

# Macrobenthic communities of the Santa Maria Basin on the California outer continental shelf and slope

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**ABSTRACT:** We present results of a 2.5 yr survey of the macrobenthos along the California coast north of Point Conception, between Purisima Point and Point San Luis (USA), at outer-shelf and slope depths of 90 to 565 m. The study area, representing the southern offshore portion of the Santa Maria Basin, is an oceanographically complex and productive region, which is also believed to contain major petroleum deposits. This area supports a highly diverse and abundant macrobenthos, represented mostly by crustaceans (34 %), polychaetes (31 %), and molluscs (18 %). Average numbers of species and densities (up to 151 0.1 m<sup>-2</sup> and 28 826 m<sup>-2</sup>, respectively, at water depths under 200 m) equal those reported for other productive regions, such as Georges Bank and the North Sea. Spatial differences in the composition of these assemblages are related foremost to water depth in addition to variations in sedimentary and other depth-associated physical variables. Patterns of decreasing abundances and diversity with increasing depth appear to be due partly to a bottom dissolved-oxygen gradient (3.1 ml l<sup>-1</sup> at 90 m to 0.6 ml l<sup>-1</sup> at 565 m), which includes values at the low end that are below the oxygen tolerance of many benthic invertebrates. Variations in the percentage of sand explain further differences that segregate some stations of comparable depth and oxygen levels. Macrobenthic variables also show significant temporal fluctuations, although distinct seasonal cycles are hard to detect and are not repeated throughout all sampling years and stations. The occurrence of density peaks in the spring during one or more sampling years at several of the stations, however, suggests a benthic response to upwelling events, which are known to contribute to increases in new primary production and ultimately to increased energy supplies to the benthos. Results of this study provide a basis for beginning to understand natural sources of variation in the benthos of the region, which should be considered in efforts to assess potential impacts of future oil development.

## INTRODUCTION

The California outer continental shelf and slope just north of Point Conception (USA) is an oceanographically complex and productive region characterized, for example, by strong coastal upwelling (Brink et al. 1984, Kinney et al. 1990) and associated increases in new primary production (Dugdale & Wilkerson 1989). It is also an area believed to contain major new reservoirs of offshore petroleum (Rintoul 1985). The benthic ecology of this region has been poorly understood and was virtually unstudied until these recent oil discoveries.

The present study was performed as a component of a larger interdisciplinary monitoring program (Hyland et al. 1990) designed to assess potential long-term cumulative impacts of offshore oil development in the southern part of Santa Maria Basin, a geologic feature encompassing the bulk of the California continental margin between Point Conception and Monterey Bay. This is one of few studies to provide a comprehensive examination of spatial and temporal variability of offshore infauna along the California coast north of Point Conception. Previous studies of the macrobenthos of this area have been limited largely to site-specific surveys conducted around individual offshore platform

sites (unpubl. reports prepared for oil companies: Dames & Moore 1983, Engineering-Science 1984, Nekton 1983, 1984, McClelland Engineers 1985) or to broader-based reconnaissance surveys conducted at single points in time (SAIC 1986, Lissner 1989, Cimberg & Smith in press). Thompson et al. (1985) also examined macroinfaunal distributions in relation to the oxygen minimum zone at sites further north, offshore of Pt. Sur, California.

In the present paper, we present results of basic research on the structure and dynamics of the macroinfauna and on the relationships of the fauna to other natural environmental variables. Results are based on samples collected at 8 time intervals over a 2.5 yr period. The purposes of our analysis are to describe the faunal assemblages; examine their spatial and temporal patterns; and relate the faunal distributions to other environmental factors that may be of importance in controlling the observed patterns. Results reflect baseline conditions relative to oil-production in the immediate sampling area. A companion study of meiobenthic communities, sampled along with the macrofauna, is reported elsewhere by Montagna (in press).

## METHODS

**Field collections and sample processing.** The primary data base for this paper was derived from the analysis of 230 sediment samples of 0.1 m<sup>2</sup> collected along 3 cross-shelf transects of 3 stations each (encompassing depths of 90 to 410 m) and from an additional station, R-7, located ca 50 km west of Point Sal (at a depth of 565 m) in a sea valley adjacent to the Santa Lucia Bank (Fig. 1). Typically, 3 replicate samples were collected from each of the 10 stations on 8 sampling occasions: October 1986, January 1987, May 1987, October 1987, January 1988, May 1988, October 1988, and May 1989. However, Stations R-8 and R-9 were not sampled in October 1986, and Station R-7 was not sampled in May 1988. Also, only 2 replicates were obtained at Station R-3 in May 1988. An additional set of 114 samples were collected on several of the sampling occasions from a closely spaced array of 18 stations centered around Station PJ-1, the proposed site for an offshore oil and gas production platform (Platform Julius). Data from these latter samples are used here in the description of overall taxonomic composition but have been excluded from remaining analyses

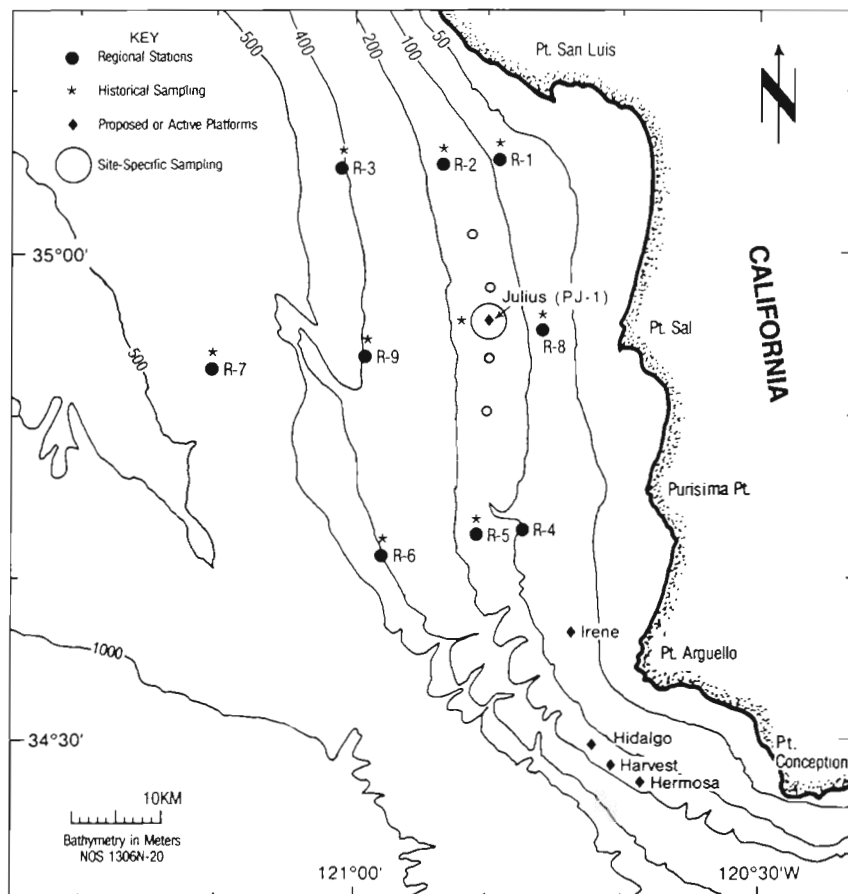


Fig. 1. Study area and station design. Historical sampling sites (asterisks) refer to coinciding sites sampled by SAIC (1986)

of regional faunal patterns and relationships of the fauna to other environmental variables.

