urtica* was common in both mid-depth and deep habitats. The arthropod *Rhepoxynius bicuspidatus* and the polychaete *Euclymeninae* sp. A were common in deep coarse and mid-depth sediment, but not in deep fine sediment.

The number of taxa and total abundance of organisms were lowest in the shallow habitat and highest in the mid-depth habitat (Table 5). Annelids comprised from 40 to 60% of the abundance in all habitats. Arthropods comprised 10 and 30% of the abundance in deep fine sediment and deep coarse sediment habitats, respectively, and 18 to 20% of the abundance in mid-depth and shallow habitats. Ophiuroids comprised 15 to 18% of the abundance in all habitats except the shallow habitat, where they were only 1% of the abundance. Conversely, mollusks were 7 to 10% of the abundance in shallow and mid-depth habitats and less than 2% of the abundance in deep habitats.

DISCUSSION

Our finding that depth is the primary habitat factor organizing southern California benthic communities is consistent with other studies of marine infaunal distribu-

tion (Hyland *et al.* 1991, Rackocinski *et al.* 1993, 1998, Oug 1998), although salinity has been found to be a more important factor in estuarine environments (Boesch 1973, Shin and Thompson 1982, Weisberg *et al.* 1997). Many early infaunal studies (Snelgrove and Butman 1994) have suggested that sediment type is a primary habitat factor organizing benthic communities, whereas we found it to be a secondary factor. This finding may, in part, be attributable to our larger study area; within a constrained depth gradient, sediment type may be a more important factor.

The size of our study area probably had an effect on our finding that latitude was not a significant factor affecting infaunal assemblage distributions. While our study area is large, stretching over 500 km of coastline, it is contained within a geographic area referred to as the Southern California Bight (SCB). The SCB is a transitional area influenced by the California Current, which brings cold, temperate ocean waters from the north, and the Davidson Counter-current, which brings warm, tropical waters from the south. These currents form an eddy that produces a single and unique biogeographic zone (Hickey 1993). If our study area had extended north of Point Conception, outside the reach of the warmer counter-current, the effect of latitude may have been more pronounced, as has been demonstrated in studies conducted in other areas of the country (Van Dolah *et al.* in press).

Descriptions of southern California benthic assemblages based upon surveys conducted between 1956 and 1961 by the Allan Hancock Foundation (Barnard and Hartman 1959; Barnard and Ziesenhenné 1960; Jones 1964, 1969) produced similar findings. First, these investigators found that differences in assemblages were related primarily to depth, with sediment grain size as a secondary factor. Both the Hancock surveys and our study defined shallow, mid-depth, and deep shelf assemblages, with breaks between assemblages occurring at approximately the same depth. The lower limit of the shallow assemblage was 30 m in the Hancock surveys and 32 m (depending upon the sediment type) in our study. The lower limit of the mid-depth assemblage was 92 m in the Hancock surveys and 115 m in our study, although we did find extensions as shallow as 80 m depending upon sediment grain size. Species composition in the primary shallow (*Nothria-Tellina*) and mid-depth assemblages (*Amphiodia urtica*) were also similar between studies (Tables 6 and 7, respectively).

The Hancock surveys identified several additional assemblages that were not identified in our study (Table 8). The fact that we did not find these assemblages may

TABLE 5. Community characteristics of the four cluster groups. All values are ara weighted. CI = Confidence interval.

Characteristic	Cluster Group							
	1		2		3		4	
	Mean	(95% CI)	Mean	(95% CI)	Mean	(95% CI)	Mean	(95% CI)
Number of taxa / sample	86.6	24.0	61.6	7.0	101.0	6.6	75.9	7.9
Shannon-Wiener Diversity Index (H')	3.6	0.2	3.4	0.2	3.7	0.1	3.6	0.1
Dominance	0.1	0.0	0.1	0.0	0.1	0.0	0.1	0.0
Evenness	0.4	0.0	0.4	0.0	0.5	0.0	0.5	0.0
Total abundance / m2	4005.0	1727.4	2329.8	539.2	4908.2	464.0	3121.5	597.8
Percent abundance as:								
Annelida	41.8	6.6	63.6	8.2	50.0	2.9	51.0	3.5
Arthropoda	33.3	6.3	10.4	3.1	18.1	1.8	20.9	3.4
Ophiuroidea	16.8	4.1	15.7	15.7	17.1	2.6	1.9	0.7
Misc. Echinodermata	1.0	0.4	1.1	1.2	0.5	0.1	0.9	0.3
Mollusca	4.1	1.5	5.7	1.9	6.9	1.0	14.6	2.7
Other phyla	2.2	1.0	3.2	2.0	7.2	1.2	10.6	1.5
Total biomass (gms wet weight / m ²)	41.0	15.3	44.3	10.6	79.4	12.2	35.9	8.6
Percent biomass as:								
Annelida	28.5	7.3	44.6	9.7	30.9	3.8	34.8	4.4
Arthropoda	8.1	4.7	3.0	0.8	3.9	0.5	10.6	1.8
Ophiuroidea	43.2	8.2	34.0	0.8	41.1	5.2	8.0	2.6
Misc. Echinodermata	9.1	6.0	1.4	1.1	4.3	1.8	5.3	1.8
Mollusca	7.8	3.7	12.8	6.8	6.9	1.5	31.5	5.0
Other phyla	3.4	1.6	3.6	1.2	12.9	3.6	9.8	2.5

