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Mary Bergen · Stephen B. Weisberg · Robert W. Smith
Donald B. Cadien · Ann Dalkey · David E. Montagne
Janet K. Stull · Ronald G. Velarde
J. Ananda Ranasinghe

Relationship between depth, sediment, latitude, and the structure of benthic infaunal assemblages on the mainland shelf of southern California

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Abstract A regional benthic survey was conducted in 1994, and the data were used to assess the relationship among three habitat factors (depth, sediment grain size, and latitude) and 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 (10–200 m deep) from Point Conception, California, to the United States–Mexico international border. The relationship between habitat and assemblages was investigated by conducting a 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. Analysis of data from 175 uncontaminated sites yielded four habitat-related benthic infaunal assemblages along the southern California coastal shelf: a shallow-water assemblage from 10–32 m, a mid-depth assemblage between 32 and 115 m, and two deep-water (115–200 m)

assemblages, one in fine and one in coarse sediments. These empirically defined points in the depth and sediment grain size gradients can be used to define reference habitats for the development of biocriteria. Benthic abundance and diversity were greatest in the mid-depth assemblage, conforming to predictions for benthic assemblages in regions of upwelling. Within the 500 km of coastline examined, latitude was not an important factor in defining assemblages.

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M. Bergen · S. B. Weisberg · J. A. Ranasinghe (✉)
Southern California Coastal Water Research Project,
7171 Fenwick Lane, Westminster, CA 92683, USA

e-mail: anandar@sccwrp.org

Tel.: +1-714-3729218; Fax: +1-714-8949699

R. W. Smith
Ecoanalysis, P.O. Box 1537, Ojai, CA 93024, USA

D. B. Cadien · D. E. Montagne · J. K. Stull
Los Angeles County Sanitation Districts, P.O. Box 4998,
Whittier, CA 90607, USA

A. Dalkey
City of Los Angeles, Environmental Monitoring Division,
12000 Vista Del Mar, Playa Del Rey, CA 90293, USA

R. G. Velarde
City of San Diego, 4918 N. Harbor Drive, Suite 101,
San Diego, CA 92106, USA

Present address:

M. Bergen
P.O. Box 729, Ojai, CA 93024-0729, USA

Introduction

Biological populations are typically distributed along habitat gradients in a complex set of continuums that can lead to community zonation. 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 are biological criteria that are being introduced by the U.S. Environmental Protection Agency to supplement existing chemical and toxicity criteria in water quality standards (USEPA 1991). They require definition of reference condition, which typically varies as a function of habitat (Weisberg et al. 1997; Van Dolah et al. 1999). 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 and Jones 1987;

Thompson et al. 1987, 1993b; Zmarzly et al. 1994; Diener et al. 1995; Stull 1995) because of its perceived importance in determining 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 Ziesenhenné 1960). Recurrent group analysis by Jones (1964, 1969) also suggested that depth and sediment grain size were important factors. Analysis of data collected between 1975 and 1978 from 11 mainland shelf areas between Point Conception and San Diego (Fauchald and Jones 1979a, b, 1983) supported earlier findings. These studies provide important information about the structure of benthic assemblages but they were not designed to assess the relationship between physical factors and the structure of assemblages. Here we present analysis of a regional benthic survey 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. Our hypothesis was that there are discontinuities in the composition of benthic infaunal assemblages at specific depths, sediment grain sizes, and latitudes; our objective was to identify the depths, grain sizes, and latitudes at which these discontinuities occur.

Materials and methods

Between July 13 and August 22 1994, benthic samples were collected from 251 sites on the continental shelf (10–200 m deep) from Point Conception, California, to the United States–Mexico international border. Sites were selected randomly and stratified by

depth zone (inner shelf 10–25 m, middle shelf 26–100 m, and outer shelf 101–200 m). 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 1 week. Samples for sediment grain size, total organic carbon (TOC), and sediment chemistry [trace metals, dichlorodiphenyltrichloroethane (DDT), polychlorinated biphenyls (PCBs), and polycyclic aromatic hydrocarbons (PAHs)] were taken from the top 2 cm of a second grab sample. The chemistry data were used to eliminate contaminated sites from our analysis.