Samples were obtained with a Hessler-Sandia 0.25 m<sup>2</sup> box corer partitioned into 25 individual 0.01 m<sup>2</sup> subcores. From each sample, 10 subcores were removed from the corer and prepared for macroinfaunal analysis. Remaining subcores were used for analysis of meiofauna, hydrocarbons, trace metals, sediment grain-size, total organic carbon, sediment shear strength, redox conditions, distribution of mineral types, radioisotope profiles, and bioturbation processes. Near-bottom hydrocasts were also taken at or near each station to provide measurements of dissolved oxygen, salinity, pH, and temperature. A subset of these variables was selected to examine possible relationships with the macroinfaunal data.

The upper 10 cm of each subcore obtained for macroinfaunal analysis were live-sieved through a 0.3 mm screen with filtered seawater. All 10 subcores from the same box core were recombined during this sieving process, yielding a total surface area of 0.1 m<sup>2</sup> per replicate sample. Material retained on the screen was preserved with ca 10 % buffered formalin. Once samples were returned to the laboratory, they were resieved on a nest of 0.5 mm and 0.3 mm screens and transferred to 70 % ethanol. The 0.5 mm fraction was used for analysis of macroinfauna; the 0.3 mm fraction was archived.

Samples were sorted in the laboratory under dissecting microscopes and were stained with a saturated solution of rose bengal, for 4 to 24 h, to facilitate the sorting process. All individuals were enumerated and identified to the species level wherever possible. Colonial forms and temporary members of the benthos were excluded from all data analyses. Unidentifiable juveniles and damaged specimens were excluded from most data analyses except estimates of density. A quantitative species list can be obtained from the senior author.

**Data analyses.** Data were analyzed by a combination of the following methods: inspection of species lists to examine taxonomic composition and dominant species (10 most abundant species by station); calculation of species diversity and other community characteristics; numerical classification to identify patterns of faunal similarity; analysis of variance (ANOVA) to test for the significance of spatial and temporal differences; and multiple discriminant analysis to examine relationships between the macroinfauna and other environmental variables. Procedures provided in SAS (1985) were used to perform ANOVA (PROC GLM) and multiple discriminant analysis (PROC CANDISC). A customized package of statistical subroutines was used for the diversity measures and numerical classification.

Measures of diversity and other community characteristics consisted of numbers of individuals and of species,  $S$ ; the Shannon information function,  $H'$  (Shannon & Weaver 1949); and the associated evenness component,  $J'$  (Pielou 1966). Base 2 logarithms were used to calculate  $H'$ .

Normal (Q-mode) numerical classification (Boesch 1977) was performed on data transformed to  $\log_{10}(x+1)$ . Group-average sorting (= unweighted pair-group method; Sneath & Sokal 1973) was used as the clustering method and Bray-Curtis similarity (Bray & Curtis 1957) was used as the resemblance measure. Results are expressed here in the form of dendrograms in which samples have been ordered into groups of increasingly greater similarity based on resemblances of component-species abundances.

A sequence of 3-way, 2-way, and 1-way ANOVA models was used to test for the significance of main effects of depth, time, transect location, and their interactions on the following response variables: number of species, density of total fauna, and densities of selected dominant species. Student-Newman-Keuls multiple range tests were used in conjunction with ANOVA to locate where significant differences exist between the various levels of each class variable. Data were transformed to  $\log_{10}(x+1)$ . An alpha value of 0.05 was selected as the significance level.

As recommended by Green & Vascotto (1978), multiple (canonical) discriminant analysis was used to determine whether the group separation derived by numerical classification of the macroinfaunal species data can be explained by other measured environmental variables. The other variables used are sediment organic matter (total organic carbon, expressed as % dry wt), mean particle size (in phi units), sorting coefficient (quartile deviation, in phi units), % sand, % silt, % clay, near-bottom dissolved oxygen (ml l<sup>-1</sup>), density of all meiofaunal members (size range = 0.063 to 0.50 mm), density of protozoan meiofauna, and density of metazoan meiofauna. Physical variables and meiofaunal variables were tested separately. All data were transformed to  $\log_{10}(x+1)$ , unless already in log form (e.g. variables expressed in phi units). The discriminant analysis was used to derive a reduced set of discriminant functions that best describe the separation of the predeclared station groups based on data represented by the different environmental variables. Total structure coefficients, which are the correlations between the original variables and the discriminant scores on each function, served as a measure of the relative contribution of each variable to group separation. Station groups were then plotted in the reduced discriminant space and interpreted visually in light of those variables that accounted for the majority of the separation.

Table 1. Summary of major taxonomic groups

Taxonomic group	Number identifiable taxa	% Total identifiable taxa
Phylum Porifera <sup>a</sup>	1	0.1
Phylum Cnidaria <sup>a</sup>		
Class Hydrozoa	20	2.3
Class Anthozoa	37	4.2
Phylum Platyhelminthes	1	0.1
Phylum Nemertina	16	1.8
Phylum Priapulida	1	0.1
Phylum Sipuncula	5	0.6
Phylum Mollusca		
Class Gastropoda	85	9.6
Class Aplacophora	17	1.9
Class Bivalvia	67	7.6
Class Scaphopoda	10	1.1
Phylum Echiura	5	0.6
Phylum Annelida		
Class Polychaeta	278	31.4
Class Oligochaeta	6	0.7
Phylum Arthropoda		
Class Pycnogonida	5	0.6
Class Crustacea		
Subclass Ostracoda	31	3.5
Subclass Cirripedia <sup>a</sup>	1	0.1
Subclass Malacostraca		
SupOrd Peracarida		
Mysidacea <sup>a</sup>	13	1.5
Cumacea	52	5.9
Tanaidacea	18	2.0
Isopoda	18	2.0
Amphipoda	153	17.3
SupOrd Eucarida		
Euphausiacea <sup>a</sup>	8	0.9
Decapoda <sup>a</sup>	10	1.1
Phylum Bryozoa <sup>a</sup>	4	0.5
Phylum Brachiopoda	1	0.1
Phylum Echinodermata		
Class Stelleroidea		
Asteroidea	2	0.2
Ophiuroidea	12	1.4
Class Echinoidea	4	0.5
Class Holothuroidea	3	0.3
Phylum Hemichordata	1	0.1
Phylum Chordata		
Subphy. Urochordata <sup>a</sup>	1	0.1
<i>Total</i>	<i>886</i>	<i>100</i>

<sup>a</sup> Colonial forms and temporary members of the benthos are excluded from all data analyses

## RESULTS

### Taxonomic and zoogeographic composition

A total of 886 species representing 15 phyla (Table 1) have been identified among 444 989 specimens encountered in all samples (344 cores). Most (551) have been identified to species level. The remaining

335 species are recognized as distinct taxa but have been given provisional codes because they are either new to science or not known to the participating taxonomists. The actual number of species encountered is probably much higher considering the presence of an additional 339 unidentifiable taxa represented by indeterminate juveniles or fragments of specimens (not included in Table 1). The largest percentages of identifiable taxa are represented by crustaceans (34 %, mostly peracarida) and polychaetes (31 %). Gastropods (10 %) and bivalves (8 %) contribute the next highest percentages of species. Together these 4 classes account for 83 % of all taxa.

The study area is located at the boundary separating 2 major zoogeographic provinces, the Oregonian and Californian, as defined by Valentine (1966). An examination of the latitudinal ranges of ca 75% of the polychaetes, crustaceans (except cumaceans), and molluscs encountered in the present study revealed that the majority (69 %) have northern affinities, either as members of the Oregonian Province (32 %) or as wide-ranging northern species (37 %). Species with primarily southern affinities comprise 26 % of the fauna, most (22 %) being members of the California Province and the remaining ones having wide-ranging southern distributions. Five percent of the taxa examined appear to be endemic to the study area.

