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Megabenthic Assemblages of Coastal Shelves, Slopes, and Basins off Southern California

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Abstract.—Megabenthic invertebrate assemblages from soft sediments on the mainland shelf and San Pedro and Santa Monica Basin slopes and floor were identified based on 1203 otter trawl collections made between 1971 and 1985 at depths ranging from 10 to 915 m. Major changes in species composition and abundances occur at mid-slope (~300 m) and at the basin sills (~715 m). The mainland shelf assemblage (10–137 m) is dominated by the sea urchin *Lytechinus pictus* and the prawn *Sicyonia ingentis.* This assemblage is heterogeneous in space and time, with sub-assemblages that reflect severe contamination and large storms and/or El Nino. The basin slopes are dominated by the echinoids, *Allocentrotus fragilis, Brissopsis pacifica,* and *Brisaster latifrons.* The latter two species may exist in kilometer scale herds on the slopes, but they are absent below the basin sills (737 m). Galatheid crabs are the most abundant megafauna in the San Pedro and Santa Monica Basins. Species composition of all assemblages appeared to be seasonally stable, but *S. ingentis* and the tuna crab *Pleuroncodes planipes* increased by several orders of magnitude during El Nino. Numbers of megafaunal species, individuals, and biomass were highest on the basin slopes reflecting elevated levels of organic material in the sediment. Numbers of individuals and biomass increased on the lower slopes (500–800 m), following El Nino. Although organic material is highest in the basins, the numbers of species and individuals were much lower than on the lower slopes. Near anaerobic conditions in the basins probably exclude many species.

The large invertebrates that inhabit soft sediments on the sea floor are the most obvious biological component of the benthos and usually contribute most to benthic community biomass (Haedrich et al. 1980; Smith and Hamilton 1983). Megabenthos are usually defined operationally (e.g., Rex 1981), and in this paper they are animals larger than 4.2 cm, the mesh size of the otter trawl net used for sampling. Megabenthos are different from macrobenthos in size and species composition. Macrobenthos are usually collected with grab or core samplers and are defined as animals retained on a 0.5 mm sieve. While there may be some overlap in the kinds of animals collected by grabs, corers, and trawls, the species collected by trawling are usually quite different due to differences in animal size, motility, and population dispersion.

The purpose of this study was to determine spatial and temporal patterns in megabenthic species composition, abundances, and biomass from otter trawls collected on the mainland shelf and from the San Pedro and Santa Monica Basin