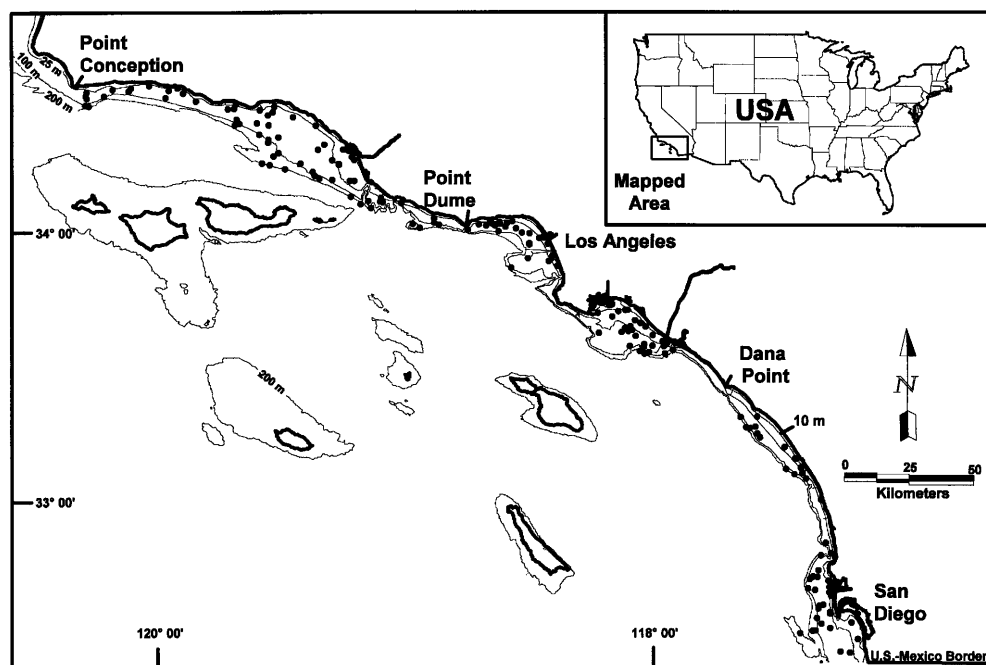
Infaunal samples were sorted into six major taxonomic categories (annelids, arthropods, mollusks, ophiuroids, other echinoderms, and other phyla), and the wet weight of each group was measured. Specimens were then identified to the lowest practical taxon following the nomenclature of SCAMIT (1994) and enumerated. Sediment chemistry samples were analyzed in the laboratory using standard methods; details are provided in Schiff (2000).

Because our 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) more than three 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 (4) the sample was in an area surrounding a stormwater or municipal wastewater outfall. After these exclusions, 175 stations remained for analysis (Fig. 1).

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 using non-parametric statistics. Three physical habitat attributes were examined: depth, percent fines (<63 μ m grain size) in the sediment, and latitude.

Cluster analysis was conducted using flexible sorting of Bray–Curtis dissimilarity values with $\beta = -0.25$ (Bray and Curtis 1957; Lance and Williams 1967; Clifford and Stephenson 1975). Data were square-root transformed and then standardized by the species

Fig. 1 Map of sites used in the cluster analysis



mean of abundance values higher than zero to reduce the influence of dominant species (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 to reduce the distortion of ecological distances caused by joint absences of a high proportion of species; the distortion occurs due to the non-monotonic truncated joint species distribution. Prior to cluster analysis, species occurring at fewer than 15 sites (8.6%) were eliminated except when the total abundance of the species was ≥ 50 individuals.

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 the 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 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. Probabilities were not adjusted to account for multiple testing because we were only interested in controlling the comparisonwise error rate.