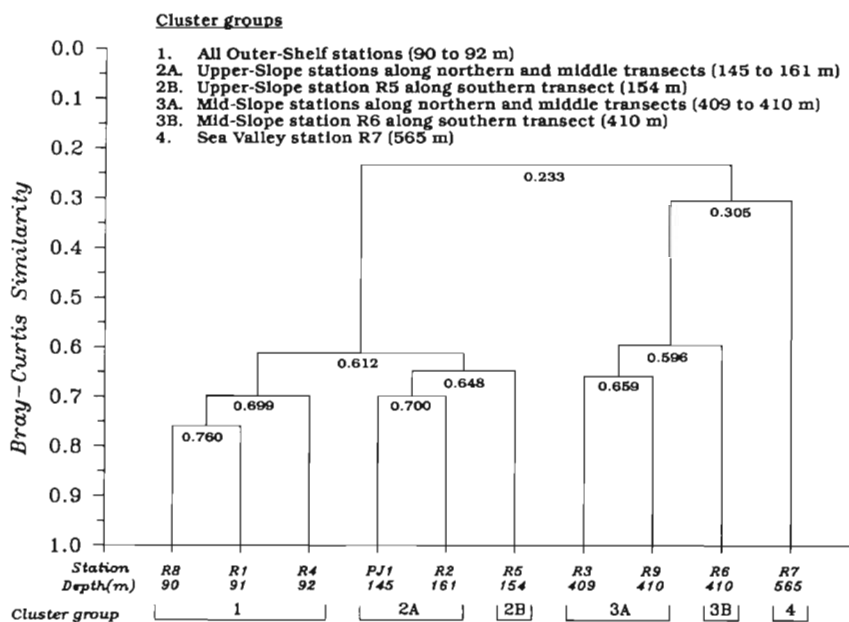
### Numerical classification

Numerical classification of samples combined over all replicates and cruises from the various regional stations defines 4 major groups reflecting depth-related differences in macroinfaunal species composition (Fig. 2). These groups consist of all outer-shelf stations at depths of about 90 m (R-8, R-1, and R-4 = Cluster Group 1); all upper-slope stations at depths of 145 to 161 m (PJ-1, R-2, and R-5 = Cluster Group 2); all mid-slope stations at depths of about 410 m (R-3, R-9, and R-6 = Cluster Group 3); and the sea-valley station R-7 at 565 m (Cluster Group 4). These variations with depth appear to be related to the near-bottom oxygen gradient (see below). Additional environmental factors (e.g. % sand) may explain the remaining differences that segregate Stations R-5 (Group 2B) and R-6 (Group 3B) along the southern transect from corresponding stations of comparable depth.

### Dominant species

Dominant (10 most abundant) species and estimates of their abundances by station are presented in Table 2. These species account for more than 50 % of

Fig. 2. Dendrogram resulting from clustering of stations, using group-average sorting, and Bray-Curtis similarity. Samples within each station are combined over all replicates and cruises (except Oct 1986 and May 1988 cruises are deleted to create equal sample sizes among stations). Station pairs with similarities  $\geq 0.650$  are placed within the same cluster group



the cumulative percent abundance of all species at a given station. The data are averaged over all sampling times and arranged to allow visual comparisons between depths and transect locations.

Among outer-shelf and upper-slope stations (90 to 161 m; Cluster Groups 1 and 2) the most persistent and strongly ranked dominants are the 2 polychaetes *Mediomastus ambiseta* and *Chloeia pinnata*. Other important co-dominants are the polychaetes *Minuspio (Prionospio) lighti*, *Levinsenia gracilis* and *Pholoe glabra*. Ophiuroids (*Amphiodia urtica*) are also characteristic of the shallowest stations (90 to 92 m), and several dominant species of crustaceans (3 amphipods, 1 tanaid, and 1 isopod) are increasingly abundant among the southern stations within this depth range. The *Amphiodia* influence at the shallower depths suggests some resemblance of our outer-shelf fauna to the *Amphiodia-Cardita* association described by Jones (1969) for shelf sites south of Point Conception. However, in the present study, *Amphiodia* is not the highest ranked dominant and, while *Cyclocardia ventricosa* (= *Cardita*) is present at moderately low densities, the clams *Parvilucina tenuisculpta* and *Acila castrensis* are ranked as the dominant molluscs. The outer-shelf to upper-slope stations in the present study also bear some resemblance to the 'shelf' (Site Group 1) and 'upper-slope' (Site Groups 4 and 6) stations described in the 'Phase I Reconnaissance Study' conducted previously in the same study area (SAIC 1986). For example, species such as *Amphiodia urtica*; the polychaetes *Spiophanes berkeleyorum*, *S. missionensis* and *Chloeia pinnata*; and the clam *Acila castrensis* are mentioned as co-dominants at these depths in both

studies. However, a striking difference is the complete absence of *Mediomastus ambiseta* in the earlier Phase I study.

At the deeper mid-slope stations (410 m; Cluster Group 3), *Mediomastus ambiseta* drops out as a dominant and the polychaetes *Chloeia pinnata* and *Nephtys cornuta* become the 2 most persistent and strongly ranked dominants. These deeper stations are also characterized by the absence of *Minuspio lighti* and by increasing dominance of several other polychaete species (*Maldane sarsi*, *Chaetozone* nr. *setosa*, *Minuspio* sp. A, *Cossura rostrata* and *Cossura candida*); oligochaetes (*Tectidrilus diversus*); crustaceans (including the cumaceans *Leucon magnadentata*, *Eudorella pacifica*, and *Eudorella* sp. 1 and the amphipods *Pseudharpinia excavata* and *Harpiniopsis fulgens*); and 2 species of molluscs (the scaphopod *Cadulus californica* and the bivalve *Huxleyia munita*). SAIC (1986) also describes a 'mid-slope' assemblage (Site Group 8) centered on approximately the 400 m isobath and containing *Chloeia pinnata* and *Maldane sarsi* as co-subdominants. However, unlike the present study, their study did not mention *Nephtys cornuta* as a dominant and listed the snail *Amphissa bicolor* as the highest ranked dominant at this depth.

The deepest station (R-7; Cluster Group 4) is characterized by an overwhelming dominance of the phoxocephalid amphipod *Harpiniopsis epistomata*, which accounts for over 50% of the total faunal abundance. Station R-7 is also characterized by the absence of *Mediomastus ambiseta*, a decline in the relative dominance of *Chloeia pinnata*, and an increase in the dominance of *Maldane sarsi*. This

Table 2. Dominant macroinfaunal species (A = Amphipoda, B = Bivalvia, C = Cumacea, I = Isopoda, O = Oligochaeta, Op = Ophiuroidea, Ost = Ostracoda, P = Polychaeta, S = Scaphopoda, Si = Sipuncula, T = Tanaidacea). Densities averaged over all sampling periods