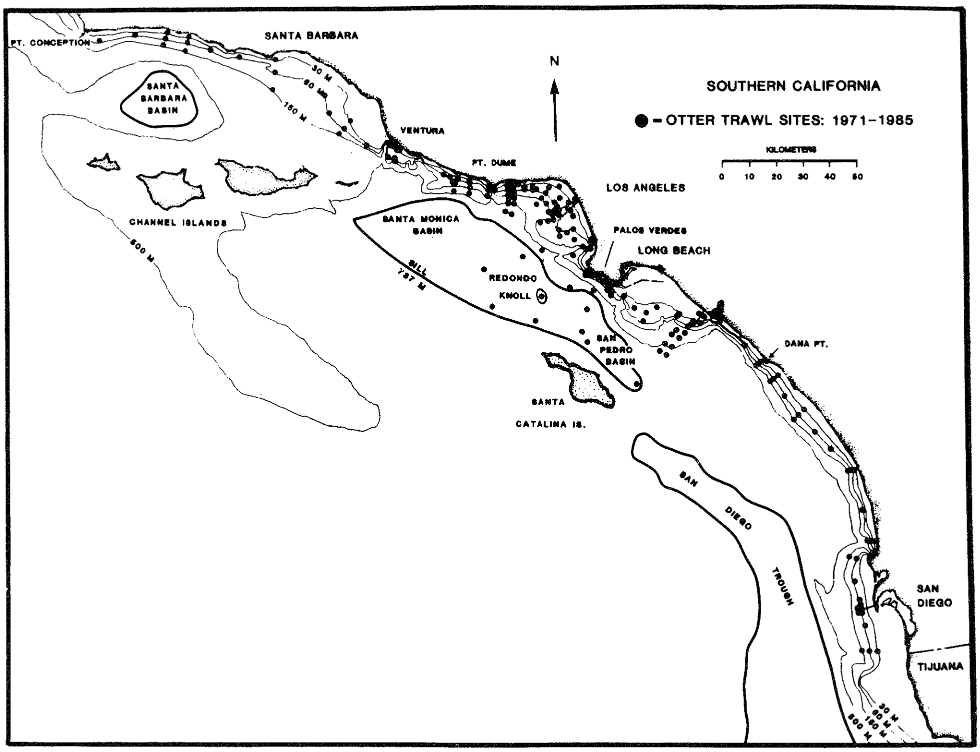


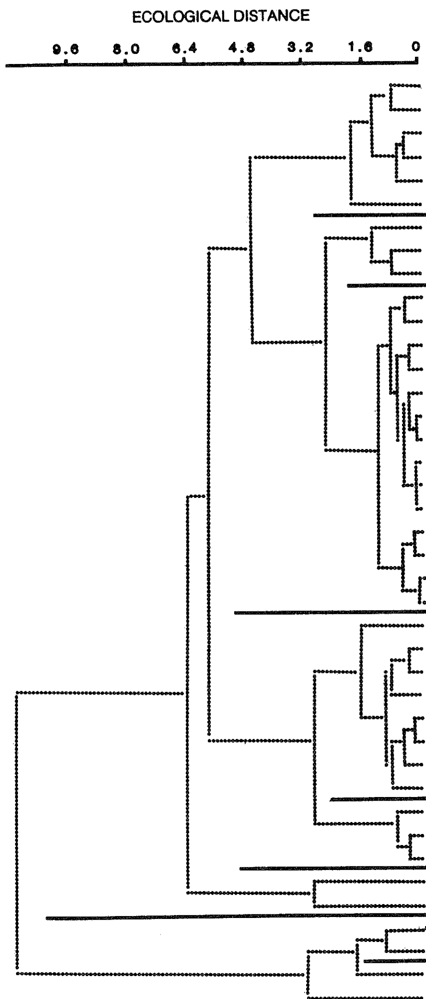
Fig. 1. Chart of southern California coast showing locations of otter trawls collected between 1971–1985.

included. However, single occurrences and taxa above genus were omitted unless they were monospecific or deemed essential for the interpretation of the data. A total of 191 megabenthic species were used in the analysis.

Identification of megabenthic assemblages in space and time was accomplished

Table 1. Sources of data used in this study. CSDOC = County Sanitation Districts of Orange Co., LACSD = Los Angeles County Sanitation Districts, LAOMA = Los Angeles-Orange Co. Metropolitan Area, LARWQCB = L.A. Regional Water Quality Control Board. * indicates data from waste discharge monitoring reports by the agency referenced.

Area-Survey	No. of sites	No. of trawls	Depths (m)	Years	Reference
Ventura-Oxnard	18	19	14–300	1978–82	City of Oxnard*
Santa Monica Bay	66	82	10–300	1977–84	Hyperion Treatment Plant*
Palos Verdes Pen.	35	617	23–137	1971–84	LACSD*
Orange County	12	276	18–137	1976–84	CSDOC*
San Diego	12	59	60–80	1978–84	City of San Diego*
60 m survey	52	52	60	1977	Word and Mearns 1979
Reference survey	38	38	30–150	1985	Thompson et al. 1987b
CSDOC DEEP	16	48	300–627	1981–83	Thompson et al. 1984
LAOMA	8	8	549–915	1977	Mearns et al. 1978b
LARWQCB	4	4	780–877	1985	SCCWRP unpubl.
Totals	261	1203	10–915	1971–85	



