

RELATIONSHIPS BETWEEN WAVE DISTURBANCE AND ZONATION OF BENTHIC INVERTEBRATE COMMUNITIES ALONG A SUBTIDAL HIGH-ENERGY BEACH IN MONTEREY BAY, CALIFORNIA

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ABSTRACT

Benthic marine invertebrate communities were organized along a gradient of wave-induced substrate motion on the subtidal high-energy beach in Monterey Bay, California. Two general zones were distinguished from 6 to 30 m of water. A shallow zone (<14 m) contained sediments that were commonly disrupted by wave activity and it was primarily occupied by small, mobile, deposit-feeding peracarid and ostracod crustaceans. Patterns of crustacean morphology and mobility were related to their depth zonation. Few animals lived in permanent tubes or burrows in the crustacean zone. Wave disturbance decreased with increasing water depth, while the numbers of sessile and semisessile species, commensal animals, and suspension or selective-surface-deposit feeders increased. The deeper zone (>14 m) was dominated by polychaete worms living in relatively permanent tubes and burrows. A variety of descriptive-correlative evidence indicates that community zonation is strongly influenced by wave-induced bottom disturbance. The evidence includes: 1) a positive correlation between water depth and the numbers of tube dwellers, burrow dwellers, and commensal animals which apparently cannot establish or maintain populations in shifting sediments; 2) other depth and thus substrate disturbance related natural history patterns; 3) a positive correlation between the strength of wave activity and the width and depth limits of the faunal zones (i.e., when wave disturbance is more intense, the crustacean zone ends and the polychaete zone begins in deeper water); 4) a correspondence between the largest decrease in polychaete population size and the season and location of greatest wave activity (winter months at the shallowest station); and 5) a marked similarity between community zonation along a depth-dependent gradient of oscillatory substrate motion (gently sloping sandflats) and the zonation along a constant depth gradient of creeping substrate motion (submarine canyon ridge). Other explanations are inconsistent with these biological patterns and, thus, wave disturbance is apparently the major physical process affecting community zonation.

Sedimentary environments are dynamic and strongly influenced by water currents and the physical and biological properties of the sediment. These animal-sediment relations have become a major focus of benthic community studies since the pioneering work of Sanders (1958, 1960) and Rhoads and Young (1970) and were recently reviewed by Rhoads (1974) and Gray (1974). This previous work was primarily restricted to wave-protected embayments where deposition and re-suspension of fine sediments is a major process. In contrast, the open-coastal environment is commonly subjected to oceanic swell which has a dramatic effect on substrate motion (e.g., Komar 1976). Although sediment scour and motion are major sedimentary processes affecting the shallow parts of most continental shelves, little is known

about their effect on the establishment and maintenance of soft-bottom communities.

The large areal scale of gradients in wave-induced bottom disturbance and the corresponding community patterns are difficult to manipulate experimentally. However, potential relationships between wave disturbance and community zonation can be explored by a posteriori correlations and by a priori use of "natural experiments" (sensu Cody 1974). While communities are often organized along gradients of environmental variability (Whittaker 1962, 1967; Mills 1969; Nichols 1970), the complex interactions between physical and biological regulatory processes are rarely understood. The descriptive and experimental studies in the marine rocky intertidal habitat are an important exception (e.g., Connell 1961; Dayton 1971; Ricketts et al. 1972; Stephenson and Stephenson 1972; Paine 1974; Lubchenco and Menge 1978). This study has two primary objectives: to describe the zonation of benthic inverte-

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brates along a subtidal high-energy beach; and to examine the relationship between community zonation and wave-induced bottom disturbance. Understanding the role of this predominant physical process is critical to subsequent studies of biological phenomena and their interactions with the physical sedimentary environment.

METHODS

The study area was in central Monterey Bay, Calif., on the sandflats adjacent to the Monterey Submarine Canyon and along a ridge in the canyon head (Figure 1). The southern sandflat transect was the main study site (Figures 1, 2). Stations in 6 (M-1), 9 (M-2), 14 (M-3), 18 (M-4), and 24 m (M-5) of water were sampled at approximately the same time from June 1971 to June 1974. Three stations (9, 18, 24 m) were sampled

along the northern sandflat from August 1974 to June 1975 (Figure 1; N stations). The maximum interval between sampling periods was 3 mo. Therefore, samples were taken during at least the four major seasons at each station. The two deepest stations along the northern sandflat (N-5, 30 m; N-6, 40 m) were only sampled in May 1975. Samples were treated separately to document seasonal patterns and were combined over the study period for each station to examine general zonal patterns.

A third, but much shorter transect (40 m long) was located along a flat ridge in the head of the Monterey Submarine Canyon (Figure 1). Four stations were established at 10 m intervals and at a constant water depth of 14 m. One end of the transect (station D) was highly disturbed by the slumping of sediment down an adjacent terrace wall. No sediment slumping occurred along the opposite end of the transect (station A) (see Environmental Setting section). The movement of sediment by slumping was measured by periodic depth soundings along the terrace wall and by diver observations and measurements at permanent underwater stations. Divers measured the distance from the bottom to the tops of the steel station rods at monthly intervals from May to November 1972. Periodic visual observations of station migrations and algal accumulations proceeded until mid-1974.

All samples and field observations were made by divers using scuba. Routine samples were taken with diver-held can corers (length = 17 cm; area = 0.018 m²) and were washed over a 0.5 mm screen in the laboratory. Eight replicate can cores were usually taken in a haphazard fashion (Fager 1968) at each station on each sampling date. The can corers were 3-lb coffee cans with both ends removed. Animal and sediment loss were prevented by water-tight snap-on plastic lids. Residues were fixed in 4% formaldehyde and transferred to 70% ethanol after sorting. The macrofaunal invertebrates were identified to species (i.e., nematodes, foraminiferans, and copepods were excluded).

A long, diver-operated corer (length = 60 cm; area = 0.018 m²) was used to document the vertical distribution of organisms within the sediment at southern sandflat stations in 9, 18, and 30 m of water during August 1972. To maintain the strata and minimize animal movement through them, the corers were held horizontally after sample procurement. Some cores were sectioned immediately in the boat and others were sectioned within an

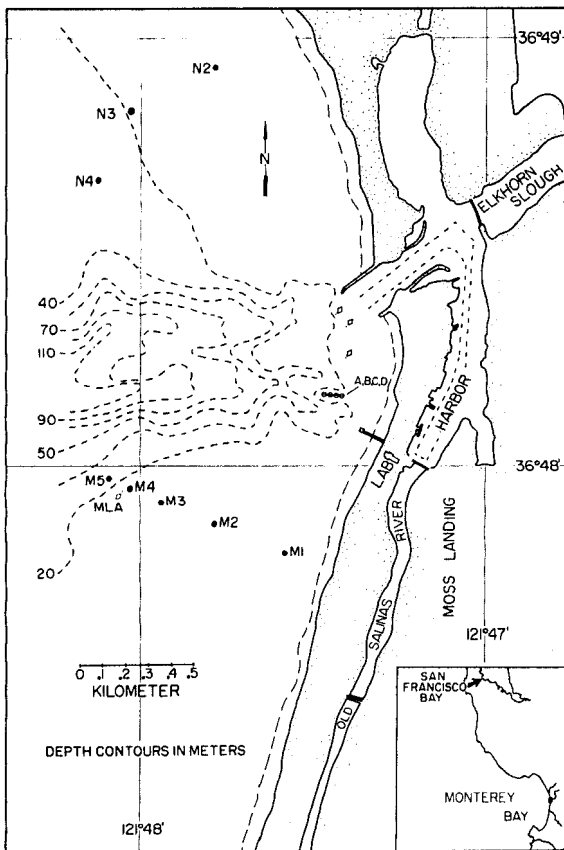


FIGURE 1.—Southern (M) and northern (N) sandflat stations and the canyon transect (A-D) in central Monterey Bay, Calif. N-5 and N-6 were directly east of N-4, 0.5 and 1 km, respectively.

hour at the laboratory. Biomass was calculated from samples taken with a hydraulic suction dredge (Brett 1964) in August 1972. Vertical layers were excavated from a 0.25 m² cylinder and collected separately in 1 mm mesh bags. Animals were weighed after being removed from 70% ethanol and air-dried for 10 min. These weights were converted to grams of organic material with the conversion factors of Lie (1968).

Animals swimming near the bottom were sampled with a funnel trap, an inverted funnel (20 cm in diameter) with the spout leading up and into a holding jar. Legs held the traps within several centimeters of the bottom. These traps were set periodically throughout the entire year, primarily at M-2 (Figure 1; 9 m).

The availability of polychaete larvae was estimated by the settlement of larvae into plastic collecting jars. The jars were wide-mouth gallon containers (mouth diameter = 10.5 cm; volume = 4.5 l) held vertically in a rack at a height of 1 m from the bottom. Jars were collected at 14-day intervals from September 1972 to June 1975 at station M-4 (Figure 1; 18 m). No sediment was placed in the jars, but a 1 or 2 cm layer of seston accumulated during each interval. The jars were covered with a galvanized mesh (1 cm square) to prevent the entrance of fish. The jar contents were washed over a 0.25 mm screen and preserved in 4% formaldehyde. Postsettlement polychaetes were identified to species.