Species	Northern transect		Middle transect		Southern transect		
	Ind. m <sup>-2</sup>	Cum %	Species	Ind. m <sup>-2</sup>	Cum %	Species	
	<b>R-1 (91 m)</b>		<b>R-8 (90 m)</b>		<b>R-4 (92 m)</b>		
<i>Mediomastus ambiseta</i> (P)	1869	13.9	<i>Minuspio lighti</i> (P)	2206	13.4	<i>Photis lacia</i> (A)	3049
<i>Chloea pinnata</i> (P)	995	21.2	<i>Pholoe glabra</i> (P)	1582	23.0	<i>Mediomastus ambiseta</i> (P)	2240
<i>Minuspio lighti</i> (P)	871	27.7	<i>Mediomastus ambiseta</i> (P)	1381	31.4	<i>Myriochele</i> sp. M (P)	2215
<i>Cossura pygodactylata</i> (P)	725	33.1	<i>Chloea pinnata</i> (P)	1267	39.1	<i>Chloea pinnata</i> (P)	2210
<i>Pholoe glabra</i> (P)	703	38.3	<i>Nephtys cornuta</i> (P)	761	43.8	<i>Photis</i> spp. (A)	1583
<i>Amphiodia urtica</i> (Op)	585	42.6	<i>Amphiodia urtica</i> (Op)	624	47.6	<i>Photis californica</i> (P)	1508
<i>Levinsenia gracilis</i> (P)	634	47.3	<i>Cossura pygodactylata</i> (P)	552	50.9	<i>Typhlotanais</i> sp. A (T)	870
<i>Nephtys cornuta</i> (P)	517	51.1	<i>Levinsenia gracilis</i> (P)	406	53.4	<i>Sopiophanes missionensis</i> (P)	865
<i>Typhlotanais</i> sp. A (T)	344	53.7	<i>Parviticina tenuisculpta</i> (B)	352	55.5	<i>Praxillella pacifica</i> (P)	813
<i>Nephasoma diaphanes</i> (Si)	330	56.2	<i>Tharyx</i> spp. (P)	336	57.6	<i>Minuspio lighti</i> (P)	724
All fauna [336 species] <sup>a</sup>	13496	100.0	All fauna [386 species] <sup>c</sup>	16447	100.0	All fauna [419 species] <sup>a</sup>	28826
	<b>R-2 (161 m)</b>		<b>PJ-1 (145 m)</b>		<b>R-5 (154 m)</b>		
<i>Mediomastus ambiseta</i> (P)	1622	18.1	<i>Mediomastus ambiseta</i> (P)	1870	146	<i>Mediomastus ambiseta</i> (P)	2510
<i>Levinsenia gracilis</i> (P)	642	25.2	<i>Chloea pinnata</i> (P)	1029	22.6	<i>Chloea pinnata</i> (P)	1177
<i>Tectidrilus diversus</i> (T)	575	31.6	<i>Minuspio lighti</i> (P)	729	28.3	<i>Tharyx</i> spp. (P)	934
<i>Minuspio lighti</i> (P)	562	37.9	<i>Exogone lourie</i> (P)	581	32.8	<i>Photis californica</i> (A)	843
<i>Cossura pygodactylata</i> (P)	475	43.2	<i>Cossura pygodactylata</i> (P)	491	36.7	<i>Minuspio lighti</i> (P)	675
<i>Nephtys cornuta</i> (P)	426	47.9	<i>Levinsenia gracilis</i> (P)	485	40.5	<i>Sopiophanes berkeleyorum</i> (P)	567
<i>Chaetozone</i> nr. <i>setosa</i> (P)	355	51.9	<i>Sopiophanes berkeleyorum</i> (P)	438	43.9	<i>Photis lacia</i> (A)	559
<i>Sopiophanes berkeleyorum</i> (P)	331	55.6	<i>Nephtys cornuta</i> (P)	376	46.8	<i>Prochelator</i> sp. A (I)	472
<i>Trachyleberis simiensis</i> (Ost)	316	59.1	<i>Typhlotanais</i> sp. A (T)	336	49.4	<i>Sopiophanes missionensis</i> (P)	470
<i>Acila castrensis</i> (B)	314	66.0	<i>Amphiodia urtica</i> (Op)	328	52.0	<i>Levinsenia gracilis</i> (P)	469
All fauna [275 species] <sup>a</sup>	8982	100.0	All fauna [318 species] <sup>a</sup>	12818	100.0	All fauna [358 species] <sup>a</sup>	16076

Table 2 (continued)

Northern transect			Middle transect			Southern transect		
Species	Ind. m <sup>-2</sup>	Cum %	Species	Ind. m <sup>-2</sup>	Cum %	Species	Ind. m <sup>-2</sup>	Cum %
<b>R-3 (409 m)</b>			<b>R-9 (410 m)</b>			<b>R-6 (410 m)</b>		
<i>Chloëia pinnata</i> (P)	1010	21.3	<i>Chloëia pinnata</i> (P)	921	24.0	<i>Chloëia pinnata</i> (P)	2233	33.2
<i>Levinsenia gracilis</i> (P)	850	39.2	<i>Nephtys cornuta</i> (P)	820	45.4	<i>Nephtys cornuta</i> (P)	774	44.7
<i>Nephtys cornuta</i> (P)	668	53.3	<i>Tectidrilus diversus</i> (O)	351	54.5	<i>Tectidrilus diversus</i> (O)	531	52.6
<i>Leucon magnadentata</i> (C)	401	61.7	<i>Maldane sarsi</i> (P)	263	61.4	<i>Chaetozone nr. setosa</i> (P)	500	60.0
<i>Chaetozone nr. setosa</i> (P)	350	69.1	<i>Chaetozone nr. setosa</i> (P)	164	65.7	<i>Huxleyia munita</i> (B)	243	63.6
<i>Cadulus californicus</i> (S)	197	73.3	<i>Cadulus californicus</i> (S)	90	68.0	<i>Cossura rostrata</i> (P)	217	66.8
<i>Eudorella pacifica</i> (C)	121	75.9	<i>Levinsenia gracilis</i> (P)	75	70.0	<i>Maldane sarsi</i> (P)	215	70.0
<i>Pseudoharpinia excavata</i> (A)	104	78.1	<i>Eudorella</i> sp. 1 (C)	75	71.9	<i>Minuspio</i> sp. A. (P)	154	72.3
<i>Minuspio</i> sp. A. (P)	83	79.9	<i>Leucon magnadentata</i> (C)	72	73.8	<i>Cossura candida</i> (P)	139	74.4
<i>Cossura rostrata</i> (P)	64	81.3	<i>Harpiniopsis fulgens</i> (A)	66	75.5	<i>Cossura pygodactylata</i> (P)	96	75.8
All fauna (165 species) <sup>b</sup>	4750	100.0	All fauna (159 species) <sup>c</sup>	3837	100.0	All fauna (215 species) <sup>a</sup>	6732	100.0
			<b>R-7 (565 m)</b>					
			<i>Harpiniopsis epistomata</i> (A)	1448	50.8			
			<i>Maldane sarsi</i> (P)	231	58.9			
			<i>Nephtys cornuta</i> (P)	219	66.6			
			<i>Araphura</i> sp B (T)	171	72.6			
			<i>Minuspio</i> sp. A (P)	161	78.3			
			<i>Limnodriloides</i> sp. 1 (O)	100	81.8			
			<i>Cadulus californicus</i> (S)	52	83.6			
			<i>Saturnia</i> nr. <i>ritteri</i> (B)	50	85.4			
			<i>Chloëia pinnata</i> (P)	47	87.0			
			<i>Isocirrus</i> sp. A (P)	36	88.3			
			All fauna (116 species) <sup>c</sup>	2849	100.0			

<sup>a</sup>Total of 24 0.1 m<sup>2</sup> samples (3 replicates on each of 8 cruises: Oct 86, Jan 87, May 87, Oct 87, Jan 88, May 88, Oct 88, May 89)