NODAL GROUP	NO. OF SITES W	NO. OF SITES S	YEARS	DEPTHS (M)	ASSEMBLAGE
28	2	4	72-83	23-62	
15	1	6	72-76	23-137	
7	6	3	71-73	23-137	Pre-1980
24	15	12	71-84	23-137	Palos Verdes Shelf
27	17	3	71-79	18-137	
8	2	1	71-77	60-137	
26	7	6	77-84	18-23	Post-1981
23	4	2	71-83	23	Storm/El Niño
20	6	4	76-84	18-37	
9	5	7	73-82	23-45	
17	10	18	72-81	18-23	
19	13	12	72-84	18-23	
13	14	8	74-81	23-137	
31	23	16	71-84	18-51	
32	24	20	73-84	14-61	
12	24	20	73-84	18-128	Normal
2	22	13	74-84	10-61	Mainland shelf
3	13	14	73-84	18-60	
35	11	12	76-84	18-61	
22	25	17	73-84	18-137	
16	39	49	73-84	23-137	
36	44	57	75-84	27-137	
40	42	84	71-84	23-137	
11	3	1	73-74	61-137	
14	28	31	74-84	45-150	
34	13	11	73-84	60-150	
21	20	10	77-84	60-137	Outer-shelf-
25	33	38	73-84	60-150	Upper-slope
18	61	46	71-84	27-137	
29	16	10	72-83	23-200	
33	11	11	74-83	137-379	
1	4	5	81-83	300-385	
4	4	2	81-83	315-490	Mid-slope
6	5	5	81-83	478-490	
30	2	4	72-83	23-137	"Short" Trawls
10	1	0	73	137	
5	8	7	77-85	478-780	Lower-slope
38	2	0	77	549-641	
37	2	1	77-85	715-878	Sub-Sill
39	2	1	77-85	823-877	Basins

Fig. 2. Dendrogram from classification analysis of otter trawl data. Nodal groups and ecological distance are explained in the text.

at depths shallower than 50 m peaked in 1979. Abundances at 51–100 m peaked in 1981, then decreased in 1982, during the storms and El Nino. By 1985 mean abundances decreased to less than 100 trawl^{-1} at all depths. Factors that may cause the peaks in abundance are not known.

This species often forms "herds" on the shelf, but solitary individuals may also be collected. Based on grab and box core samples, the herds may be up to 50×10^3 m^2 in size, and are usually composed of several age classes. Average population densities on the shelf range up to 12 m^{-2}, but within herd densities are probably much higher (Fauchald and Jones, 1979; SCCWRP unpubl).

L. pictus also inhabits the Channel Island shelves, and offshore ridges and banks off southern California where they are even more abundant than on the mainland shelf (up to 110 m^{-2}) and may range deeper (to 390 m; Fauchald and Jones 1983).

Table 2. Continued.

Assemblage:		Pre-1980 Palos Verdes	Post-1981 storm, El Nino	Normal mainland shelf	Outer shelf-upper slope	Mid-slope	Lower slope	Basins
Depth range (m):		23–137	18–37	10–137	45–315	300–490	478–780	715–878
No. of trawls:		78	29	658	343	25	17	6
Species	Taxon							
Porifera	(p)	+ (.03)	0	+ (.06)	+ (.02)	+ (.08)	+ (.82)	+ (.67)
Spirontocaris sica	(c)	0	0	R	.3 (.07)	11 (.56)	31 (.82)	68 (.50)
Munida quadrispina	(c)	0	0	0	.2 (.02)	1 (.16)	11 (.59)	115 (.50)
Pennatula phosphorea	(cn)	0	0	0	0	.2 (.16)	14 (.59)	19 (.33)
Liponema brevicornis	(cn)	0	0	0	0	.2 (.12)	2 (.41)	30 (.50)
Munidopsis hystrix	(c)	0	0	0	R	0	4 (.47)	177 (.83)