Results

Sequential analysis of the dendrogram splits yielded four habitat-related benthic infaunal assemblages along the southern California coastal shelf (Fig. 2). The first split (split 1 of Fig. 2) was primarily associated with depth; 96% of the sites separated along the 32 m depth contour (Fig. 3). Percent fines differed significantly between the two station groups (Table 1) but served 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 (Fig. 3). Presumably, the shallow water biota extend into deeper waters under high-energy conditions and deep water biota extend into shallow water under low-energy conditions.

The next split in the deeper group (split 3) was based on depth (Table 1) with 96% of the sites segregating at 115 m (Fig. 4). 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. The next split in the deep group (split 5) was based on grain size, with 96% of the sites segregating on a threshold of 45% fines (Fig. 5). This was the only split in which depth was not a significant variable.

Although depth and latitude were significantly different (Table 1) for the other split in the deep group (split 4) they segregated less than 95% of the sites, failing our criteria for habitat differentiation. Therefore, these sites were all included in a mid-depth (32–115 m) group defined at split 3.

The next split in the shallow group (split 2) failed our criteria for habitat differentiation in a similar manner, resulting in a single shallow (10–32 m) group defined at split 1. Although split 2 was significant for depth and grain size (Table 1), there was broad overlap in depth and grain size for sites on either side of the split.

Biological characterization

The shallow habitat fauna were the most distinctive, with nearly 70% of the most common and abundant species (i.e. those occurring in more than 60% of the samples with average abundance greater than 20/m²) prevalent only in the shallow habitat (Table 2). Although these species were found in other habitats, they were relatively rare. Most of the remaining species were generalists, with all except one common and abundant in all habitats.

The two most distinctive species in the shallow assemblage were the amphipod *Amphideutopus oculatus* and the brachiopod *Glottidia albida* (Table 2). The polychaete *Spiophanes bombyx*, the amphipod *Ampelisca cristata*, and the bivalves *Macoma yoldiformis* and *Tellina modesta* were also characteristic of shallow habitats.

Fig. 2 Dendrogram illustrating the station groups identified by cluster analysis. The number of dendrogram branches (stations) in each group is shown. Splits 1–5 identify dendrogram branch points referred to elsewhere in the text and figures

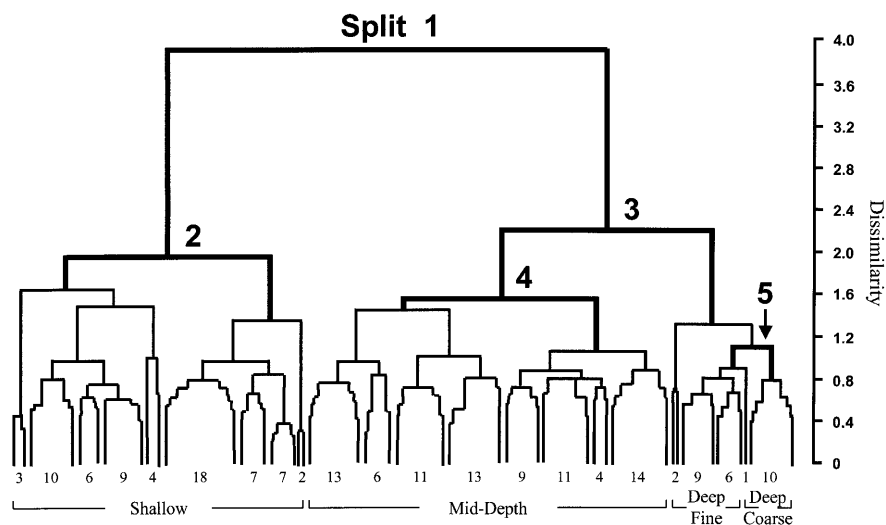


Fig. 3 Distribution of cluster groups from dendrogram split 1 (see Fig. 2) relative to depth and sediment type. *a* Stations in the “shallow” branch; *b* stations in the “mid-depth” and “deep” branches