<sup>b</sup>Total of 23 0.1 m<sup>2</sup> samples (2 replicates on May 88 cruises, plus 3 replicates on remaining 7 cruises listed in Footnote 'a')

<sup>c</sup>Total of 21 0.1 m<sup>2</sup> samples (3 replicates on 7 of the cruises listed in Footnote 'a'; R-8 and R-9 not sampled in Oct 86; R-7 not sampled in May 88)

Table 3. Summary of community variables (all replicates and cruises combined within stations)

Station	Transect	Depth (m)	Ind. m <sup>-2</sup>	(Ind. m <sup>-2</sup> ) <sup>a</sup>	Av. S 0.1 m <sup>-2</sup>	Total S	H'	J'
R-1	North	91	13496	17100	121	336	5618	0.669
R-2	North	161	8983	9864	85	275	5210	0.643
R-3	North	409	4750	4836	46	165	4108	0.557
R-8	Mid	90	16447	19214	141	386	5577	0.649
PJ-1	Mid	145	12818	14840	108	318	5570	0.670
R-9	Mid	410	3837	3996	45	159	4222	0.577
R-7	Mid	565	2849	2964	26	116	3123	0.455
R-4	South	92	28826	30771	151	419	5631	0.646
R-5	South	154	16076	16885	123	358	5564	0.656
R-6	South	410	6732	7063	61	215	4229	0.546

<sup>a</sup>Includes unidentifiable juveniles and damaged specimens

station corresponds to the deep-slope and Santa Lucia Valley group (Site Group 10) of the Phase I study (SAIC 1986), although both *Harpiniopsis epistomata* and *Maldane sarsi* are described in that study as being co-dominants of a separate Santa Lucia Bank and Arguello Canyon group (Site Group 11).

#### Diversity and related community characteristics

A summary of diversity and other community characteristics for the various regional stations is given in Table 3. There are distinct depth-related trends in these variables along all 3 transects. Densities of total fauna, numbers of species, and species diversity ( $H'$ ) all decrease as a function of increasing depth. The evenness component ( $J'$ ) shows similar differences, with the lowest values associated with the deepest stations, although the pattern is less clear among some of the shallower stations. There is also a general trend of increasing numbers of individuals and species from the northern to the southern transect.

#### Statistical analysis of spatial and temporal patterns

Plots of the average number of species per sample and total faunal density versus sampling time are given in Figs. 3 & 4. The plots are arranged to allow direct visual comparisons between depths within a transect or between transects within a given depth range. Three-way ANOVAs were run on these data initially to test null hypotheses of no significant mean differences ( $p \leq 0.05$ ) due to the main effects of cruise, depth, transect location, and their interactions. Tests on both response variables resulted in Type I error probabilities below 0.05 ( $p = \text{near zero to } 0.04$ ) for each of the main effects and all 2-way

and 3-way interactions. Additional 2-way and 1-way ANOVA models with multiple-range tests were applied to portions of the data separately to provide a means for determining which levels of the main effects were significant and for interpreting the various interactions. Although detailed ANOVA out-

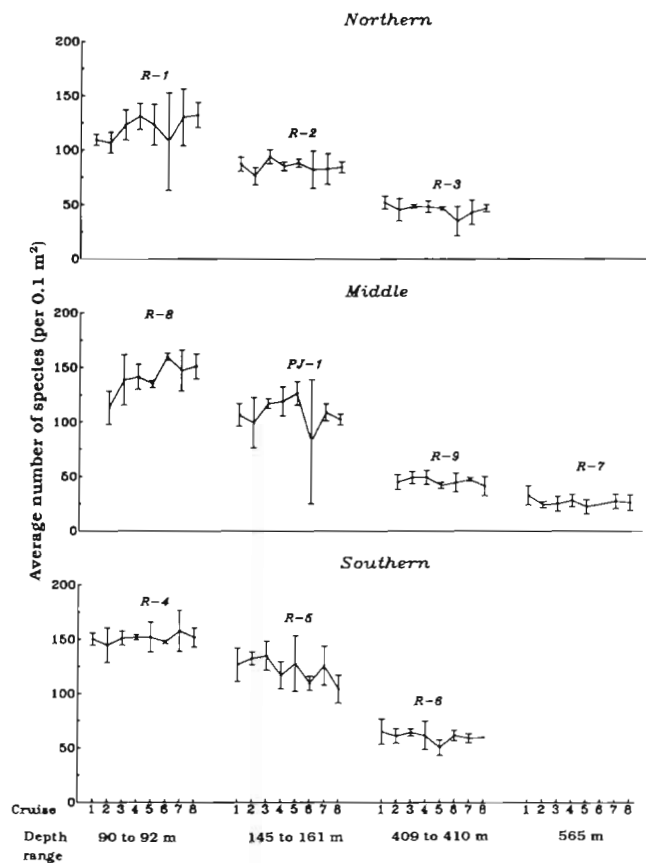


Fig. 3. Average number of macrofaunal species per sample (based on average of 3 replicate 0.1 m<sup>2</sup> samples) and 95 % confidence intervals plotted against time (cruises). Cruises: 1 = Oct 86; 2 = Jan 87; 3 = May 87; 4 = Oct 87; 5 = Jan 88; 6 = May 88; 7 = Oct 88; 8 = May 89



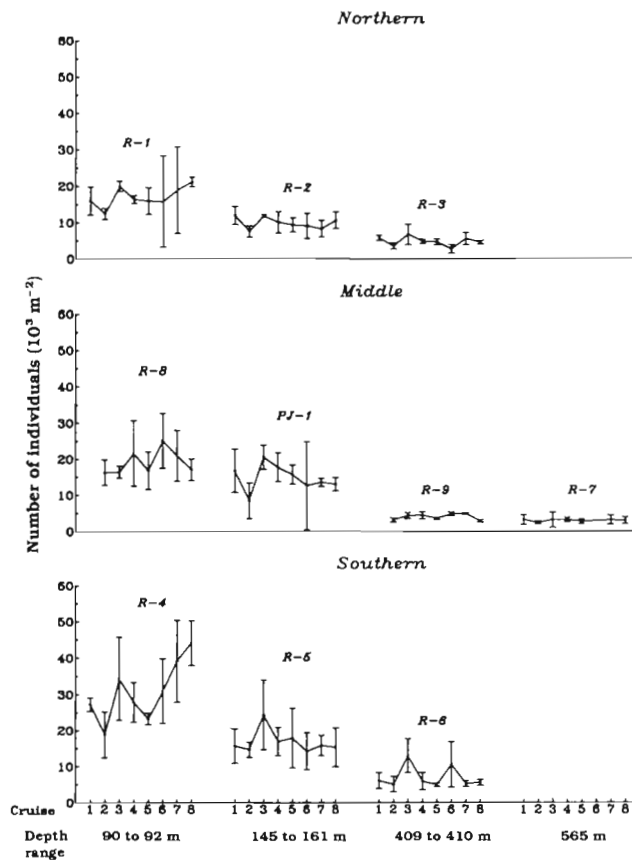


Fig. 4. Macroinfaunal densities (number of individuals  $\times 10^3$   $m^{-2}$ , based on average of 3 replicate  $0.1$   $m^2$  samples) and 95 % confidence intervals plotted against time (cruises). Cruises: 1 = Oct 86; 2 = Jan 87; 3 = May 87; 4 = Oct 87; 5 = Jan 88; 6 = May 88; 7 = Oct 88; 8 = May 89

puts are not included in this paper, resulting Type I error probabilities are discussed to help interpret patterns of variation observed in the plots.