Diver observations of sediment movements and current patterns were frequent. Direct measurements of wave height and wave period were also made in the northern bay from September 1971 to February 1973. They were recorded by the Corps of Engineers from Santa Cruz Pier approximately 18 km from the study area. Although wave heights were generally greater in the central bay, the seasonal patterns were similar throughout the bay.

Feeding and burrowing observations were made in the laboratory and gut contents were examined under a compound microscope. If an animal contained only sediment, it was called a deposit feeder. Some deposit feeders also preyed on other infauna in an aquarium.

ENVIRONMENTAL SETTING

Central Monterey Bay is characterized by high-energy beaches (*sensu* Clifton et al. 1971) that have a relatively gentle seaward slope and a well-developed winter berm. The most distinct

physiographic feature is the large Monterey Submarine Canyon (Figure 1). Prevailing wind and wave direction is from the northwest. Wave refraction in relation to bottom topography concentrates wave energy on the northern sandflat and disperses wave energy in the canyon head and along a portion of the adjacent southern sandflat. Width of the breaker zone and wave height increase dramatically to the north and south of the canyon head (Gordon 1974).

Wave-generated bottom currents have primary control over the sedimentary environment of a beach. Clifton et al. (1971) gave a detailed description of wave-generated depositional structures in the high energy-nearshore environment along the southern coast of Oregon. The same major depositional structures and zones were present in central Monterey Bay. The relative position of the nearshore and offshore is illustrated in Figure 2. The bulk of the faunal sampling and other field observations was performed in the offshore area (Figure 2).

Strong longshore tidal currents can produce lingooid and undulatory small ripples (Reineck and Singh 1973) that trend perpendicular to the ripples produced by oscillating wave-generated currents. Both types were observed at the stations in 18 m of water and deeper, and often resulted in a complicated maze of discontinuous ripple crests. In shallower water, wave-generated currents were more intense and dominated the depositional structure. They produced ripple crests in the fine sand that were more or less continuous and normal to the direction of wave arrival. During periods of large winter swell, conditions at the 9 m station were very similar to those described for the "outer planner facies" of the nearshore by Clifton et al. (1971). Here, ripple marks were obliterated by wave currents and the sediment moved in sheet flow. Fager (1968) observed similar "miniature sandstorms" on the sandflats adjacent to the Scripps Institution of Oceanography in southern California.

The bottom threshold velocity of sediment movement is highly dependent on water depth. Given the narrow range of grain size distributions among the sandflat stations (Table 1), the predominant factors controlling the threshold of sediment movement along the sandflat transects were undoubtedly water depth, wave height, and wave period (Komar 1976). Since unidirectional longshore currents had a decreasing impact on the surface sedimentary structures with decreasing

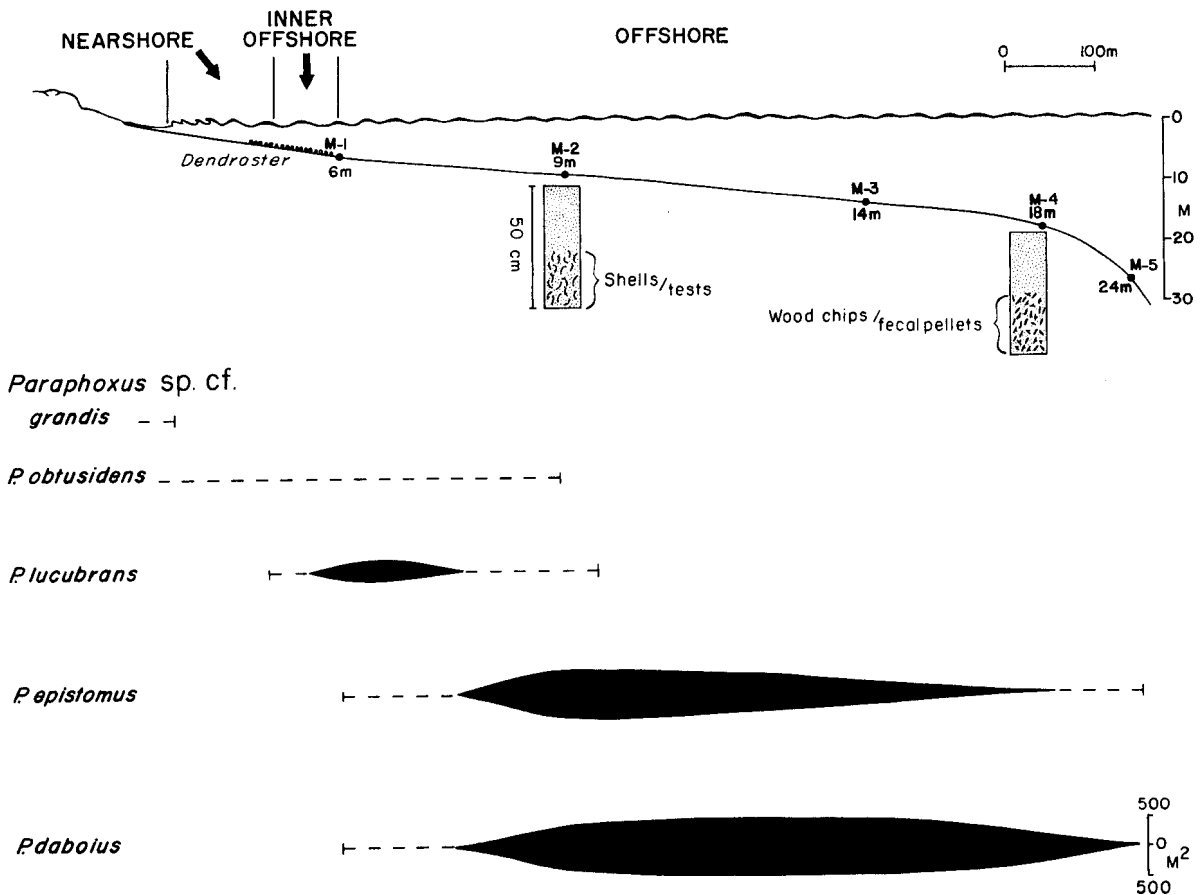


FIGURE 2.—Schematic profile of the beach along the southern transect showing sediment profiles from long cores and the zonation of paraphoxid amphipods in Monterey Bay, Calif.

TABLE 1.—Characteristics of the surface sediments along southern (M) and northern (N) transects in Monterey Bay, Calif. (mean \pm 95% confidence limits).

Station	Depth (m)	n samples	Md (ϕ) ¹	% fine sand (0.250-0.062 mm)	% silt (<0.062 mm)	Coefficient sorting ²	% organic carbon
M-1	6	6	2.93 \pm 0.30	94.4 \pm 5.4	1.0 \pm 1.3	0.44 \pm 0.03	0.08 \pm 0.012
M-2	9	11	3.27 \pm 0.04	91.4 \pm 3.6	8.1 \pm 3.8	0.47 \pm 0.04	0.13 \pm 0.020
M-4	18	7	3.39 \pm 0.05	93.3 \pm 1.5	6.2 \pm 1.5	0.38 \pm 0.02	0.10 \pm 0.050
M-5	24	7	3.53 \pm 0.05	87.6 \pm 2.0	10.8 \pm 1.6	0.43 \pm 0.02	0.18 \pm 0.020
N-2	9	3	3.04 \pm 0.20	96.1 \pm 7.0	1.0 \pm 0.1	0.42 \pm 0.20	—
N-3	18	3	3.15 \pm 0.03	95.5 \pm 3.6	1.3 \pm 1.9	0.42 \pm 0.03	—
N-4	24	3	3.06 \pm 0.10	88.9 \pm 14.0	2.0 \pm 0.3	0.54 \pm 0.30	—

¹ ϕ = $-\log$ (median diameter).

²Folk and Ward (1957); higher coefficient equals poorer sorting.

water depth, the primary sediment movements were caused by waves intercepting a shoaling bottom.

An increase in wave height and a decrease in wave period both cause an increase in the velocity of sediment movement (Komar 1976). As a result,

winter wave conditions should cause the greatest sediment motion (Figure 3). Hundreds of dives and years of qualitative observations of wave activity indicated a strong gradient in substrate movement with changing depth along the sandflats as well as considerably greater sediment motion dur-

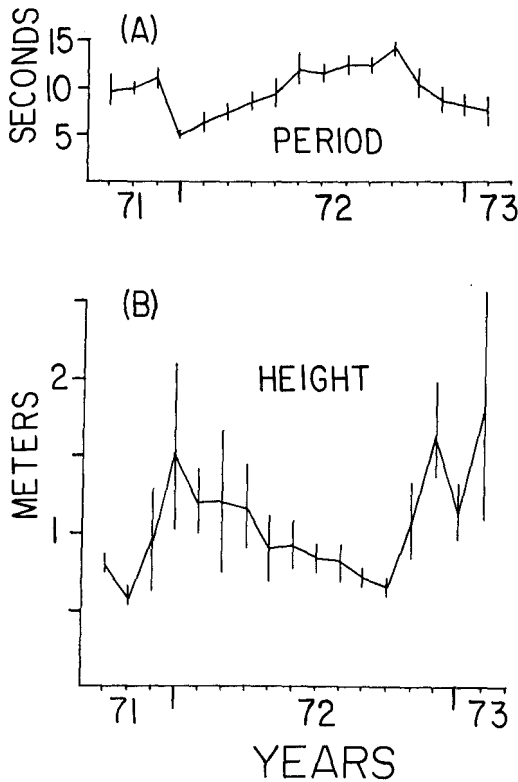


FIGURE 3.—Monthly wave periods (A) and heights (B) during 1971-73 at the Santa Cruz pier in northern Monterey Bay, Calif. (means and ranges).