TABLE 6. Comparison of common species in Nothria-Tellina assemblage and shallow depth (cluster group 4).

Old Species Name	Current Name	Percent Occurrence	
		Nothria-Tellina Assemblage	Cluster Group 4 Shallow
<i>Chaetozone</i> spp.	<i>Chaetozone corona</i> , <i>C. setosa</i>	98.2*	71.2
<i>Amphiodia urtica</i>	<i>Amphiodia urtica</i>	98.2	45.4
<i>Prionospio pinnata</i>	<i>Paraprionospio pinnata</i>	96.4*	86.4
<i>Lumbrineris</i> spp.	<i>Lumbrineris</i> spp.	96.4	71.2
<i>Haploscoloplos elongatus</i>	<i>Leitoscoloplos elongatus</i>	92.7*	34.8
<i>Prionospio malmgreni</i>	<i>Prionospio</i> Sp. A and B (SCAMIT), <i>Apoprionospio pygmaea</i>	90.9*	80.3
<i>Tellina buttoni</i>	<i>Tellina modesta</i>	89.1	75.8
<i>Ampelisca cristata</i>	<i>Ampelisca cristata</i>	80.0	69.7
<i>Goniada</i> spp.	<i>Goniada brunnea</i> , <i>G. maculata</i>	80.0*	27.3
<i>Paraphoxus epistomus</i>	<i>Rhepoxynius menziesi</i>	74.6	62.1
<i>Nuculana taphria</i>	<i>Nuculana taphria</i>	74.6	36.4
<i>Nereis procera</i>	<i>Nereis procera</i>	72.7	48.5
<i>Spiophanes missionensis</i>	<i>Spiophanes missionensis</i>	70.9	87.9
<i>Nephtys</i> spp.	<i>Nephtys caecoides</i> , <i>N. cornuta franciscana</i> , <i>N. feruuginea</i>	70.9*	72.7
<i>Thalanesa spinosia</i>	<i>Sigalion spinosa</i>	70.9*	60.6
<i>Argissa hamatipes</i>	<i>Argissa hamatipes</i>	70.9	28.8
<i>Turbonilla</i> sp.	<i>Turbonilla</i> sp.	67.3	47.0
<i>Cadulus</i> sp.	<i>Gadila</i> sp.	67.3	0.0
<i>Nothria elegans and iridescens</i>	<i>Onuphis elegans, iridescens and Sp. 1 (SCAMIT)</i>	66.7*	59.1
<i>Tharyx tessellata</i>	<i>Monticellina</i> spp., <i>Aphelochaeta</i> spp.	65.5	59.1
<i>Glottidia albida</i>	<i>Glottidia albida</i>	63.6*	74.2
<i>Mediomastus californiensis</i>	<i>Mediomastus</i> spp.	61.8	63.6
<i>Olivella baetica</i>	<i>Olivella baetica</i>	60.0	34.8
<i>Diastylopsis tenuis</i>	<i>Diastylopsis tenuis</i>	60.0*	22.7
<i>Spiophanes bombyx</i>	<i>Spiophanes bombyx</i>	58.2	78.8
<i>Amphicteis scaphobranchiata</i>	<i>Amphicteis scaphobranchiata</i>	43.6	60.6
<i>Amphideutopus oculatus</i>	<i>Amphideutopus oculatus</i>	40.0	68.2
<i>Owenia collaris</i>	<i>Owenia collaris</i>	20.0	69.7
<i>Ampharete labrops</i>	<i>Ampharete labrops</i>	0.0	69.7

TABLE 7. Comparison of commo species in the *Amphiodia urtica* assemblage and mid-depth (cluster group 3).