**Numbers of species.** Fig. 3 shows the general pattern of decreasing numbers of species with depth. Mean numbers of species (averaged over all replicates and cruises within a station) range from 121 to 151  $0.1$   $m^{-2}$  at stations along the 90 m isobath to 26  $0.1$   $m^{-2}$  at Station R-7 (565 m). Differences between depths are highly significant ( $p = 0.0001$  to  $0.009$ ) on all sampling occasions along all 3 transects. The effect of time, however, is interactive with a combination of both depth and transect location. For example, along the middle transect significant differences due to time occur only at the shallowest station R-8 ( $p = 0.0004$ ); in contrast, along the southern transect significant differences occur at the 2 deeper stations R-5 ( $p = 0.006$ ) and R-6 ( $p = 0.027$ ). Along the northern transect there are no significant differences due to time at  $p \leq 0.05$ . The interaction of time and depth is significant along both the middle ( $p = 0.036$ ) and southern ( $p = 0.0006$ ) transects.

Transect location has a significant effect on species numbers within all 3 depth zones. There are significant differences between transects (at  $p \leq 0.05$ ) on all cruises except C7 ( $p = 0.118$ ) at 90 m; on all cruises except C6 ( $p = 0.354$ ) at 145 to 161 m; and on all cruises at 410 m. On several cruises, however, stations from the northern vs middle transects and from the middle vs southern transects do not differ significantly from one another at  $p \leq 0.05$ . Although overall community structure and composition appear to be relatively uniform among stations of similar depth (based on cluster analysis), ANOVA results indicate significant mean differences in numbers of species along isobaths, especially for stations that are far apart. This source of variation seems to reflect the general trend of increasing numbers of species from the northern to the southern transect (Fig. 3, Tables 2 & 3).

**Density of total fauna.** Fig. 4 reveals the general pattern of decreasing macrofaunal density with depth. Mean densities (averaged over all replicates and cruises within a station) range from 17 100 to 30 771  $m^{-2}$  at stations along the 90 m isobath to 2964  $m^{-2}$  at Station R-7 (565 m). Mean differences between depths are significant ( $p = 0.0001$  to  $0.023$ ) on all cruises along all transects. In contrast, significant temporal differences (at  $p \leq 0.05$ ) occur only at Stations R-2 ( $p = 0.018$ ) and R-3 ( $p = 0.0008$ ) along the northern transect, at Station R-9 ( $p = 0.0001$ ) along the middle transect, and at Station R-4 ( $p = 0.0001$ ) along the southern transect. The interaction of time and depth is highly significant along the middle ( $p = 0.011$ ) and southern ( $p = 0.0001$ ) transects and relatively insignificant ( $p = 0.272$ ) along the northern transect. Thus, as in the case for numbers of species, temporal variability in density is affected by a combination of depth and transect location.

Similar to the effect on numbers of species, the effect of transect location on density is significant within all 3 depth zones. There are significant differences between transects at  $p \leq 0.05$  on all cruises except C6 ( $p = 0.120$ ) at 90 m; on all cruises except C6 ( $p = 0.545$ ) and C8 ( $p = 0.076$ ) at 145 to 161 m; and on all cruises except C2 ( $p = 0.063$ ), C4 ( $p = 0.228$ ), and C7 ( $p = 0.621$ ) at 410 m. Thus variation within a depth stratum must be taken into account when interpreting bathymetric patterns over broad areas.

### Multiple discriminant analysis

Mean values of other measured environmental variables for the 6 station groups defined by numerical classification of the macroinfaunal species data are given in Table 4. Multiple (canonical) discriminant analysis was performed to identify the variables that best account for the station groupings, as a means of

Table 4 Untransformed mean values of abiotic environmental variables (D. Hardin, Kinnetic Laboratories, Inc., pers. comm.) for station groups defined by numerical classification of macroinfaunal species data. DO = dissolved oxygen, TOC = total organic carbon

Station cluster group	Stations included	Depth (m)	Mean grain size ( $\phi$ )	Sorting ( $\phi$ )	Percent sand	Percent silt	Percent clay	DO ( $\text{ml l}^{-1}$ )	TOC (%)
1	R1, R8, R4	91	4.3	1.3	24.4	67.4	8.1	3.1	0.63
2A	PJ1, R2	153	4.7	1.6	10.6	76.4	12.8	2.7	0.99
2B	R5	154	4.0	1.4	53.3	41.0	5.0	2.7	0.52
3A	R3, R9	409	4.9	1.7	5.0	82.1	12.8	1.3	1.41
3B	R6	410	4.2	1.2	34.4	59.1	6.4	1.0	0.66
4	R7	565	5.0	2.5	4.0	64.3	31.6	0.6	2.55

determining what environmental factors are important in structuring the macroinfaunal communities. A separate test to examine the possible influence of meiofaunal variables on macrofaunal distributions produced an insignificant second discriminant function, not interpretable graphically. Thus, subsequent discussion focuses on the 8 abiotic environmental variables shown in Table 4. Among-group differences based on these variables are highly significant ( $F$  statistics =

29 to 12 179,  $df = 8, 116$ ) as are the first 2 discriminant functions (Function I:  $F = 124.4$ ,  $df = 40, 508$ ; Function II:  $F = 20.1$ ,  $df = 28, 423$ ). Fig. 5 shows the separation of the groups of stations on the first and second discriminant functions, which account for 99.56 and 0.28 %, respectively, of the among-group variance (cumulative percent = 99.84). Because additional functions add little to the interpretation, evaluation of group separation is based on the interpretation of these 2 functions. The total structure coefficients (Table 5) aid in this interpretation by providing a measure of the relative importance of each variable in discriminating among the groups (see similar application by Weston 1988).

The 6 groups are separated on DFI largely as a result of differences in depth and near bottom levels of dissolved oxygen. Group 1 consists of the shallowest outer-shelf stations (mean depth = 91 m) characterized by the highest levels of dissolved oxygen (mean =  $3.1 \text{ ml l}^{-1}$ ). Groups 2A and 2B represent upper-slope stations (153 m) with mean oxygen levels of  $2.7 \text{ ml l}^{-1}$ . Groups 3A and 3B represent mid-slope stations (409 m) with mean oxygen levels of  $1.0$  to  $1.3 \text{ ml l}^{-1}$ . Group 4 consists of the sea-valley station R-7, which has the greatest depth (565 m) and lowest mean oxygen level ( $0.6 \text{ ml l}^{-1}$ ).

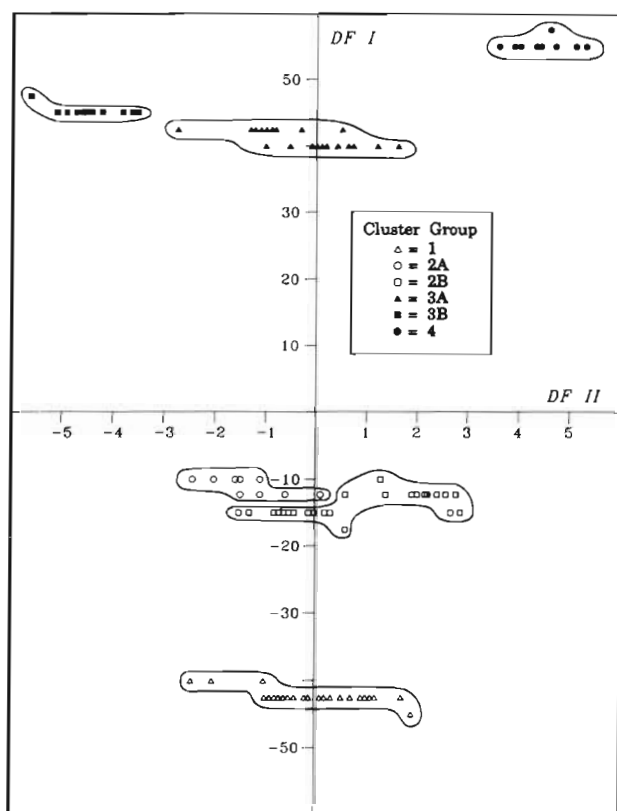


Fig. 5. Separation of station cluster groups on the first 2 discriminant functions (DF I and II). Note that 33 observations are hidden