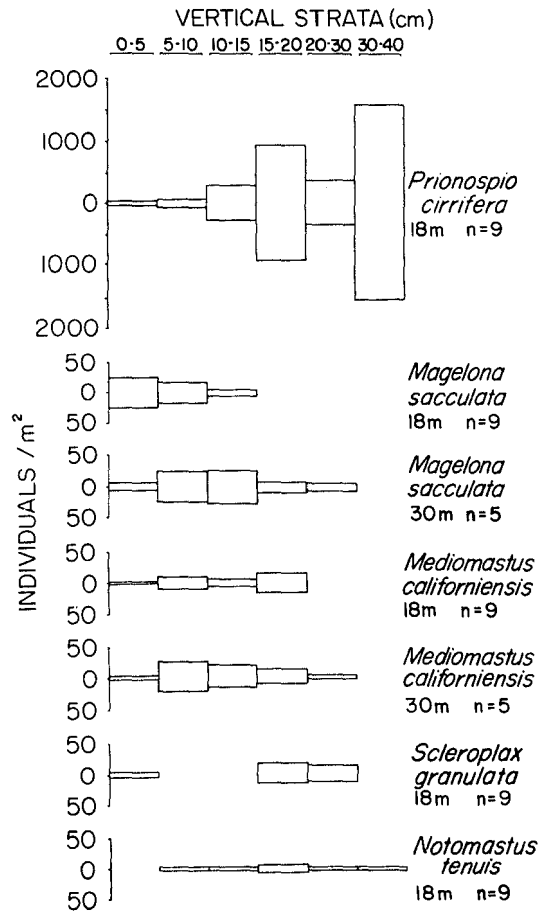


FIGURE 4.—Vertical distribution of invertebrate species living deep in the sediment in Monterey Bay, Calif. (mean per layer based on n cores 50 cm long).

ing the late fall and winter months. These observations are consistent with theoretical expectations (Komar 1976).

Examination of the residue retained by the 0.5 mm mesh screen during the processing of vertical strata from the long cores revealed additional characteristics of the depositional environment. At the 9 m station, strata below 25 cm contained broken tests and spines of the sand dollar *Dendraster excentricus*, broken mollusc shells, and rounded, olive-green silt stones. The surface stratum (top 25 cm) was homogenous fine sand (Figure 2). Similar stratification was observed by Howard and Reineck (1972) in the upper offshore of a low-energy beach along Sapelo Island, Ga. This concentration of shells and tests probably resulted from physical winnowing or reworking during severe storms.

Long cores from 18 and 30 m had no shell/test strata. Instead, there was a concentration of woody chips of terrigenous, riverine origin and a

high density of large oblong fecal pellets (1 mm length) below 25-30 cm in the sediment (Figure 2). The fecal pellets belonged to the deposit-feeding capitellid polychaete *Notomastus tenuis*, which lives deep in the sediment column (Figure 4). Although fecal pellets were produced in situ, the wood chips had been deposited on the surface and were either buried by subsequent deposition or by the biological reworking of the upper sediment layers. Many large deposit feeders burrowed to a depth of 20-30 cm (Figures 4, 5, 6). Nevertheless, this deposit would not persist at the shallower depths of stronger physical winnowing.

In summary, surface ripple mark patterns, the composition of deep sediment layers, frequent field observations, and theoretical predictions indicate a unidirectional gradient in substrate motion highly dependent on depth.

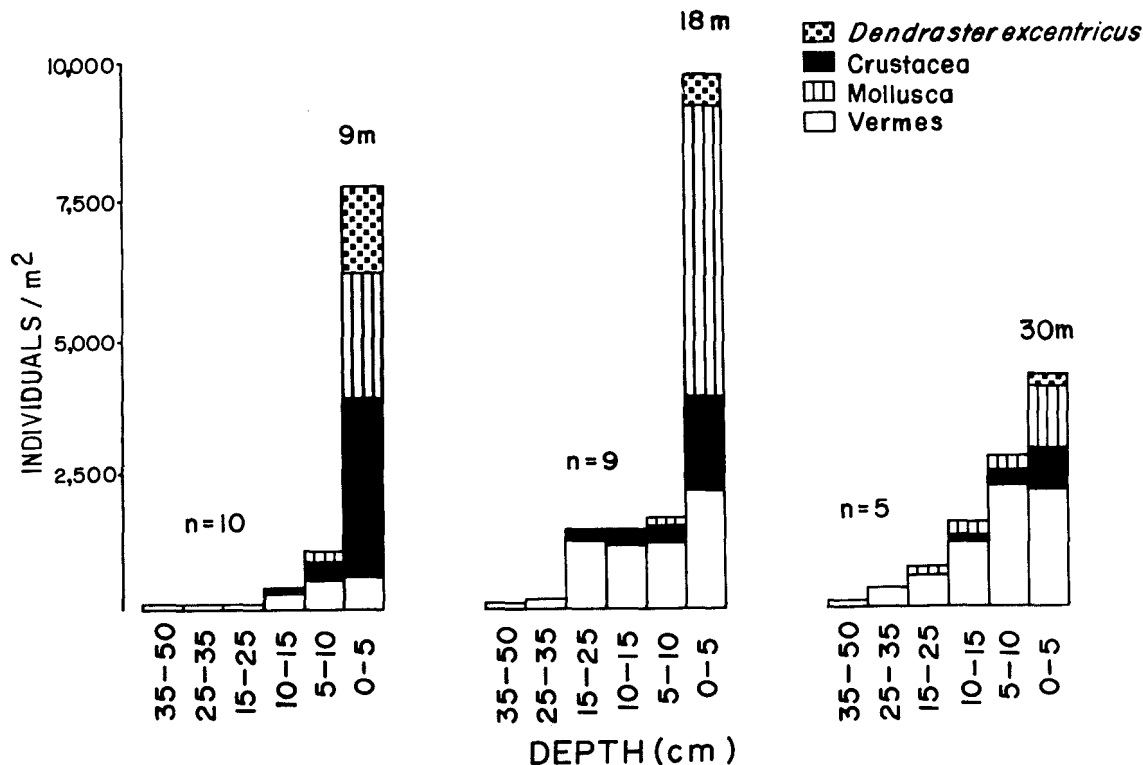


FIGURE 5.—Mean number of individuals per square meter per long core layer in n long cores in Monterey Bay, Calif. Vermes are 90% polychaetes and include enteropneusts, phoronids, oligochaetes, and nemerteans.

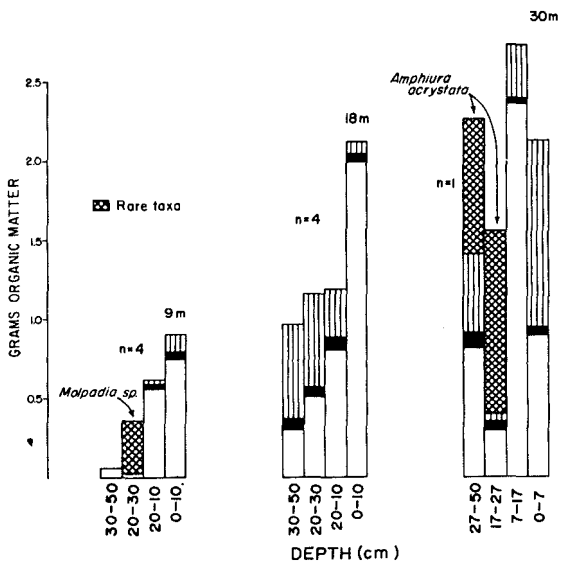


FIGURE 6.—Mean biomass of animals per suction dredge layer in Monterey Bay, Calif. (except at 30 m, where n = 1). Rare taxa indicated. See Figure 5 for bar legend.

Sediment movements in the canyon head included unidirectional down-canyon creeping and slumping as well as oscillatory movements. Diver observations and measurements at permanent bottom stations indicated a general shoaling of shallow (5-15 m) terrace walls and an accumulation of drift plants (primarily *Ulva lobata*, *Macrocystis pyrifera*, *Zostera marina*) during the summer and early fall. Slumping of terrace walls and down-canyon flushing of channels were coincident with the first fall storms and continued through the winter (see Arnal et al. 1973). The same seasonal cycle of sediment accumulation and flushing was observed at the heads of the Scripps and La Jolla Submarine Canyons (Shepard and Dill 1966).

One of the major slumping events occurred at the shoreward end of the flat canyon ridge. Sediment crept down the terrace wall (5-14 m), across the ridge (14 m), and into the deeper canyon channel (25 m). The slumping was evidenced by a change in the position of the terrace wall, the exposure of consolidated mud outcrops on the ter-

race after the fall storms, and the down-canyon movements of station markers along this part of the ridge. The change in the terrace wall position was reflected in a 1 or 2 m increase in the depth of a midwall reference station and in the shifting of the wall base closer to the permanent stations on the ridge. The station markers (rods) at station C and especially D were also moved and slanted in a down-canyon direction. Furthermore, a large ship anchor, dropped in slightly deeper water below station D, moved about 10 m in the same down-canyon direction (Arnal et al. 1973). In contrast, the station stakes at stations A and B remained in a vertical position and did not move. The slumping of the terrace wall during the fall and winter was observed in other years and in other parts of the canyon head as well (Arnal et al. 1973; pers. obs.).