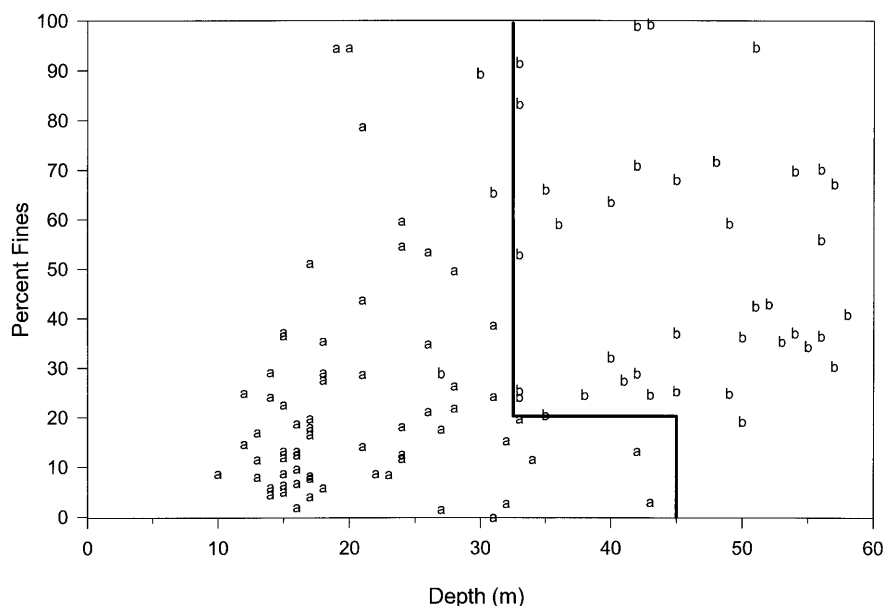


Table 1 Range of values for depth, percent fines, and latitude for stations in each division of the cluster dendrogram. Bolded pairs indicate significant difference in median

Cluster split	Range			
	Depth (m)	Fines (%)	Latitude	<i>n</i>
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

Fifty-six percent of the species in the mid-depth assemblage were distinctive (Table 2). The most abundant distinctive species were the polychaete *Sthenelanelia uniformis* and phoronids in the genus *Phoronis*. The polychaetes *Prionospio* sp. A and *Paramage scutata* and the ostracod *Euphilomedes carcharodonta* were also common. Of the remaining species, five were universal across habitats, two were shared with both deep habitats, two were shared with the deep coarse habitat, one was shared with the deep fine habitat, and one was shared with the shallow habitat.

Twenty nine percent of the species in the deep fine habitat and 35% of the species in the deep coarse habitat were distinctive (Table 2). In the deep fine sediment assemblage, four species were distinctive: the polychaetes *Maldane sarsi*, *Levinsonia* spp., *Cossura* spp., and *Laonice appelloefi* (Table 2). In the deep coarse sediment assemblage, six species were distinctive: the brittlestar *Amphiodia digitata*, the ostracod *Euphilomedes producta*,

the polychaetes *Chloeia pinnata* and *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* and the polychaete *Pectinaria californiensis* were common in both mid-depth and deep habitats. The amphipod *Rhepoxynius bicuspidatus* and the polychaete Euclymeninae sp. A were common in the deep coarse and mid-depth habitats, but not in deep fine sediments.

Five polychaete taxa, including at least four species, were common in all four assemblages (Table 2). The species were *Spiophanes missionensis* and *Paraprionospio pinnata*, which were identified to species, and *Mediomastus californiensis* and *M. ambiseta*, which were included under *Mediomastus* spp. The two *Mediomastus* species co-occur in fair abundance off the coast of southern California but often cannot be identified because many individuals fragment and the posterior fragments that bear diagnostic characters are too small to be retained on 1-mm sieves. *Lumbrineris* spp. and Maldanidae, the other two widespread and common taxa, each comprise several species that may or may not individually be widespread.