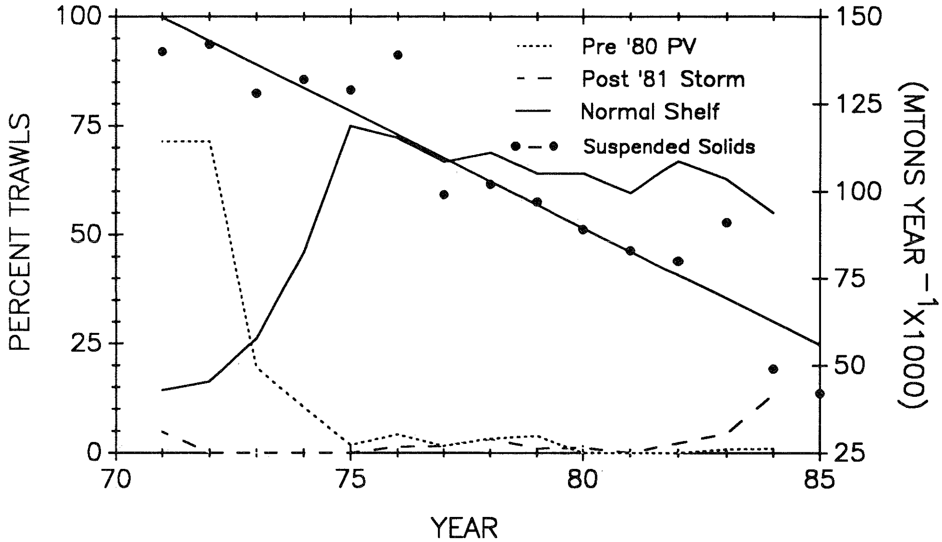


Fig. 4. Percentages of trawls classified in the normal mainland shelf and shelf sub-assemblages each year. Data include all shelf depth sites 10–137 m. Trends in annual mass emissions of suspended solids from PV outfall are alsc shown (data courtesy of Los Angeles Co. Sanitation Districts).

The existence of this sub-assemblage during the 1970's corresponds to a period of severe sediment contamination from the Los Angeles County Sanitation District's (LACSD) sewage outfall which discharged over 140×10^3 mtons yr^{-1} of suspended solids (particulate material resistant to sewage treatment) on the PV shelf. During this study, improved treatment and source control programs greatly reduced the amount of suspended solids discharged from the outfall (Fig. 4). A direct relationship between suspended solids emissions and altered benthos was shown by Mearns and Word (1982), and the demise of the pre-1980 PV sub-assemblage may also be related to decreased solids emissions.

Below emission rates of about 130×10^3 mtons yr^{-1} of suspended solids, normal megabenthos began to inhabit the area. By 1980, the benthic habitat off PV had apparently improved and the samples collected there were usually classified with the normal mainland shelf assemblage.

Another sub-assemblage of the normal mainland shelf assemblage occurred only at the shallowest shelf sites (18–37 m) between 1982–1984 (Fig. 2). Sites from Palos Verdes, Santa Monica Bay, and Orange County were included in this sub-assemblage, but none of 7 sites sampled off Ventura were included. Prior to 1982, only a few sites were occasionally classified in this sub-assemblage, but by 1984, 19% of the mainland shelf sites were classified in this group (Fig. 4). This increase corresponds with severe winter storms and El Nino that occurred in 1982.

As in the pre-1980 PV assemblage, there were no species unique to this sub-assemblage. The most common and abundant species, *L. pictus* and *A. verrilli,* were also dominant in the normal mainland shelf assemblage, but were collected in reduced abundances in this assemblage. Other species such as the anomuran crab *Paguristes ulreyi* and the brachyuran crab *Portunis xantusii* were more common and abundant than in the normal shelf group. The latter species is a warm water crab, normally with a more southern distribution (Garth and Stephenson m, but they may range to sill depths, beyond the depth range of the other echinoids. In contrast with *B. latifrons,* they were more abundant on the San Pedro slope than on the Santa Monica slope.

The two irregular echinoids may occur in large scale herds (kilometers) on the slopes (Thompson et al. 1987a). Their burrowing creates a considerable amount of surface disturbance in slope sediments, but the effects of this activity on other slope benthos is unstudied.

Lower slopes.—The lower basin slopes assemblage inhabited sites between 478–780 m including a site on Redondo Knoll between the San Pedro and Santa Monica Basins. This assemblage was dominated by echinoderms. *B. pacifica* was the most common and abundant species, but ophiuroids and asteroids were also common and abundant (Table 2). Several species, the asteroid *Thrissacanthias penicillatus,* the gastropod *Bathybembix bairdii,* and the endemic demersal siphonophore *Dromalia alexanderii,* were collected only on the lower slopes.

There were differences in the abundances of some species between the San Pedro and Santa Monica Basin lower slopes. The epizoic ophiuroid *Asteronyx longifissus* was an order of magnitude more abundant on the Santa Monica Basin slope, but the asteroid *Myxoderma platyacanthum* was an order of magnitude more abundant in the San Pedro Basin slope. Factors that influence these differences are not known.