The four ridge stations (A-D) were established along a gradient of substrate motion. Station D was nearest to the slump zone and station A was farthest from the terrace wall, where there was no evidence of sediment slumping. The animals were sampled once along the transect in December 1972. Although there were no significant differences in the median diameter of the sediment and the sorting coefficients among the four stations ($P > 0.1$; Kruskal-Wallis test, Conover 1971), the surface sedimentary structures indicated the persistence of the substrate disturbance gradient from October to December. During this entire period, the sandy sediment was well consolidated and formed parallel ripple marks at stations A and B, but was poorly consolidated and had no ripple marks at stations C and especially D (the area of creeping).

This change in substrate consolidation and ripple mark patterns was not caused by changes in tidal or oscillatory-wave currents. Tidal and longshore currents did not vary along the 40 m transect. Moreover, since oscillatory bottom currents primarily depend on the grain size, water depth, wave height, and wave period (Komar 1976), which were all constant along the transect, the bottom threshold of sediment movement by these currents did not differ among the ridge stations. Therefore, the slumping gradient cannot be quantified in terms of resuspended material or bottom current velocity. On the other hand, poorly consolidated sandy sediments characterized all the slump areas we observed in the canyon head and were also documented in a large slump near the Scripps Canyon in southern California (VanBlaricom 1978; pers. obs.). These slumping events

are extremely difficult to quantify because they have never been witnessed (see Shepard and Dill 1966). Nevertheless, the observations and indirect measurements indicate a unidirectional gradient of substrate motion related to the distance from slumping canyon walls and channeling topography. Stations A (low movement) and D (high movement) represent the ends of this gradient.

OFFSHORE ZONATION PATTERNS ALONG THE SOUTHERN SANDFLAT

The gradational nature of the invertebrate assemblages was apparent from the changes in species abundance along the offshore transect (Table 2). The crustaceans were the numerically dominant group at the 6 and 9 m stations (M-1 and M-2). The density of crustacean species and individuals was highest at 9 m (Figures 7, 8). Six of the seven most abundant species at this station were crustaceans (Table 2). The number of crustaceans decreased steadily seaward of 9 m. The 14 m station was a distinct transition zone between a shallow offshore crustacean assemblage and a deeper polychaete assemblage (Table 2; Figure 7).

The 6 m station was located at the seaward edge of a large bed of *Dendraster excentricus*. The width of the sand dollar bed increased with distance from the canyon head. It was approximately 40 m at the southern sandflat transect (Figure 1) and >75 m wide 2 km to the south. Merrill and Hobson (1970) described a protected open coast *D. excentricus* bed which was similar to the local situation.

Crustacean Zone

Crustaceans

The abundant animals of the shallow-water zone were small, actively burrowing, deposit-feeding amphipods and ostracods (Table 2). The amphipods belonged to three typically sand-dwelling families, Oedicerotidae, Phoxocephalidae, and Haustoriidae, and the ostracods to the Philomedidae. Each family was represented mainly or exclusively by one genus of several species and each species was often found within distinct depth limits.

The genus *Eohaustorius* contained the only representatives of the subfamily Haustoriinae on this coast (Bousfield 1970). Temporal variations in *Eohaustorius sencillus* and *E. sawyeri* were relatively complementary at the 6 m station and may

TABLE 2.—Ten most abundant species at each station along southern transect in Monterey Bay, Calif. Data are number/square meter \pm 95% confidence limits and percent frequency of occurrence in n samples in parentheses. \times = species that ranked 11-17 in abundance; B = semipermanent burrow; T = tube dweller.

Species	Crustacean zone			Polychaete zone	
	M-1, 6 m $n = 106$	M-2, 9 m $n = 107$	M-3, 14 m $n = 30$	M-4, 18 m $n = 141$	M-5, 24 m $n = 28$
Crustacea:					
<i>Euphilomedes longiseta</i>	854 \pm 209 (81)	397 \pm 110 (62)			
<i>Eohaustorius sencillus</i>	351 \pm 105 (60)	1,234 \pm 165 (100)	333 \pm 127 (80)		
<i>Paraphoxus lucubrans</i>	298 \pm 72 (68)				
<i>E. sawyeri</i>	182 \pm 50 (58)				
<i>Synchelidium</i> spp.	143 \pm 44 (59)				
<i>P. obtusidens</i>	66 \pm 21 (31)				
<i>Euphilomedes oblonga</i>		1,064 \pm 204 (87)	513 \pm 220 (93)	\times	
<i>P. daboius</i>		799 \pm 176 (94)	970 \pm 209 (100)	402 \pm 61 (91)	\times
<i>P. epistomus</i>		722 \pm 116 (98)	320 \pm 94 (97)		
<i>E. carcharodonta</i>		397 \pm 116 (76)	\times	\times	
Mollusca:					
<i>Olivella pycna</i>	309 \pm 479 (37)				
<i>Tellina modesta</i>	55 \pm 17 (43)	738 \pm 182 (93)	132 \pm 61 (63)	722 \pm 171 (68)	309 \pm 121 (93)
<i>Mysella aleutica</i>		386 \pm 110 (81)	\times		
<i>Protothaca staminea</i>			\times	105 \pm 39 (44)	\times
Polychaeta:					
<i>Prionospio pygmaea</i> T, B	110 \pm 50 (19)	\times	149 \pm 72 (60)	237 \pm 50 (84)	573 \pm 342 (68)
<i>Scoloplos armiger</i>	105 \pm 33 (56)				
<i>Armandia bioculata</i>		276 \pm 133 (32)			
<i>Magelona sacculata</i> B	\times	237 \pm 72 (61)	303 \pm 171 (80)	1,174 \pm 231 (94)	628 \pm 220 (100)
<i>Amaena occidentalis</i> B		\times	204 \pm 72 (87)	138 \pm 39 (57)	276 \pm 110 (68)
<i>Mediomastus californiensis</i>		\times	182 \pm 66 (80)	331 \pm 50 (93)	1,053 \pm 231 (96)
<i>Northria elegans</i> T		\times	116 \pm 44 (67)	242 \pm 28 (96)	435 \pm 94 (100)
<i>Lumbrineris luti</i> B				226 \pm 28 (94)	242 \pm 50 (93)
<i>P. cirrifera</i> T, B				193 \pm 99 (55)	303 \pm 132 (89)
<i>Nephtys cornuta</i>				\times	325 \pm 105 (93)
<i>Edwardsia</i> sp. (Anthozoa) B				\times	150 \pm 62 (80)

indicate a well-defined boundary between the two populations (Figure 9). No *Eohaustorius* were captured in funnel traps, indicating that much of the life history occurs on or within the sediment.

The genus *Paraphoxus*, in contrast to *Eohaustorius*, has a wide depth distribution in Monterey Bay (Barnard 1960). Four species occurred along the subtidal transect in much greater densities than populations from deeper portions of the bay (Barnard 1960; Hodgson and Nybakken 1973) and in more well-defined zones (Figure 2). A fifth species was the intertidal *Paraphoxus* sp. cf. *grandis*, a new species (Slattery in prep.).

There is an obvious relationship between certain morphological characteristics and the depth zonation of *Paraphoxus* spp. Larger species reached their peak abundance in shallower water (Table 3). *Paraphoxus* sp. cf. *grandis* and *P. obtusidens* were giants relative to the other three species (Table 3). This large size may be an adaptation to strong sediment motion (Sameoto 1969; Fincham 1971). In contrast, *P. epistomus* and *P. lucubrans* were more streamlined and slightly larger than the deepest species, *P. daboius*. *Paraphoxus daboius* was small and had poorly developed eyes (Table 3). It lived in the calmest water (i.e., deepest) and finest sediment and was the only peracaridean crustacean commonly found

below 5 cm in the long cores. *Paraphoxus* were captured by the funnel traps (Table 4).

Euphilomedid ostracods were among the most abundant crustaceans (Table 2). They occasionally occurred in funnel traps (Table 4). In contrast, cumaceans were not abundant on the bottom (Table 2), but were numerous in funnel traps (Table 4). A number of other rare bottom dwellers were also abundant in the funnel traps, including the oedicerotid amphipods *Synchelidium shoemakeri*, *Synchelidium* spp., and *Monoculodes spinipes*; other amphipods *Atylus tridens*, *Tiron biocellata*, and *Megaluropus longimerus*; and a number of mysids (Table 4).