The numbers of taxa and total abundance of organisms were lowest in the deep fine sediment habitat and highest in the mid-depth habitat (Table 3). Annelids made up 42–64% of the abundance in all habitats. Arthropods contributed 10 and 33% of the abundance in deep fine sediment and deep coarse sediment habitats, respectively, and 18 and 21% of the abundance in mid-depth and shallow habitats. Ophiuroids made up 16–17% of the abundance in all habitats except the shallow habitat, where they contributed only 2% of the abundance. Conversely, mollusks contributed 4–7% of the abundance in deep and mid-depth habitats and 15% of the abundance in shallow habitats.

Fig. 4 Distribution of cluster groups from dendrogram split 3 (see Fig. 2) relative to depth and sediment type. *a* Stations in the “mid-depth” branch; *b* stations in the “deep” branch

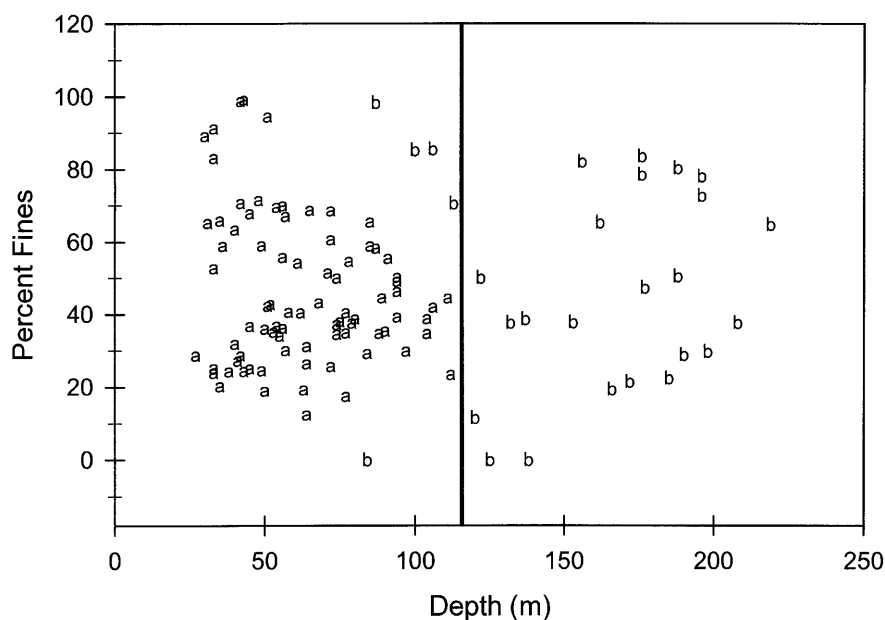
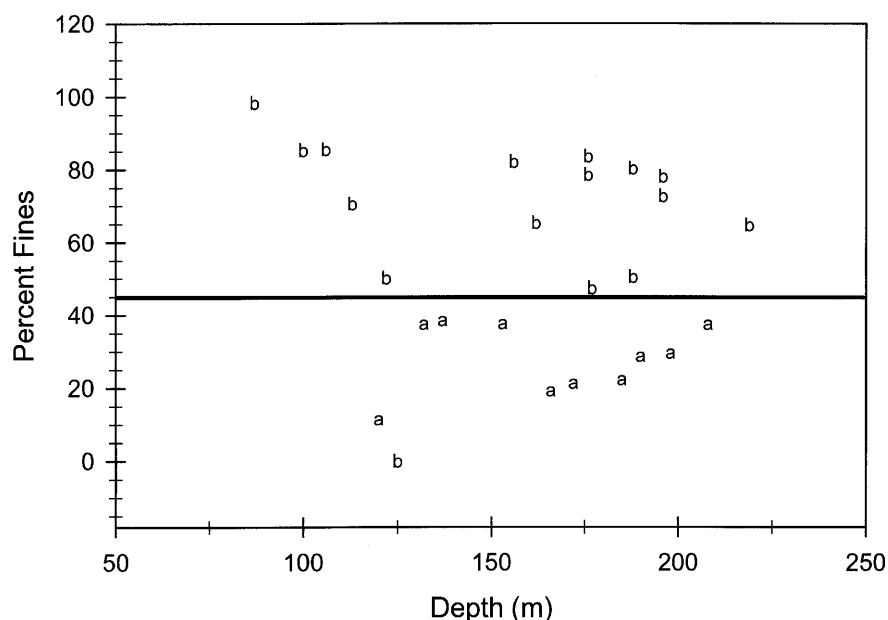