In 1982–1983, during El Nino, several species were collected on the lower slopes that were not collected in the 1977 or 1981 samples. These included the asteroids *Brisingella exilis, Ceremaster* sp., *Dipsacaster eximius,* and *Henricia polyacantha,* the pelecypod *Cyclopecten* sp., and the polychaete *Aphrodita japonica.*

Another feature of the lower slopes (and basins) was the sharp increase in the frequency of collection of sponges (Table 2). Hartman (1955) reported the occurrence of a "glass sponge zone" that ringed the lower slopes of the nearshore basins near sill depth. Several species of sponges were collected from these sites, but we have not identified them. These sponges provide a habitat for numerous ophiuroids, polychaetes, sipunculans, and fish. Factors that cause this increase in sponges near, and below the sills are not known.

Basin floors.—The sill depth of the San Pedro Basin is 737 m (Emery 1960) which corresponds closely to the separation of the lower slope and basin floor assemblages shown in the classification analysis. Eight trawls were collected below the sills in 1977 and 1985. One site located on the deepest part of Santa Monica Basin (915 m) was classified with the outer shelf-upper slope group because *P. planipes* was collected there. Another site (780 m) was inhabited by a diverse fauna, including echinoderms, and was classified as a lower slope site. Another site shallower than the sill (715 m) was inhabited by typical basin fauna, without echinoderms. These faunal variations around the sill demonstrate a variable lower slope-basin assemblage boundary in space and time.

The species composition of the megafauna in the basins is very different from the lower slope. Echinoderms were not collected on the basin floors. Instead, two species of galatheid crabs *Munidopsis hystrix* and *Munida quadrispina* were most abundant. Actually, the small gastropod *Mitrella permodesta* was most abundant in trawls, but it is a macrofaunal species (<4.2 cm, the trawl net size).

Below 850 m, Santa Monica Basin may be anoxic (Gorsline ms.) and has been considered biologically impoverished based on grab and core samples (Hartman

Table 3. Pooled mean (S.D.) number of species, individuals, and biomass per trawl in each megabenthic assemblage.

Megabenthic assemblage	No. trawls	Species	Individuals	Biomass (wet kg.)
Pre-1980 PV	78	5.8 (3.7)	68.3 (200.4)	3.0 (3.9)
Post-1981 storm/El Nino	29	5.6 (3.7)	101.0 (345.2)	0.9 (1.1)
Mainland shelf	658	13.1 (6.5)	577.0 (1539.0)	6.6 (11.3)
Outer shelf-upper slope	343	13.7 (6.0)	1869.5 (5347.4)	30.7 (53.5)
Mid-slope	25	18.0 (5.0)	4944.9 (4626.5)	64.2 (73.8)
Lower slope	17	29.5 (11.5)	3874.2 (6409.0)	48.6 (28.9)
Basins	6	11.0 (2.3)	1027.3 (1624.4)	3.9 (4.7)

1955, 1966; Fauchald and Jones 1979, 1983). However, all trawl samples from below the sills contained megabenthic organisms.

Trends in Numbers of Species, Individuals, and Biomass

The mean number of megafaunal species, individuals, and biomass per trawl increased over shelf and slope depths to maximum values in the mid- and lower slope assemblages (Table 3). Below the basin sills, these parameters decreased to values similar to those on the shelf. The large amounts of variation in these averages reflect both within-depth spatial heterogeneity (e.g., herds of urchins) and temporal variation.

Despite this variation, there were significant differences in some of these parameters between some of the classification assemblages. The pre-1980 PV and post-1981 storm/EL Nino sub-assemblages of the mainland shelf had significantly lower numbers of species and individuals than any other assemblage (Table 3; Duncan's multiple range test, $\alpha = 0.05$; Steel and Torrie 1960). Reduced abundances and biomass are typical of assemblages in contaminated areas (Pearson and Rosenburg 1978) and assemblages subjected to severe natural disturbances (Connell 1978). Although both anthropogenic and natural factors reduced numbers of species and individuals, megabenthic species composition (as measured by classification analysis) was somewhat different in response to each type of perturbation.