No general correlation exists between swimming tendency and species zonation within the crustacean zone. Although more active *Paraphoxus* species were found in shallow water, nonswimming *Eohaustorius* spp. lived at the same depths. Moreover, the cumaceans and oedicerotid amphipods were active swimmers (Table 4) and occurred in relatively low numbers throughout the crustacean zone. On the other hand, there were distinct morphological patterns suggesting greater swimming among shallower species within particular groups (i.e., *Paraphoxus* and *Euphilomedes* species); however, these groups and others may enter the water column for very differ-

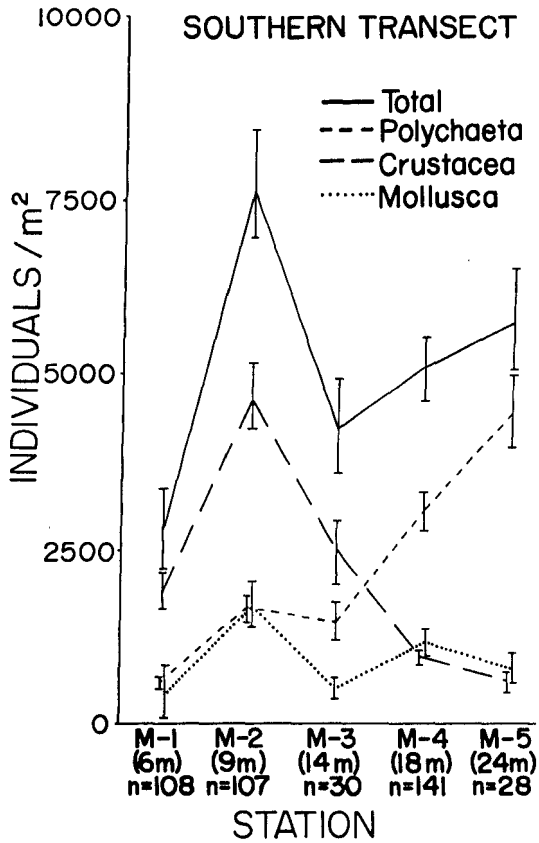


FIGURE 7.—Mean number of individuals per square meter and 95% confidence limits of major groups along the southern transect in Monterey Bay, Calif. (estimates based on n can cores).

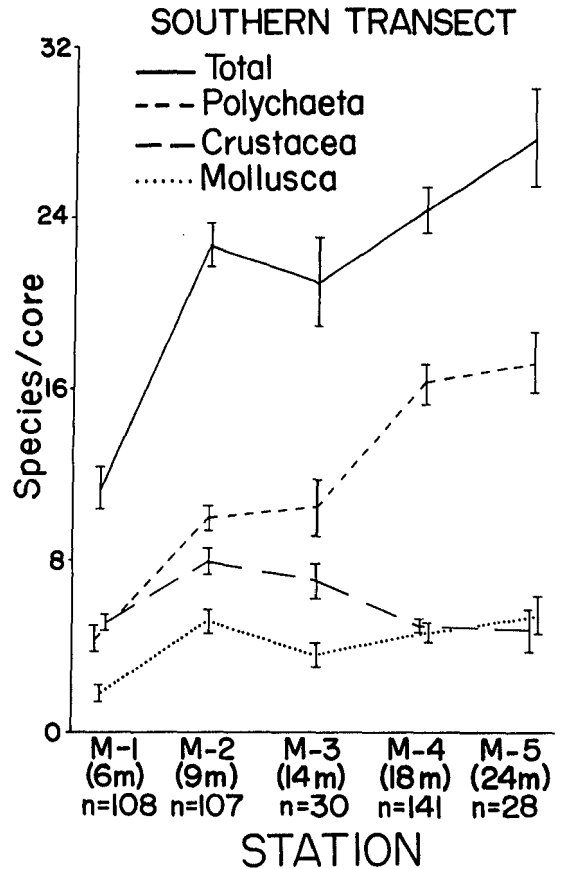


FIGURE 8.—Mean number of species per can core (0.018 m²) and 95% confidence limits of major groups along the southern transect in Monterey Bay, Calif.

ent reasons (e.g., mating, food, substrate movements). Despite these differences, almost all the crustaceans in the crustacean zone were active, free-burrowing species and few inhabited tubes.

Other Animal Groups

The polychaetes were much less abundant than crustaceans in the crustacean zone (Table 2; Figure 7). *Scoloplos armiger*, *Chaetozone setosa*, *Nephtys caecoides*, and *Dispio uncinata* were the most characteristic species at the shallowest station (M-1). *Prionospio pygmaea* and *Magelona sacculata* maintained highly ephemeral populations near the surf zone (see Seasonal Patterns). The uncommon onuphid *Onuphus eremita* was only encountered at 6 m (M-1). In general, the more frequent members of the polychaete as-

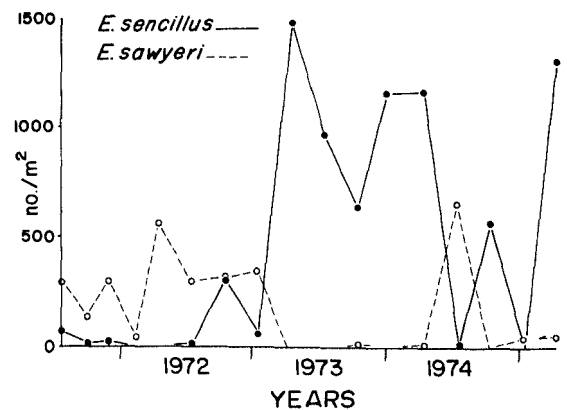


FIGURE 9.—Complementary temporal variations of *Eohaustorius sencillus* and *E. sawyeri* at M-1 (6 m) in Monterey Bay, Calif.

TABLE 3.—Gradation of adult morphological characters in the five species of parapoxid amphipods in Monterey Bay, Calif.

Character	<i>Parapoxus</i> sp. cf. <i>grandis</i>	<i>P.</i> <i>obtusidens</i>	<i>P.</i> <i>lucubrans</i>	<i>P.</i> <i>epistomus</i>	<i>P.</i> <i>daboius</i>
Depth of dispersion center		<6 m	≥6 m	9 m	14 m
Mean size (mm) mature females (±SD)	15±2.5	12±2.2	4.5±0.8	3.7±0.4	2.8±0.2
Ratio of eye diameter to body length	1:35	1:39	1:17	1:33	1:56
Ratio of inner ¹ to outer ramus of uropod III	1:1.09	1:1.04	1:1.1	1:1.5	1:4.2
Number of individuals measured	10	10	20	20	20

¹Higher ratio indicates more foliose uropod used in swimming.

TABLE 4.—Abundance of crustaceans caught in funnel traps at station M-2 (9 m) in Monterey Bay, Calif. (410 trap days).

Species	No. trapped	Species	No. trapped
Amphipods:		Cumaceans:	
<i>Synchelidium shoemakeri</i>	160	<i>Diastylopsis tenuis</i>	57
<i>Parapoxus daboius</i>	79	<i>Lamprops carinata</i>	35
<i>Atylus tridens</i>	66	<i>Hemilamprops californica</i>	27
<i>Tiron biocellata</i>	40	<i>Mesolamprops bodegensis</i>	25
<i>Monoculodes spinipes</i>	40	<i>Cyclasopsis</i> spp.	9
<i>P. epistomus</i>	11	<i>Anchicolorous</i>	
<i>Megaluropus longimerus</i>	1	<i>occidentalis</i>	4
Ostracods:		Mysids:	
<i>Euphilomedes</i>		<i>Neomysis kadiakensis</i>	550
<i>carcharodonta</i>	12	<i>Acanthomysis</i> spp.	250
<i>E. longiseta</i>	7	Others	50
<i>E. oblonga</i>	5		

semblage at M-1 were mobile deposit feeders. The most abundant polychaetes at M-2 (9 m) were species that maintained larger populations in deeper water. The one exception, *Armandia brevis*, had a low frequency of occurrence (Table 2), was highly opportunistic, and primarily lived in more protected areas (Oliver 1979).

Polychaete Zone

The polychaete zone (Table 2) was characterized by animals that require a more stable substratum to establish and maintain burrows and tubes. Most of the polychaetes living exclusively in the shallow crustacean zone did not have permanent tubes or burrows (Table 2). This was true of all the crustaceans. The gradual change in ripple mark and vertical sedimentary structure discussed previously reflected this increase in substrate stability. There were several other distinct visual changes between the two zones. The most conspicuous were the increase in burrow openings and tube fragments and the density of large siphons of the goeuduck, *Panopea generosa*, which was first encountered in the transition area (14 m).

Polychaetes

The polychaetes *Magelona sacculata* and *Nothria elegans* were abundant at the deeper stations (Table 2). The onuphid *N. elegans* lived in a verti-

cal tube constructed of clean sand. Laboratory observations and gut contents indicated that *N. elegans* was a surface-deposit feeder, scavenger, and predator. *Magelona sacculata* lived in a burrow and was a surface-deposit and suspension feeder. The gut contents of 25 *M. sacculata* were mainly amorphous organic matter with very little sand.

Many other polychaetes were generally more abundant in deeper water. These included the spionids *Prionospio cirrifera* and *P. pygmaea* and the large terebellid *Amaeana occidentalis* (Table 2). *Amaeana occidentalis* constructed a burrow with a mucus-impregnated wall and was capable of extensive burrowing activity in the laboratory. The mouth was often positioned a centimeter or more below the substrate surface with the tentacles extended through the sediment and into the overlying water. The gut contents of *A. occidentalis* and *Prionospio* spp. were similar to those of *M. sacculata*. Apparently, they scrape fine material from the sediment-water interface and catch suspended particles.