Fig. 5 Distribution of cluster groups from dendrogram split 5 (see Fig. 2) relative to depth and sediment type. *a* Stations in the “deep coarse” branch; *b* stations in the “deep fine” branch



Discussion and conclusions

The southern California benthic assemblages we describe are similar to assemblage descriptions based on surveys conducted between 1956 and 1961 by the Allan Hancock Foundation (Barnard and Hartman 1959; Barnard and Zieshenne 1960; Jones 1964, 1969). The Hancock surveys and our study both defined shallow, mid-depth, and deep shelf assemblages, with breaks between assemblages occurring at approximately the same depth. The deeper limit of the shallow assemblage was 30 m in the Hancock surveys and 32 m (depending upon the sediment type) in our study. The deeper 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 4 and 5, respectively).

The Hancock surveys identified several additional assemblages that were not identified in our study (Table 6). The fact that we did not find these assemblages may be attributable to differences in sampling methodology, differences in the methods used to define the assemblages, or both. The Hancock sampling was conducted using an orange peel grab, which samples

Table 2 Average abundance of species with frequency of occurrence greater than 60% and average abundance of at least 20/m² in each cluster group. All values are area weighted

Species	Taxonomic group	Average abundance (number/m ²)			
		Cluster group			
		1 Deep coarse	2 Deep fine	3 Mid-depth	4 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 ^a	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>Leptochelia 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

^a All Maldanids except 11 identified species

large organisms (e.g. *Mooreonuphis* spp., *Brisaster latifrons*) better than 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* assemblages. 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*,

Table 3 Community characteristics of the four cluster groups. All values are area weighted. *CI* Confidence interval

Characteristic	Deep coarse sediment <i>n</i> = 10		Deep fine sediment <i>n</i> = 16		Mid-depth <i>n</i> = 81		Shallow <i>n</i> = 66	
	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 (<i>H'</i>)	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/m ²	4005.0	1727.4	2329.8	539.2	4908.2	464.0	3121.5	597.8
Percent abundance of								
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 (g wet weight/m ²)	41.0	15.3	44.3	10.6	79.4	12.2	35.9	8.6
Percent biomass of								
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

may disappear if depositional patterns change. In fact, both *L. pelodes* and *Cyclocardia ventricosa* are now relatively rare with mean abundances of only 30.9 and 24.6 m⁻², respectively, at sites of occurrence in our study. In contrast, Jones (1969) reported that *C. ventricosa* was co-dominant with *Amphiodia* on the outer Point Conception and Santa Barbara shelves and mean *L. pelodes* abundances were 100 m⁻² in silt deposits further inshore in the same area. Stull et al. (1986) documented a case in which *L. pelodes* mass-recruited to the shelf off the Palos Verdes peninsula in southern California, achieved biomass and numeric dominance for a period of 3–4 years, and subsequently collapsed to near absence. Thus, the fact that we did not find the *Listriolobus* or the *Cyclocardia-Amphiodia urtica* assemblages in our study may simply be because these two species are now less abundant.

Thompson et al. (1993a) 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 this *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. Although the assemblages are similar, Thompson found the transition between the two assemblages at depths of 150–160 m rather than 90–115 m.

The primary difference among the survey results is that one deep-water assemblage was defined in the Hancock surveys and Thompson et al. (1993a) 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. Thompson et al. (1993a) mentioned that assemblages in sandy sediment are different but did not list a separate coarse-sediment assemblage. 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.