Table 5. Total structure coefficients (TSC) of abiotic environmental variables on the first 2 discriminant functions (DF). Coefficients of variables considered important on each function are underlined. DO = dissolved oxygen, TOC = total organic carbon

Variable	TSC	
	DF I	DF II
Depth (m)	<u>0.998</u>	0.057
Grain size ( $\phi$ )	0.118	0.343
Sorting ( $\phi$ )	0.591	<u>0.736</u>
Percent sand	-0.407	<u>-0.649</u>
Percent silt	0.010	0.269
Percent clay	0.376	0.437
DO ( $\text{ml l}^{-1}$ )	<u>-0.810</u>	-0.127
TOC (%)	0.617	<u>0.677</u>

DFII reveals the influence of percent sand, sediment organic matter, and sediment sorting on the separation of Group 2B from Group 2A, and Group 3B from 3A. Group 2B consists of Station R-5, which has a depth and mean concentration of dissolved oxygen similar to those of Group 2A; however, the sediment of Station R-5 has a much higher percentage of sand and lower amount of organic carbon in comparison to those of the more northern stations along the same isobath (PJ-1 and R-2). Similarly, Station R-6, which comprises Group 3B, has a depth and mean concentration of dissolved oxygen similar to those of Group 3A; however, the sediment at Station R-6 has a much higher percentage of sand and lower amount of organic matter in comparison to those of the more northern stations along the same isobath (R-3 and R-9). The sediment at Station R-6 also has a much lower sorting coefficient indicating a greater amount of particle sorting. Group 4 (Station R-7) is also separated on DFII from other deeper-water stations comprising Groups 3A and 3B and further exemplifies the influence of these same 3 sediment variables. The sediment at Station R-7 has the lowest percentage of sand, highest amount of sediment organic matter, and the highest sorting coefficient among all stations.

## DISCUSSION

### Spatial patterns of species diversity and abundances

This study reveals distinct patterns of decreasing macrofaunal abundances and diversity with increasing water depth. Similar patterns have been reported in other areas off the coast of southern California (Fauchald & Jones 1978, SAIC 1986) and central and northern California (Lissner 1989). However, the pattern of species diversity is at variance with results of classic studies conducted in the western North Atlantic, which show that the diversity of a variety of macrofaunal taxa increases with depth from the shelf to upper-rise depths of about 2300 to 2800 m (Sanders 1968, Rex 1981) and then decreases again with increasing distance onto the abyssal plain (Rex 1981). Both the abundances and diversity of macrofauna have been shown to increase with depth across the shelf off New England (Neff et al. 1989) and in the Middle Atlantic Bight (Boesch 1979). Such differences demonstrate that efforts to predict faunal patterns in relation to depth gradients in the ocean must take into account a complexity of factors causing variation on local or regional scales.

In the present study, stations at depths less than 200 m are characterized by the highest macrofaunal densities (8983 to 28826 m<sup>-2</sup>), numbers of species

(85 to 151 0.1 m<sup>-2</sup>), and species diversity ( $H'$ , 5.2 to 5.6). Other studies have shown much lower values for comparable depths along the California coast. SAIC (1986), for example, reports lower densities (800 to 6240 m<sup>-2</sup>), numbers of species (32 to 110 0.1 m<sup>-2</sup>), and species diversity ( $H'$ , 2.99 to 3.72) for similar shelf and upper-slope depths throughout the southern Santa Maria Basin and western Santa Barbara Channel. Fauchald & Jones (1978) report lower values (densities: 5366 m<sup>-2</sup>; numbers of species: 87 0.1 m<sup>-2</sup>; and  $H'$ : 2.6 to 3.5) for stations at depths less than 200 m in the Southern California Bight. Lissner (1989) also reports lower values (densities: 5990 to 11350 m<sup>-2</sup>; numbers of species: 86 to 97 0.1 m<sup>-2</sup>; and  $H'$ : 1.6) for stations at depths of 100 to 200 m in basins along the central and northern California coast.

The high values of macrofaunal abundance and diversity encountered in the present study are comparable to those reported for Georges Bank (densities of 2500 to 55000 m<sup>-2</sup> and  $H'$  values of 1.1 to 5.7; Neff et al. 1989) and for the North Sea in locations unaffected by oil-platform discharges (densities of 13000 to 20000 m<sup>-2</sup> and  $H'$  values of 4.3 to 5.8; Kingston 1987). These locations are recognized as being among the most productive fishing areas in the world. The large numbers of species and individuals encountered in the present study suggest that the southern portion of the Santa Maria Basin also supports a highly diverse and abundant macroinfauna. Similarly, Montagna (in press) notes that densities of meiofauna are much higher in the southern Santa Maria Basin in comparison to other well-studied regions, such as the southeastern U.S. continental shelf (Coull et al. 1982), and are comparable to those found in the North Sea (McIntyre 1964, Faubel & Hartwig 1983).

The high diversity of benthos in the region may be related to the fact that the southern Santa Maria Basin is at a zone of biotic transition between 2 zoogeographic provinces: the Oregonian province north of Point Conception and the California Province to the south (Valentine 1966). The macrofauna, for example, include possible endemic species and representatives from both the northern and southern provinces. High abundances could be related to the prominent upwelling events in the area, which contribute to new primary production (Dugdale & Wilkerson 1989) and ultimately to increased supplies of organic material transported to the benthos. The spring upwelling season coincides with periodic peaks in the abundances of total macrofauna and some of the dominant species (e.g. *Chloëia pinnata* and *Nephtys cornuta*; plots not included) although the overall temporal patterns for these species are variable from year to year (see below). Silicate and nitrate concentrations are also generally higher in surface waters during

spring when upwelling events are more common (Hyland et al. 1990).

The above macrofauna comparisons seem valid considering they are based on samples that were all processed with the same size sieves (0.5 mm). However, other general methodological differences (e.g. live-specimen vs preserved-specimen sieving; different groups of taxonomists) may account for the higher densities and species numbers found in this study relative to those reported by SAIC (1986) for overlapping sampling sites in the southern Santa Maria Basin portion of their study. Thus the apparently higher densities and diversity of benthic fauna in the present study area, relative to other regions along the California coast to the north or south, should be interpreted with some caution until additional comparisons can be made. Nonetheless, the present results still demonstrate that the study area supports an abundant and diverse benthic fauna comparable to other regions of known, high biological productivity.

#### Temporal variability

Results of ANOVA provide evidence of significant temporal variability in both abundances and numbers of species. Because stations were sampled randomly at each point in time, it is possible that spatial patchiness among replicates, which is pronounced particularly among the shallower stations (Figs. 3 & 4) is a source of the observed differences among sampling times. However, several lines of evidence suggest that these temporal fluctuations are the result of biological processes rather than sampling error. For example, temporal changes in density during the first year of sampling form a pattern common among most stations (all but R-8 and R-9). This pattern consists of a low during the first winter (Jan 1987), a peak during the following spring (May 1987), and another low beginning in the second autumn (Oct 1987) and continuing through the second winter sampling (Jan 1988) (Fig. 4). This same within-year pattern is not repeated in its entirety at all stations in subsequent years. However, additional density peaks in May of 1988 or 1989 occur at several stations (R-4, R-8, R-1, R-2, R-6). Density lows during October also occur in subsequent years at 2 stations (R-2 in May 1989, R-6 in May 1988).