In general, a higher proportion of animals was found in lower vertical sediment strata from the polychaete zone (>14 m depth) compared with the crustacean zone (Figures 5, 6). This was expected due to the greater number of tube- and burrow-dwelling inhabitants. Coincident with this increase was an increase in known or suspected commensal or symbiont animals. These included the pinnotherid crabs *Scleroplax granulata* (Figure 4) and *Pinnixa franciscana* and several species of polynoid polychaetes. Although Day (1967) described the paraonid polychaetes as shallow surface burrowers, almost half of the individuals of the three local species (*Aricidea suecica*, *Aedicira pacifica*, and *Paraonides platybranchia*) were found below 10 cm in the sediment (9 individuals in 0-10 cm and 7 in 10-20 cm).

Several rather small species also burrowed deep into the sediment. The capitellid polychaete *Mediomastus californiensis* was generally <1 cm long after preservation and was found throughout the sediment column (Figure 4). Additionally, the

small (< 1 cm long) *Prionospio cirrifera* was found as deep as 30-40 cm in the sediment (Figure 4). It was the most abundant polychaete from the long cores at the 18 m station (Figure 4) and yet ranked only seventh in abundance, when the top 10 cm of the sediment was considered separately. Spionids have ciliated feeding palps and dorsal gill filaments. They generally live in mucus-lined burrows or sand tubes and feed on, or just above, the bottom surface (Hartman 1941). Perhaps *P. cirrifera* inhabits the burrows of thalassinid shrimps in a manner similar to the phoronid worm *Phoronis pallida*. In Bodega Bay, Calif., *P. pallida* is found deep in the sediment in association with *Upogebia pugettensis* (Thompson 1972). The lower portion of the phoronid tube is constructed of relatively coarse sand and the distal end is composed of fine black sediment where the tube passes through the burrow wall of *U. pugettensis*. The tube is oriented normal to the shrimp burrow such that the lophophore can be extended into the burrow for feeding and respiration (Zimmer²). Coincidentally, the highest concentration of *P. cirrifera* per vertical stratum (175) was found deep (30-40 cm) in the only core that contained a large thalassinid, *Callianassa* sp.

It is important to note that these vertical patterns were not artifacts resulting from migration down the core or from physical disturbance. Corers were oriented horizontally while out of water and quickly cut by extruding the core from the corer bottom. Moreover, animals that were known to live very near to the sediment-water interface were not displaced (e.g., small bivalves, crustaceans, and *Nephtys cornuta*).

Other Animal Groups

Although the density of crustaceans was very low in the polychaete zone (Figure 7), the number of tube-dwelling forms was greater (e.g., *Ampelisca* and *Photis* species). Variations in the number of individuals and species of bivalve molluscs (Figures 7, 8) were due to periodical heavy settlement along the entire transect. Juvenile mortality was almost complete and very few specimens were observed that were larger than a few millimeters. The same observation was made by Muss (1973) in the Øresund in Denmark. The

most abundant local bivalves were *Tellina modesta* and *Mysella aleutica* (Table 2). The distribution of *T. modesta* was correlated with the percentage of silt in shallow-water sediments by Barnard (1963). Large individuals were observed in the northern bay and in Moss Landing Harbor, where the fine sediment fraction was greater than that along the transects. There were also high numbers of small (1 mm) juvenile bivalves present in the surface strata of the long cores (Figure 5); however, most of the biomass of molluscs in the lower, hydraulically dredged strata was due to a few large individuals of *Solen sicarius* and *Macoma* spp. (Figure 6).

Ophiuroid communities are generally found at depths ranging from 45 to 90 m in southern California (Barnard and Ziesenhenné 1961). Large individuals of *Amphiura acrystata* were found deep in the substrate at the 24 m station. The animal's oral disc was usually 10-15 cm below the surface and its arms extended through the sediment into the water column. All observed individuals appeared to be suspension feeding. The density of *A. acrystata* was <1/m² at the 24 m station, but increased to 1 or 2/m² south of the study area.

NORTHERN SANDFLAT

The northern sandflat received larger waves and the bottom surge was consistently greater than that along the southern sandflat. The theoretical difference in relative wave energy reaching both beaches was estimated from a detailed wave refraction diagram.³ Assuming wave arrival from the northwest and wave period of 14 s, the total energy reaching the southern transect is only three-quarters of that arriving at a comparable segment of the northern beach. The southern stations also had finer sediment compared with the same northern depths (Table 1). During winter storms, wave heights in the northern area were often more than a meter higher than those at the southern study site. These differences only occurred close to the canyon in the vicinity of the sampling transects and were corroborated by hundreds of scuba diving observations of substrate motion and wave swell on the two sandflats.

If the primary control of the offshore zonation pattern is due to wave-induced substrate motion,

²R. Zimmer, Professor, Biology Department, University of Southern California, Los Angeles, CA 90007, pers. commun. June 1973.

³U.S. Army Corps of Engineers wave refraction diagrams 14-51-1, 1948.

then faunal zones should be shifted into deeper waters by an increase in wave activity. The difference in wave energy arriving at the two sides of the canyon allows a partial test of this hypothesis. As predicted, the animal zones described on the southern sandflat were wider and shifted toward deeper water on the northern sandflat (Figures 7, 10). Density of crustaceans was highest in 18 m of water, the transition zone was wider, and polychaetes did not increase in number until 30 m (Figure 10). Nevertheless, the shape of the curves in Figures 7 and 10, and thus the gross zonal patterns, were remarkably similar. The abundant species were the same on both sides of the canyon, but the rank orders of abundance were not identical (Oliver 1979). Abundance of the numerically dominant crustaceans and the total number of crustaceans was significantly higher along the northern transect (Figures 7, 10). Presumably, this increase was related to the extension of the crustacean zone into deeper water.

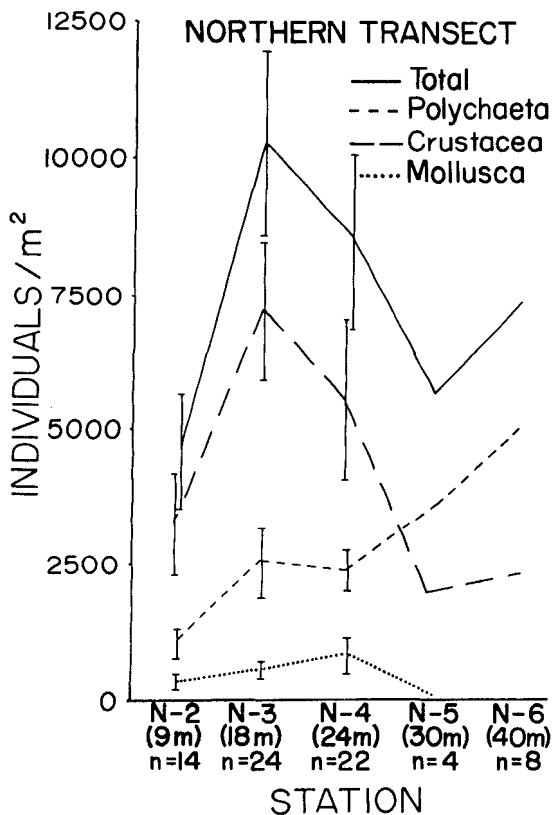


FIGURE 10.—Mean number of individuals per square meter and 95% confidence limits of major groups along northern transect in Monterey Bay, Calif. N-5 and N-6 were only visited once.

The predicted effect of increased wave activity on the infaunal zonation was also observed on the zonation of the sand dollar bed. During moderate to heavy sea states, the outer edge of the bed was in 6 m on the southern and in 9 m of water on the northern sandflat. In addition, the bed was more than 30 m wider along the northern transect. Therefore, the greater width and seaward depth limits of the sand dollar bed were also associated with stronger wave swell.

CANYON RIDGE TRANSECT

Faunal changes along the canyon ridge transect provide further evidence for the relationship between benthic community zonation and substrate motions. The ridge stations (A through D) traversed a substrate movement or disturbance gradient at a constant water depth of 14 m. Therefore, a number of other environmental factors that changed with water depth along the sandflats did not vary along the ridge transect. These included light, temperature, resuspension and settlement of food particles, and the zonation of predatory demersal fish (see Discussion). On the other hand, there was a distinct gradient of substrate movement along the sandflats as well as along the canyon ridge. The type of sediment movement, however, was rather different. The primary substrate movements along the sandflats were caused by wave-generated, oscillating bottom currents, which became greater with decreasing water depth. This substrate disturbance gradient was caused by a unidirectional (down-canyon) creeping of sediment which was greater at stations located nearer to the terrace walls and channels (i.e., stations D and C) (see Environmental Setting).