The mainland shelf and outer shelf-upper slope assemblages had similar numbers of species and individuals until 1982 when the number of individuals at the outer shelf sites increased considerably (Fig. 5). This increase was due to the influx of *S. ingentis* and *P. planipes* during El Nino. Biomass of the outer shelf-upper slope assemblage was consistently higher than on the mainland shelf due to the presence of large numbers of *S. ingentis.* Numbers of species, individuals, and biomass in the normal mainland shelf assemblage did not fluctuate significantly, even during El Nino.

The mid-slope assemblage had the highest number of individuals and biomass per trawl due to the large echinoid populations on the slopes as described above.

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Fig. 5. Mean number of species, individuals, and biomass in each megabenthic assemblage per year. Vertical line at 1976 separates data from off Palos Verdes only and data from all areas of the region.

following El Nino. The sharp increase in these parameters through 1985 suggests time delays in benthic effects from El Nino, but the processes involved are not known. There were no observable effects of El Nino on the basin assemblages.

The most dramatic change in megafaunal assemblages occurred near the basin sills. However, plots of sediment grain-size, organic material, and dissolved oxygen over slope and basin depths do not show any discontinuities at the sills that correspond with this major faunal break (e.g., Minard 1968; Gorsline ms.). The faunal break at the sills could be the result of episodic anoxia and flushing in the nearshore basins. Such episodes have been reported in the Santa Barbara Basin where anoxic bottom water was rapidly (weeks) flushed with water of higher oxygen concentrations, then decreased (months) back to anoxia (Sholkovitz and Gieskes 1971). Similar episodes may occur in the Santa Monica Basin (Gorsline ms.). Although episodic flushing may raise the dissolved oxygen concentration of basin water for an unknown period of time, that period of time may be insufficient for repopulation of the sub-sill basins before oxygen again decreases below megabenthic tolerances.

The presence of living megafaunal animals in the nearshore basins has not been previously reported. The sub-sill slope and floors of San Pedro and Santa Monica Basins are inhabited by up to 34 megabenthic species, but how they can exist in such low oxygen habitats is poorly understood. Current sediment biofacies models consider anoxic areas to be uninhabited by benthos (Savrda et al. 1984; J. Thompson et al. 1985). Although few basin megabenthic species are deep burrowers and their activities may not produce bioturbation, their existence should be accounted for in models of animal-sediment interactions.

The numbers of megabenthic species, individuals, and biomass per trawl increased over shelf and slope depths, opposite to decreasing trends in those parameters for the macrobenthos (Thompson and Jones 1987). Maximum numbers of megafaunal species, individuals, and biomass occurred on the lower slopes. Factors that produce these maxima are not clear, but they reflect elevated levels of organic material. Although levels of organic material are even higher in the basins (6%, Gorsline ms.), dissolved oxygen concentrations may limit the kinds and abundances of megafauna there.

Previous collections of shelf megabenthos in Santa Monica Bay (Carlisle 1968) produced similar species composition as presented in this paper. Megabenthos collected from the Channel Is. shelves and offshore banks also included many species that inhabit the mainland shelf. *Allocentrotus fragilis* and the shrimp *Pandalus jordani* were the most abundant species in trawl samples (Mearns et al. 1978a). Insular species, such as the decapods *Clythrocerus planus* and *Crangon zacae,* occur along the mainland only in areas with coarser substrata (Wicksten 1980). At basin depths, megabenthos from the San Diego Trough, Santa Barbara Basin, and the offshore basins are quite different from those reported in this paper. The Santa Barbara Basin is anoxic which excludes most megafauna (Emery and Hulsemann 1962). The San Diego Trough is dominated by ophiuroids which do not occur in the northern nearshore basins (Barham et al. 1967). The San Diego Trough has no sill, thus the bottom water contains more dissolved oxygen (0.7 ml l^{-1}, Smith 1974) than in the northern nearshore basins. In the offshore basins, ophiuroids and holothuroids are dominant (Fauchald and Jones 1979; Smith and Hamilton 1983). These basins are deeper (>1000 m) but also have slightly higher

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