Old Species Name	Current Name	Percent Occurrence	
		<i>Amphiodia urtica</i> Assemblage	Cluster Group 3 Mid-Depth
<i>Amphiodia urtica</i>	<i>Amphiodia urtica</i>	100.00*	96.3
<i>Pectinaria californiensis</i>	<i>Pectinaria californiensis</i>	98.15*	92.6
<i>Pholoe glabra</i>	<i>Pholoe glabra</i>	94.44	65.4
<i>Paraphoxus bicuspidatus</i>	<i>Rhepoxynius bicuspidatus</i>	92.59	65.4
<i>Heterophoxus oculatus</i>	<i>Heterophoxus oculatus</i>	90.74	66.7
<i>Paraphoxus similis</i>	<i>Foxiphalus similis</i>	88.89	37.0
<i>Ampelisca brevisimulata</i>	<i>Ampelisca brevisimulata</i>	87.04	88.9
<i>Prionospio pinnata</i>	<i>Paraprionospio pinnata</i>	87.04	85.2
<i>Axinopsis serricatus</i>	<i>Axinopsida serricata</i>	85.19*	55.6
<i>Prionospio malmgreni</i>	<i>Prionospio</i> Sp. A and B (SCAMIT), <i>Apoprionospio pygmaea</i>	85.19	90.1
<i>Paraonis gracilis</i>	<i>Levinsenia</i> spp.	85.19	48.1
<i>Ampelisca pacifica</i>	<i>Ampelisca pacifica</i>	85.19	64.2
<i>Terebellides stroemi</i>	<i>Terebellides californica</i> , <i>T. reishi</i> , <i>T. sp. Type C</i>	85.19	76.5
<i>Gnathia crenulatifrons</i>	<i>Gnathia crenulatifrons</i>	81.48	71.6
<i>Metaphoxus frequens</i>	<i>Metaphoxus frequens</i>	81.48	12.3
<i>Sternaspis fossor</i>	<i>Sternaspis fossor</i>	77.78*	58.0
<i>Glycera capitata</i>	<i>Glycera nana</i>	77.78*	74.1
<i>Lumbrineris cruzensis</i>	<i>Lumbrineris</i> spp.	74.07	79.0
<i>Goniada brunnea</i>	<i>Goniada brunnea</i> and <i>G. maculata</i>	70.37	60.5
<i>Haploscoloplos elongatus</i> (actually <i>H. pugettensis</i>)	<i>Leitoscoloplos pugettensis</i>	70.37	30.9
<i>Cossura candida</i>	<i>Cossura</i> spp.	68.52	56.8
<i>Leptosynapta albicans</i>	<i>Leptosynapta</i> spp.	68.52	23.5
<i>Haliophasma geminata</i>	<i>Haliophasma geminatum</i>	66.67	34.6
<i>Aruga oculata</i>	<i>Aruga oculata</i>	64.81	8.6
<i>Nephtys furruginea</i>	<i>Nephtys furruginea</i>	62.96	45.7
<i>Ampelisca pugetica</i>	<i>Ampelisca pugetica</i>	62.96	72.8
<i>Oxydromus arenicolus</i>	<i>Podarkeopsis</i> Sp. A, <i>P. glabra</i>	61.11	28.4
<i>Spiophanes missionensis</i>	<i>Spiophanes missionensis</i>	59.30	100.0
<i>Mediomastus californiensis</i> , <i>Capitita ambiseta</i>	<i>Mediomastus</i> spp.	53.70	76.5
<i>Axiothella rubrocincta</i> , <i>Euclymene</i> spp.	<i>Euclymeninae</i> Sp. A	66.70	67.9
<i>Sthenelanellella uniformis</i>	<i>Sthenelanellella uniformis</i>	57.40	77.8
<i>Brown ostracod</i>	<i>Euphilomedes carcarodonta</i>	24.10	60.5
<i>Parvilucina tenuisculpta</i>	<i>Parvilucina tenuisculpta</i>	16.60	69.1
Unknown tanaid	<i>Leptocheilia dubia</i>	72.20	64.2
<i>Amage</i> spp.	<i>Parmage scutata</i>	9.10	66.7
<i>Tellina carpenteri</i>	<i>Tellina carpenteri</i>	38.90	60.5

TABLE 8. Benthic infaunal assemblages described in Barnard and Hartman (1959). Barnard and Ziesenhenné (1960), Jones (1964) and Jones (1969).