Despite these differences, benthic community zonation was similar along the sandflat and canyon ridge transects. The similarity is partially illustrated by the abundance of polychaetes and crustaceans (Figure 11). The most striking parallels, however, were in the distributions of individual species (Oliver 1979). Species that were highly characteristic of the shallowest sandflat stations (e.g., *Scoloplos armiger*, *Dispio uncinata*, *Onuphus eremita*, *Olivella pycna*, *Euphilomedes longiseta*) were found at stations D and C along the ridge (zone of sediment slumping). Species that were most abundant at intermediate sandflat depths were found at intermediate ridge stations, C and B (e.g., juvenile *Dendraster excentricus*,

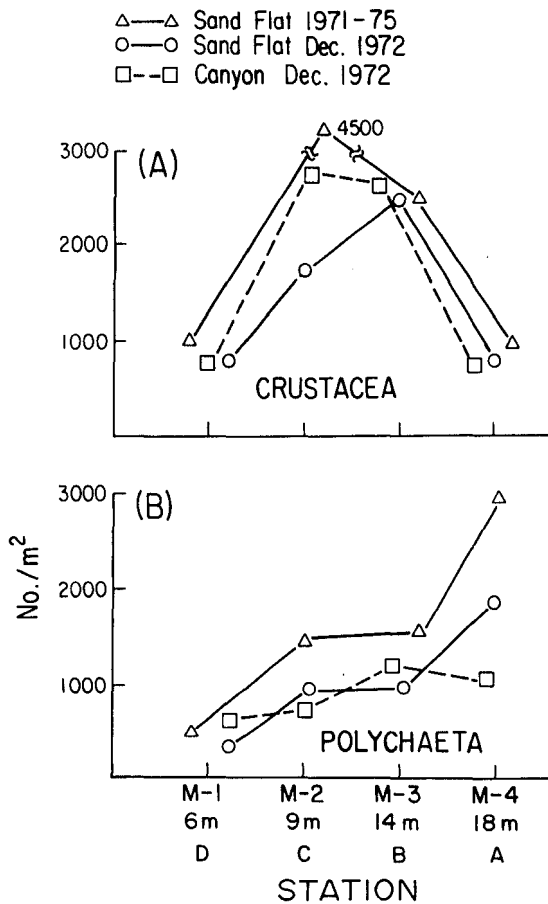


FIGURE 11.—Variations in abundance of crustaceans and polychaetes along the canyon ridge (A-D) and sandflat transects (M) in December 1972, and along the sandflat from 1971 to 1975 in Monterey Bay, Calif.

Eohaustorius sencillus, *Euphilomedes carcharodonta*). Finally, several polychaetes (*Nothria elegans*, *Amaeana occidentalis*, *Lumbrineris luti*, *Magelona* spp.) that were common in deeper water were most abundant at ridge stations B and especially A (farthest from sediment slumping).

There were only a few statistically significant correlations between the abundance of individual species along the sandflat and canyon transects ($P < 0.05$). Since the correlations involved four pairs of stations, there were just 2 degrees of freedom in determining the significance of a product-moment correlation coefficient (Snedecor and Cochran 1967). With 2 degrees of freedom, a significant ($P < 0.05$) coefficient must be at least $r = 0.95$. However, there were more positive correlation coefficients computed for the individual

species than expected by chance alone. Eighteen of the most abundant 23 species (those inhabiting both transects at $>1/\text{core}$) had positive coefficients. Assuming no correlation between the two transects (i.e., independence), the probability of 18 positive correlation coefficients is 0.019 (sign test, Snedecor and Cochran 1967). The probability is less when only the species with relatively distinct zonation patterns are considered ($P < 0.01$). The average correlation coefficient among these species is 0.54 ± 0.12 (95% CL). Therefore, although few individual species showed a statistically significant correlation in abundance along the sandflat and canyon transects, there was a significant trend in positive correlation when the abundant species were considered together.

In summary, benthic community zonation along the gently sloping sandflats (6-18 m) was similar to the zonation along a constant depth transect on the canyon ridge (14 m). This similarity was observed despite differences in substrate disturbance (oscillating vs. unidirectional creeping) and transect lengths (almost 1 km vs. 40 m).

SEASONAL PATTERNS

Seasonal changes in polychaete abundance were more regular than those of the crustaceans (Figures 12, 13). The lowest polychaete abundance generally occurred in the late fall and the winter (Figure 12). The most dramatic population de-

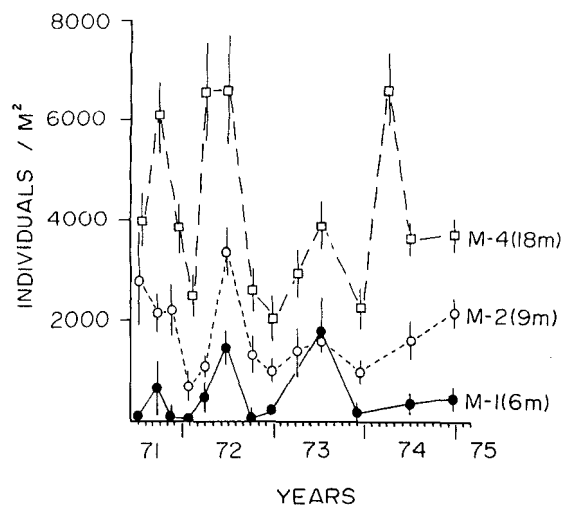


FIGURE 12.—Temporal variations in number of polychaete individuals at three depths along the southern sandflat in Monterey Bay, Calif. (means and 95% confidence limits).

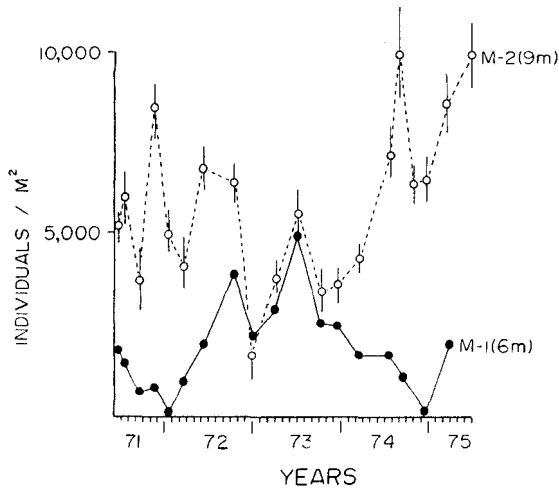


FIGURE 13.—Temporal variations in number of crustacean individuals along the southern transect in Monterey Bay, Calif. (means and 95% confidence limits).

creases, to zero in some cases, were at the shallowest station (Figure 12; M-1, 6 m). Because of the shallow water depth, wave-induced substrate motions were most severe at this station (see Environmental Setting). Furthermore, seasonal substrate movements were greatest during the late fall and winter, when wave heights were large and wave periods short (Figure 3). Therefore, the lowest polychaete numbers were found during that time (late fall and winter) and at the water depth (6 m) corresponding to the greatest substrate motions.

Many environmental factors had a general seasonal trend similar to wave activity. Water temperature, river runoff, and phytoplankton standing stocks also had marked winter-summer variations in Monterey Bay (Oliver et al.⁴). However, wave-induced sediment motion was one of the only seasonal factors that changed with water depth and was, thus, coincident with the depth and seasonal changes in polychaete abundance. The depth-dependent changes in resuspended particulate material are treated in the discussion.

Prionospio pygmaea, *Armandia brevis*, and *Magelona sacculata* settled into the crustacean zone (M-1 and M-2), but rarely survived to adult size. Their frequency of occurrence at the shal-

lower stations was much lower than it was in deeper water (Table 2). Moreover, the low population abundance during the winter was not simply a result of seasonal changes in larval availability. Although some polychaete species appeared to have a relatively seasonal pattern of larval availability (e.g., *M. sacculata*), the larvae of other species (e.g., *N. elegans* and *P. cirrifera*) were present throughout the year (Figure 14).

The seasonal peaks in polychaete abundance in deeper water (M-4, 18 m) were largely due to the

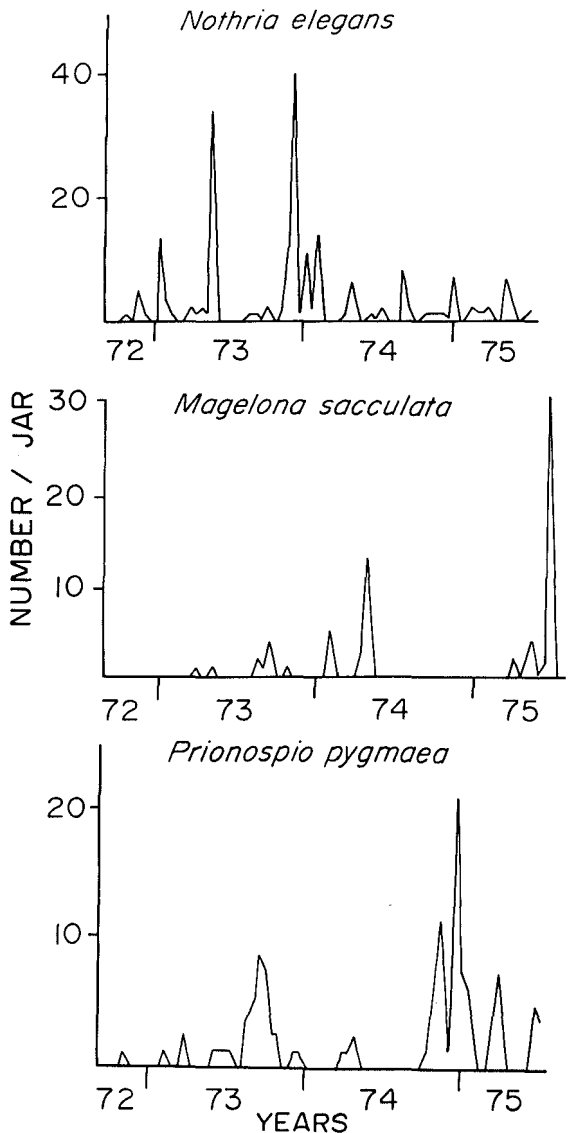


FIGURE 14.—Abundant sandflat polychaetes collected in larval settling jars at the 18 m station (M-4) in Monterey Bay, Calif.