The occurrence of density peaks in May could very well represent a benthic response to increased sedimentation of phytodetritus, as a result of upwelling events which typically occur in the study area during the spring and summer (Kinney et al. 1990). Densities of one of the dominant polychaetes, *Chloeia pinnata* (plots not included), exhibited strong peaks during one or more of the May sampling periods at all stations.

These peaks usually resulted from large blooms of juveniles. For example, at Station R-6, *C. pinnata* increased from 63 to 7800 m<sup>-2</sup> between January and May 1987, and from 380 to 6200 m<sup>-2</sup> between January and May 1988. These blooms, represented mostly by small juveniles, coincide with peaks in total faunal densities observed at this same station (Fig. 4). The polychaete *Nephtys cornuta* also exhibited occasional peaks in density during the spring upwelling period. Similarly, in the companion study of meiobenthic communities, Montagna (in press) suggests that increased meiofaunal densities in autumn 1987 could be a lagged benthic response to upwelling conditions. However, in both studies, distinct seasonal cycles are difficult to detect and are not repeated throughout all sampling years and stations.

#### Relationships between macrofaunal and other environmental variables

Near-bottom dissolved oxygen, which decreases with depth, could be an important controlling factor in depth-related biological changes. Fig. 6 illustrates the close correlation between oxygen and macrofaunal densities. The decrease in oxygen with depth is attributable to the fact that the oxygen minimum zone impinges upon the continental slope off California at depths (500 to 700 m; Emery 1960) that encompass our deepest station, R-7 (565 m). The dysaerobic levels of oxygen observed at Station R-7, which average about 0.6 ml l<sup>-1</sup>, approach values (<0.15 ml l<sup>-1</sup>) shown to be lethal to some benthic invertebrates under laboratory conditions (Theede 1973). Rhoads et al. (1971) also note that the diversity of benthic invertebrates in several oxygen-deficient marine basins drops markedly as oxygen falls below the range of 1.0 to 0.3 ml l<sup>-1</sup>.

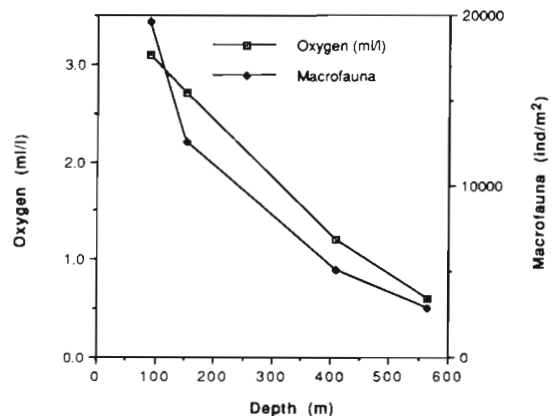


Fig. 6. Comparison of depth-related patterns in macrofaunal densities and dissolved oxygen concentrations (bottom water) averaged over all sampling periods between Oct 1986 and Oct 1988

Similar patterns of low macrobenthic abundances and reduced oxygen with depth have been noted in basins along a majority of the California coast (Thompson et al. 1985, Thompson & Jones 1987, Lissner 1989, Cimberg & Smith in press) as well as in other parts of the world, including the upwelling system off Peru (Rosenberg et al. 1983), the Black Sea (Bacescu 1963), and organically enriched Scandinavian fjords (Mirza & Gray 1981, Gray et al. 1988).

The percentage of sand, which is an important variable on the second discriminant function, may explain the observed patterns of higher abundances and numbers of species at the 2 southern stations R-5 and R-6 in comparison to stations of similar depth and oxygen concentrations to the north. A possible explanation for these patterns is that the higher percentages of sand at these stations offer a greater number of microhabitats for interstitial species to exist. The importance of the fine-sand fraction in structuring macrobenthic communities has been demonstrated on the continental shelf off the coast of Cape Hatteras (Weston 1988) and throughout the Middle Atlantic Bight (Boesch & Bowen in press). As suggested by Weston (1988), higher percentages of sand relative to finer particles may also increase sediment permeability, allowing greater penetration of oxygen. This would be especially important at depths where oxygen is already limiting.

Sediment sorting and organic content are also important variables contributing to the separation of station groups, although their exact roles in controlling species numbers and abundances are harder to interpret. Gray (1974) suggests that poorly sorted sediments may support higher species diversity because of the presence of a wider variety of particle types for benthic organisms to utilize. However, in the present study, the greatest numbers of species were found at stations with sediments that had the highest sorting (least dispersion of particle sizes). Weston (1988) observed that the degree of sorting in sediments off the coast of Cape Hatteras is probably a reflection of the effect of currents on sediment mobility. Similarly, at sites in the present study that are less depositional (the shallower stations along the northern and middle transects and all stations along the southern transect), currents most likely remove the finer particles leaving a more uniform distribution of coarser particles. Thus sediment sorting in itself does not appear to play a major role in controlling macrobenthic community differences, although it serves as a useful indicator of these differences.

Several of the dominant species are carnivorous (e.g. *Nephtys cornuta*, Fauchald & Jumars 1979; *Harpinopsis epistomata*, Oakden 1984) and thus can feed upon other smaller metazoans and protozoans. How-

ever, the majority of these species are deposit feeders, which meet their nutritional requirements from ingestion and absorption of sedimentary organic matter. Although there is a logical functional link between macrobenthic organisms and sediment organic matter as a food source, in this study low macroinfaunal abundances occurred at stations where TOC concentrations were high. Thus the benthic macrofauna of the region do not seem to be limited by low amounts of organic matter. To explain a similar trend along basin slopes in the Southern California Bight, Thompson & Jones (1987) suggested that the low oxygen levels at deeper sites may limit the metabolism of the increased organic material also found at these depths. Another interpretation is that organic matter is simply a manifestation of particle size and, thus, both percent sand and TOC appear as variables that are important in discriminating between station groups. Because of the greater surface-to-volume ratio, it is commonly understood that finer particles have a proportionately greater organic content.

The present study indicates that spatial differences in the composition of macroinfaunal communities in the southern Santa Maria Basin are related foremost to depth in addition to gradients of sedimentary and other depth-associated physical variables. Low oxygen appears to be a primary controlling factor, although percent sand is also important and explains differences that segregate some stations of comparable depth and oxygen levels. While other variables, such as sediment sorting and organic content, are strong discriminators of faunal group differences, their role as controlling factors are harder to interpret, given the direction of their association with the macroinfaunal data. Other factors not measured in this study (e.g. variations in the flux and composition of detrital material or in the intensity of biological interactions such as predation and competition) might also be important in controlling these patterns.

Regardless of the source, the natural variations in these communities should be recognized in any subsequent efforts to monitor potential long-term impacts of offshore oil development. Moreover, we strongly urge that future research in the region include studies that contribute additional information on the importance of organism-oxygen relations, which could become a key consideration under drilling scenarios where the discharge of oil or organic-based muds lead to greater oxygen demands. We suggest that such research include a combination of field and manipulative laboratory experiments to determine the stability of the oxygen gradient, the effects of reduced oxygen on dominant benthic fauna independent of other environmental variables, and the mechanisms of low-oxygen tolerance.

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