The Allan Hancock Foundation surveys (Barnard and Hartman 1959; Barnard and Ziesenhenné 1960; Jones 1964, 1969) and our study all indicate that depth is the primary habitat factor organizing southern California benthic communities, which is consistent with studies of marine infauna in California and elsewhere (e.g., Hyland et al. 1991; Rakocinski et al. 1993, 1997; Oug 1998). In estuarine environments salinity is more important (Boesch 1973; Shin and Thompson 1982; Rakocinski et al. 1997; Weisberg et al. 1997). Many infaunal studies (e.g. Snelgrove and Butman 1994) suggested that sediment type is a primary habitat factor organizing benthic communities, whereas we found it to be a secondary factor. This finding may, at least in part, be attributable to inclusion of many sites at relatively small depth intervals across a broad depth range; if stations are restricted to one or a few isobaths or within a relatively narrow depth range, as is often the case, sediment differences may appear to be more important.

The size and position of our study area probably had an effect on our finding that latitude was not a significant factor affecting infaunal assemblage distributions. Although our study area was large, extending over 500 km of coastline, it included only two degrees of latitude because part of the coastline runs east–west. In

Table 4 Comparison of common species in the historical *Nothria-Tellina* assemblage and our shallow depth assemblage (cluster group 4)

Old species name	Current name	Percent occurrence	
		<i>Nothria-Tellina</i> assemblage	Shallow depth assemblage (cluster group 4)
<i>Chaetozone</i> spp. ^a	<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> ^a	<i>Paraprionospio pinnata</i>	96.4	86.4
<i>Lumbrineris</i> spp.	<i>Lumbrineris</i> spp.	96.4	71.2
<i>Haploscoloplos elongatus</i> ^a	<i>Leitoscoloplos pugettensis</i>	92.7	34.8
<i>Prionospio malmgreni</i> ^a	<i>Prionospio</i> sp. A and sp. 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. ^a	<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. ^a	<i>Nephtys caecoides</i> , <i>N. cornuta franciscana</i> , <i>N. ferruginea</i>	70.9	72.7
<i>Thalassia spinosa</i> ^a	<i>Sigalion spinosa</i>	70.9	60.6
<i>Argissa hamatipes</i>	<i>Argissa hamatipes</i>	70.9	28.8
<i>Turbonilla</i> spp.	<i>Turbonilla</i> spp.	67.3	47.0
<i>Cadulus</i> sp.	<i>Gadila</i> sp.	67.3	0.0
<i>Nothria elegans</i> , <i>N. iridescens</i> ^a	<i>Onuphis elegans</i> , <i>O. iridescens</i> and <i>Onuphis</i> sp. 1 (SCAMIT)	66.7	59.1
<i>Tharyx tessellata</i>	<i>Monticellina</i> spp., <i>Aphelochaeta</i> spp.	65.5	59.1
<i>Glottidia albida</i> ^a	<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> ^a	<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

^a Identified as dominant in the *Nothria-Tellina* assemblage

addition, the study area was 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. Point Conception is a widely recognized faunal boundary (Briggs 1974; Cross and Allen 1993).

Although 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. As Snelgrove and Butman (1994) suggested, the amounts of hydrodynamic energy and available organic material are more likely to be primary driving forces, with depth and sediment grain size as secondary correlates. The energy profile of water flow immediately above the sediment–water interface determines the size of particles in surficial sediments, which in turn affects properties such as the ease of

burrowing, which may limit the species that can survive. The greater the energy, the higher the velocity, the larger the sediment particles carried away by the water for deposition in low-energy environments, and the larger the size of particles left behind at the sediment–water interface. Depth affects the energy profile because the effects of wave energy on the bottom are usually greatest in shallow areas and decrease as the distance between the surface and bottom increases.