⁴Oliver, J. S., P. N. Slattery, L. W. Hulberg, and J. W. Nybakken. 1977. Patterns of benthic succession after dredging and dredge material disposal in Monterey Bay, California. U.S. Army Corps Eng. Waterways Exp. Stn., Tech. Rep. 0-77-27, 186 p.

settlement of *M. sacculata*. The correlation of the abundance of *M. sacculata* with the total number of polychaetes at M-4 was highly significant ($r = 0.71$; $P < 0.001$). *Magelona sacculata* generally accounted for about one-quarter of the polychaete numbers at M-4. As a result, polychaete abundance patterns in deeper water were dominated by seasonal changes in larval availability (Figure 14) and recruitment, and were not clearly related to substrate motions. This correlation between the abundance of *M. sacculata* and the total polychaete numbers decreased in shallower water (M-2, 9 m: $r = 0.34$, $P > 0.1$; M-1, 6 m: $r = 0.39$, $P > 0.1$).

In summary, seasonal abundance patterns were probably affected by a number of environmental factors including seasonal reproductive cycles and substrate motions. The recruitment or survival of polychaetes was lowest at the time of year and water depth of maximum substrate motions. Hence, the zonation of polychaetes in the crustacean zone was apparently influenced by seasonal changes in wave-induced substrate movements. On the other hand, seasonal variations in crustacean abundance and in deeper living polychaete populations could not be related to sediment motion in a simple manner.

DISCUSSION

The general zonation of benthic invertebrate communities observed in central Monterey Bay is common along much of the temperate open coast of western North America. Carey (1965, 1972), Lie (1969), and Lie and Kisker (1970) observed a high abundance of crustaceans at their shallowest sampling stations and the numerical dominance of polychaetes in deeper areas off Oregon and Washington. Barnard (1963) and VanBlaricom (1978) found the same two zones in southern California and Hodgson and Nybakken (1973) described a comparable pattern in the northern part of Monterey Bay. A similar change from a crustacean- to a polychaete-dominated assemblage was also related to wave exposure by Masse (1972) in the Mediterranean. On the other hand, Day et al. (1971) and Field (1971) did not find a rich crustacean fauna in the "turbulent" zone they described in 3-20 m on the continental shelves of North Carolina and False Bay, South Africa, respectively.

The composition of the fauna along the sandflats was similar to that found at comparable depths in

southern California, but the animal density in Monterey Bay was almost a power of 10 greater (compare Table 2 with Barnard 1963). This disparity was greatest in the crustacean zone. The differences are probably related to different sampling methods: diver corers contrasted to the orange-peel grab used in the earlier studies.

None of the previous studies provide convincing evidence for a relationship between community zonation and wave-induced substrate motions. Although the evidence from the present study is descriptive and correlative, it is consistent with many observations. The general hypothesis is that wave-induced sediment movement has a strong influence on community zonation along the subtidal high-energy beach.

Some of the strongest evidence supporting this hypothesis comes from the natural history patterns of the fauna. There was a significant positive correlation ($r = 0.92$, $P < 0.05$) between the water depth of a station and the numbers of tube builders, burrow dwellers, and commensal animals. A similar trend emerges when the animals are grouped into mobile and sedentary forms (Figure 15). Apparently, biogenic structures were difficult or impossible to establish and maintain in areas of more intense physical sediment movement. Although wave disturbance might destroy burrows and tubes and dislodge their inhabitants, some adults were tolerant of heavy sediment accumulations and capable of vertical substrate migrations (e.g., *Nothria elegans*). The zonation of polychaetes may be largely determined by the habitat selection of settling larvae (Oliver 1979).

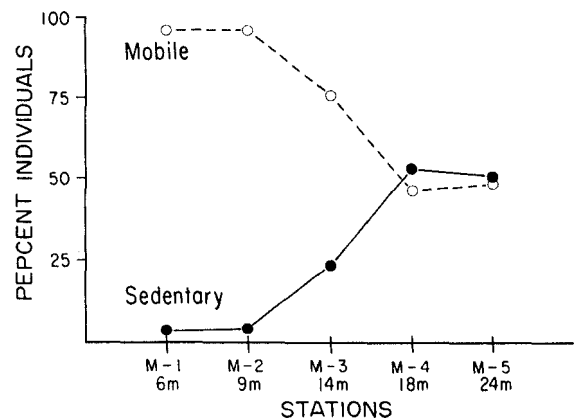


FIGURE 15.—Variations in animal motility patterns along southern sandflat in Monterey Bay, Calif. (percentage of total individuals).

Other natural history patterns also support the relationship between community zonation and substrate motion. In particular, the small peracarid and ostracod crustaceans seem well suited for life in the shifting substrate of the crustacean zone. Their durable chitinous exoskeleton and general activity probably ensure a greater survival relative to many soft-bodied and more sessile forms. Furthermore, their brooding habit and the parturition of large, armoured juveniles undoubtedly increased recruitment success. While no general pattern of crustacean mobility characterized a particular depth, almost all the crustaceans were active burrowers and few maintained a permanent tube or burrow. The lack of dependence on such structures is probably important to the persistence of these large, shallow-water populations. In addition, the most frequently occurring polychaetes in the crustacean zone were also active burrowers that did not live in permanent tubes or burrows.

Variations in zonal patterns along the two sandflats also support the wave-disturbance hypothesis. Wave activity and therefore bottom disturbance were greater along the northern sandflat, where faunal zones were wider and shifted into deeper water. At least one seasonal change in zonation was coincident with an increase in wave activity. The season (late fall and winter) and location (shallowest station, M-1, 6 m) of the greatest wave-induced bottom currents were characterized by the lowest recruitment and survival of polychaetes.

The last source of evidence supporting the hypothesis involves the canyon. While the gradient of substrate motion along the sandflat was caused by waves intercepting a shoaling bottom, the gradient of substrate motion along the canyon ridge transect was caused by unidirectional sediment slumping at a constant depth. Despite these very different types of sediment movement gradients, changes in community zonation along the canyon ridge and sandflat transects were similar. This result negates the importance of several other ecological factors that vary with water depth along the sandflat, but were held constant by the canyon contrast. These include light, temperature, the deposition and resuspension of fine food particles, and the zonation of bottom fish.

The deposition and resuspension of fine particles, which might be used as food, depend upon bottom currents. The strongest bottom currents were caused by wave swell (see Environmental

Setting). These oscillatory bottom currents are highly dependent upon water depth and other factors that did not vary along the canyon ridge transect. Thus, while there were probably significant variations in the availability of suspended particles to the different sandflat stations (i.e., their fauna), deposition and resuspension were apparently uniform along the canyon transect.

Demersal flatfish have a zonation that coincides with the zonation of bottom invertebrates. Many species of fish become more abundant with increasing water depth and are more common in the polychaete zone (Table 5). The only species that was numerous in <20 m was the speckled sanddab, *Citharichthys stigmaeus*. Its peak abundance, however, was in 14-18 m and decreased markedly in shallower depths (Ford 1965; Kukowski 1973). Since these flatfish are major predators of sand-bottom invertebrates and they primarily feed by sight (Ford 1965; VanBlaricom 1978; Hulberg and Oliver 1979), active, surface-dwelling crustaceans might be particularly susceptible prey. If this is true, the depth-related increase in bottom feeding fish might account for the correlated decrease in the shallow-water crustaceans. The changes in community zonation along the canyon ridge do not support this idea. Large and highly mobile flatfish can easily patrol the entire length of a 40 m transect.

In summary, trends in the natural history of the animals, changes in zonal patterns along the southern and northern sandflats, seasonal patterns of polychaete recruitment and survival in the shallows, and the similarity between the canyon and sandflat transects support the contention that community zonation is influenced by changes in wave-induced bottom disturbance. Alternate explanations concerning changes in physical sedimentary parameters (Table 1), the availability of suspended food, and the zonation of large flatfish are not consistent with as many observations. One potentially important alternate hypothesis could not be evaluated here. This is the effect of active crustaceans on the settlement and

TABLE 5.—Total number of species and individuals of fish and abundance of the three most common demersal flatfish in otter trawls taken in Monterey Bay, Calif. (from Kukowski 1973).

Item	15 m	36 m
No. species ¹	7.7	13.8
No. individuals	239	359
<i>Citharichthys stigmaeus</i>	33	12
<i>C. sordidus</i>	14	120
<i>Parophtyrus vetulus</i>	10	33

¹Mean number caught per 10-min tow with 20 tows at each depth.

early survival of polychaete larvae in the crustacean zone.

The most disruptive wave disturbances were caused by the mass accretion and erosion of the substrate by heavy storm swells. The local sedimentary structures indicated that severe scouring occurred at a water depth of at least 10 m and numerous diving observations revealed significant sediment movement at the deepest study stations. These periodic and catastrophic disturbances are probably more important in maintaining the zonal patterns than the average wave activity of the region. In either case, wave-induced substrate motion undoubtedly prevents the establishment and restricts the activities of many animals and directly or indirectly controls community zonation.

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