Association Name	Geographic Distribution	Depth Range	Sediment Type
<i>Prionospio malmgreni</i>	Southern California Bight	< 10 m	Sand
<i>Diopatra ornata</i>	Southern California Bight	< 30 m	Rock, gravel, shell
<i>Chaetopterus variopedatus</i> - <i>Lima dehiscens</i>	San Pedro Shelf	10-28 m	Black sand
<i>Nothria-Tellina</i>	Southern California Bight	10-35 m	Sand
<i>Amphipholus hexacanthus</i>	Patches San Pedro, Santa Monica, Oceanside	13-55 m	Fine sand
<i>Listriolobus pelodes</i>	Pt. Conception - Hueneme Canyon	30-60 m	Silt
<i>Amphiodia urtica</i> - <i>Cardita ventricosa</i>	Pt. Conception - Hueneme Canyon	55-92 m	Silty sand, sandy silt
<i>Amphiodia urtica</i>	Hueneme Canyon - Mexico	55-92 m	Silty sand, sandy silt
<i>Nothria stigmatis</i> - <i>Spiophanes bombyx</i>	Patches Santa Monica, San Pedro, Palos Verdes, San Diego	5-90 m	Red sand
<i>Pectinaria</i> - <i>Chloeia</i>	Southern California Bight	> 92 m	Sandy silt, silt

be attributable to differences in sampling methodology and/or the methods used to define the assemblages. The Hancock sampling was conducted using an orange peel grab, which samples large organisms (e.g., *Mooreonuphis* spp., *Brisaster latifrons*) that are not well sampled by the Van Veen grab used in our study. In addition, the earlier authors used large visual dominants to define the assemblages. In quantitative re-analysis of the earlier data, Jones (1969) concluded that use of dominant species to define assemblages is subjective and difficult to apply. Using recurrent group analysis, Jones determined that only two primary associations were present in the study area: the *Nothria-Tellina* and the *Amphiodia urtica*. The deep-water assemblage was considered a variant of the *Amphiodia urtica* assemblage and the other assemblages sediment subclimaxes. He discussed the theory that some dominant species, such as *Listriolobus pelodes*, may disappear if depositional patterns change. In fact, both *Listriolobus pelodes* and *Cyclocardia ventricosa* are now relatively rare. Thus, the fact that we did not find the *Listriolobus* or the *Cyclocardia-Amphiodia urtica* assemblages in our study may simply be attributable to the fact that these two species are now less common.

Thompson *et al.* (1993) also concluded that mid-depths on the mainland shelf contain a single assemblage, dominated by *Amphiodia urtica*. The assemblages identified in the Hancock surveys were considered temporal or spatial subassemblages of the *Amphiodia urtica* assemblage. Thompson also described an upper slope assemblage with many of the same species that are found in our deep fine sediment assemblages. While the assemblages are similar, Thompson found the transition between the two assemblages in 150-160 m rather than in 90-115 m of water.

The primary difference in the various survey results is that one deep-water assemblage was defined in the Hancock surveys and in Thompson *et al.* (1993); and two were defined in the present study, one in coarse sediment and one in fine sediment. The deep-water assemblage described in the Hancock surveys has elements of both deep-water assemblages described here. Apparently, the assemblages were not considered to be distinct by the investigator. Thompson *et al.* (1993) mention that assemblages in sandy sediment are different, but did not list a separate coarse-sediment assemblage. It is possible the difference may be due to sampling limitations; deep-water coarse sediment habitat is relatively rare and it is not clear how many samples were taken in deep-water coarse sediments in the earlier surveys.

While we found assemblages to be associated with depth and sediment grain size gradients, it is unlikely that either depth or sediment grain size is the real determinant of species distributions. Snelgrove and Butman (1994) have suggested that the hydrodynamic environment and the amount of organic material in the sediment are more likely to be primary driving forces, with depth and sediment grain size as secondary correlates. Our finding that the shallow assemblage is defined by a combination of depth and sediment type is consistent with the theory that hydrography is the controlling factor. Unfortunately, the hydrographic environment is difficult to measure, particularly when extreme events may be the controlling factor (Schimmelmann *et al.* 1992, Posey *et al.* 1996, Okey 1997), and the use of depth and sediment grain size as surrogates may be required. In any case, this study has provided empirically defined dividing points in the depth and sediment grain size gradients that can be used to define reference habitats.

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