Our finding that the shallow assemblage is defined by a combination of depth and sediment type is consistent with the theory that the hydrodynamic energy profile at the bottom is the controlling factor. Unfortunately, the hydrodynamic energy environment is difficult to measure, particularly when rare or extreme events are the controlling factor (Schimmelmann et al. 1992; Posey et al. 1996; Okey 1997). Therefore, depth and sediment grain size probably act as surrogates, integrating effects of the hydrodynamic environment over time. In any event, our study provides empirically defined dividing points in the depth and sediment grain size gradients that can be used to define reference habitats.

Our observation of the existence of a benthic abundance and diversity maximum at an intermediate depth

Table 5 Comparison of common species in the historical *Amphiodia urtica* assemblage and our mid-depth assemblage (cluster group 3)

Old species name	Current name	Percent occurrence	
		<i>Amphiodia urtica</i> assemblage	Mid-depth assemblage (cluster group 3)
<i>Amphiodia urtica</i> ^a	<i>Amphiodia urtica</i>	100.00	96.3
<i>Pectinaria californiensis</i> ^a	<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> ^a	<i>Axinopsida serricata</i>	85.19	55.6
<i>Prionospio malmgreni</i>	<i>Prionospio</i> sp. A and sp. B (SCAMIT), <i>Apoprionospio pygmaea</i>	85.19	90.1
<i>Paraonis gracilis</i>	<i>Levinsonia</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> ^a	<i>Sternaspis fossor</i>	77.78	58.0
<i>Glycera capitata</i> ^a	<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>	<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 ferruginea</i>	<i>Nephtys ferruginea</i>	62.96	45.7
<i>Ampelisca pugetica</i>	<i>Ampelisca pugetica</i>	62.96	72.8
<i>Oxydromus arenicolus glabra</i>	<i>Podarkeopsis glabra</i> , <i>Podarkeopsis</i> sp. A	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>Sthenelanella uniformis</i>	<i>Sthenelanella 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>Leptochelia 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

^a Identified as dominant in the *Amphiodia urtica* assemblage

Table 6 Benthic infaunal assemblages described in Barnard and Hartman (1959), Barnard and Ziesenhenné (1960), and Jones (1964, 1969)

Assemblage	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

is consistent with several previous studies off the coast of California (Fauchald and Jones 1979a, b, 1983; SAIC 1986; Thompson and Jones 1987; Lissner 1989; Hyland

et al. 1991; Thompson et al. 1993a). The patterns are the same for each study even though values of abundance and diversity are not comparable among studies because

they used different sampling devices and different mesh sizes to sieve the sediments.

It seems likely that the abundance and diversity maximum occurs at similar depths off the coast of southern California and in the Santa Maria Basin, which lies immediately to the north, despite a superficial appearance of dissimilarity. Although we report an abundance and diversity maximum at 32–115 m for the Southern California Bight (Table 3), Hyland et al. (1991) reported a maximum at “less than 200 m” in the Santa Maria Basin. Since these Santa Maria Basin data were from six stations on only the 90-m and 150-m isobaths, the maxima could well be at the same depth in both areas.

Our findings also conform to Sanders’ (1969) prediction that patterns of benthic abundance and diversity would differ under upwelling waters and other oceanic regimes. As Hyland et al. (1991) point out, the decrease in abundance and diversity with increasing depth beyond intermediate depths off southern California conflicts with the patterns off the Atlantic coast of North America, where abundance and diversity increase as depth increases monotonically down to the continental rise at 2300–2800-m (Sanders 1968; Boesch 1979; Neff et al. 1989). Sanders (1969) predicted that low benthic diversity will occur under regions of upwelling because “the abundant organic matter depletes the available oxygen as it sinks so that the bottom water contains little or no oxygen” resulting in low diversity and abundance. Although our patterns of abundance and diversity conform to Sanders’ prediction, we believe there is insufficient information to determine which of the many possible physical and biological factors drives them; we only sampled the upper-most fringes of the depth gradient and did not collect dissolved oxygen data. We hope future studies will shed light on this interesting question.

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