



## **Spatial Variation in Hard-Bottom Epifauna in the Santa Maria Basin, California: The Importance of Physical Factors**

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### *ABSTRACT*

*Hard-bottom epifauna were photographically sampled at 11 locations in the Santa Maria Basin near Platform Hidalgo. The sampling locations ranged in depth from 105 to 212 m, and were categorized as either low-relief (0.2–0.5 m) or high-relief (>1.0 m) habitat. Sampling was conducted on seven occasions between October 1986 and October 1990. Analysis of variance indicated that the 22 most common taxa varied according to depth and habitat relief, with many taxa exhibiting highest abundances in deeper high-relief locations. Some of the deep high-relief taxa also varied according to orientation on high-relief rocks, and most often faced into stronger currents. Conversely, several taxa which were most abundant in low-relief habitat often faced into weaker currents. There was a strong negative correlation ( $r = -0.988$ ) between the combined abundances of the deep high-relief taxa and the flux of suspended sediments measured with near-bottom sediment traps at each location. We suggest that the rich epifaunal assemblages that characterize deep high-relief habitat in the Santa Maria Basin are associated with a balance between the positive effects of high current speeds and the negative effects of suspended sediments.*

### **INTRODUCTION**

Rocky intertidal and shallow subtidal habitats have been extensively studied, and there are numerous physical and biological factors known to affect their community composition. For example, community composition

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has been ascribed to the processes of larval settlement (Caffey, 1985; Connell, 1985; Davis, 1987), competition and predation (Kay & Keough, 1981; Bak *et al.*, 1982; Sebens, 1985, 1986), grazing (Miller, 1982; Witman, 1985, 1987), and to physical factors; temperature (Scheer, 1984; Glynn & D'Croz, 1990), water currents (Peattie & Hoare, 1981; Dayton *et al.*, 1982; Sebens, 1984; Barry & Dayton, 1986, 1988), turbidity (Loya, 1976; Dodge & Vaisnys, 1977; Hong & Sasekumar, 1981; Hudson, 1981), and ultra-violet light (Jokiel, 1980). The rich ecological literature of rocky intertidal and shallow subtidal habitats is partly due to the ease of viewing and manipulating these habitats, and the steep gradients in physical factors which are present. Until recently, ecologists have not had the instruments to investigate deeper hard-bottom habitats, which are inaccessible by SCUBA diving.

Generally, deeper habitats have been assumed to vary less over time and space than shallower habitats. Observations have indicated deeper hard-bottom communities vary according to depth (Vinogradova, 1962; Rowe & Menzies, 1969; Carney & Carey, 1976; Hecker *et al.*, 1983), and a number of studies have suggested the importance of hydrodynamic processes in structuring these communities (Genin *et al.*, 1986; Mullineaux, 1988, 1989; Messing *et al.*, 1990). Nevertheless, few generalizations can be drawn, because of the paucity of quantitative investigations. Studies of deep hard-bottom communities are still generally limited to describing organism distributions, so that testable hypotheses can be formulated concerning the factors that affect those distributions.

The Santa Maria Basin, along the southern California shelf and slope, is the site of a multi-disciplinary study to determine the effects of discharges from petroleum platforms on the benthic environment (Hyland *et al.*, 1990; Hyland *et al.*, 1994). An emphasis has been placed upon hard-bottom communities, because of assumptions concerning their sensitivity to disturbance, and their importance as nursery areas for commercially valuable species. Hyland *et al.* (1994) discuss the effects of the platform discharges on the physical environment and biota near Platform Hidalgo. In the present study, we use the 4-year data set to evaluate the effects of factors that are not related to the platform.

The Santa Maria Basin has previously been the site of several qualitative surveys of hard-bottom communities related to petroleum exploration (Nekton, 1981; Dames & Moore, 1982, 1983; Nekton and Kinetic Laboratories, 1983; SAIC, 1986). These surveys were important for describing the visibly dominant species in the area, and for proposing factors which may affect their distributions. Nevertheless, we are not aware of previous quantitative studies over the broad range of time and space covered by the present study, either in the Santa Maria Basin or elsewhere in outer continental shelf and slope environments.

## METHODS

The study area is approximately 20 km west of Point Conception, near the western end of the Santa Barbara Channel (Fig. 1). Oceanographic processes in the area are very complex due to the confluence of the westward flow along the northern shore of the Santa Barbara Channel with the southward flow of the California Current (Savoie *et al.*, 1991). It is the site of substantial upwelling. Isobaths are oriented northwest-to-southeast, and bottom currents generally flow toward the northwest, although current-meter records contain a strong cross-shelf tidal component (Savoie *et al.*, 1991).

A reconnaissance was conducted in October 1986 of areas near Platform Hidalgo which had been indicated as hard-bottom habitat by previous geophysical surveys. Eight rocky reefs were chosen as sampling stations that were (1) at various distances from Platform Hidalgo, (2) across a range of depths, and (3) represented two types of habitat (Fig. 1 and Table 1). Low-relief habitat was defined as rocks 0.2–0.5 m in vertical relief, and high-relief habitat was defined as rocks >1.0 m in vertical relief. High-relief habitat was found only below approximately 160 m water depth.

Sampling was conducted in October 1986, July 1987, November 1987, October 1988, May 1989, October 1989, and October 1990. The epifaunal assemblages at the hard-bottom stations were sampled photographically with a remotely operated vehicle (ROV). The ROV was equipped with a video camera, a 70-mm still camera, a strobe light, two split-beam lasers,

TABLE 1  
Stations Sampled for Abundances of Hard-Bottom Epifauna near Platform Hidalgo

Station	Depth (m)	Depth category <sup>a</sup>	Habitat relief <sup>b</sup>
PH-E(L)	119	Shallow	Low
PH-F(L)	105	Shallow	Low
PH-I(L)	109	Shallow	Low
PH-J(L)	117	Shallow	Low
PH-K(H)	160	Deep	High
PH-N(L)	166	Deep	Low
PH-R(L)	212	Deep	Low
PH-R(H)	212	Deep	High
PH-U(L)	113	Shallow	Low
PH-W(L)	195	Deep	Low
PH-W(H)	195	Deep	High

<sup>a</sup> Shallow: 105–119 m. Deep: 160–212 m.

<sup>b</sup> Low-relief: 0.2–0.5 m. High-relief: >1.0 m.

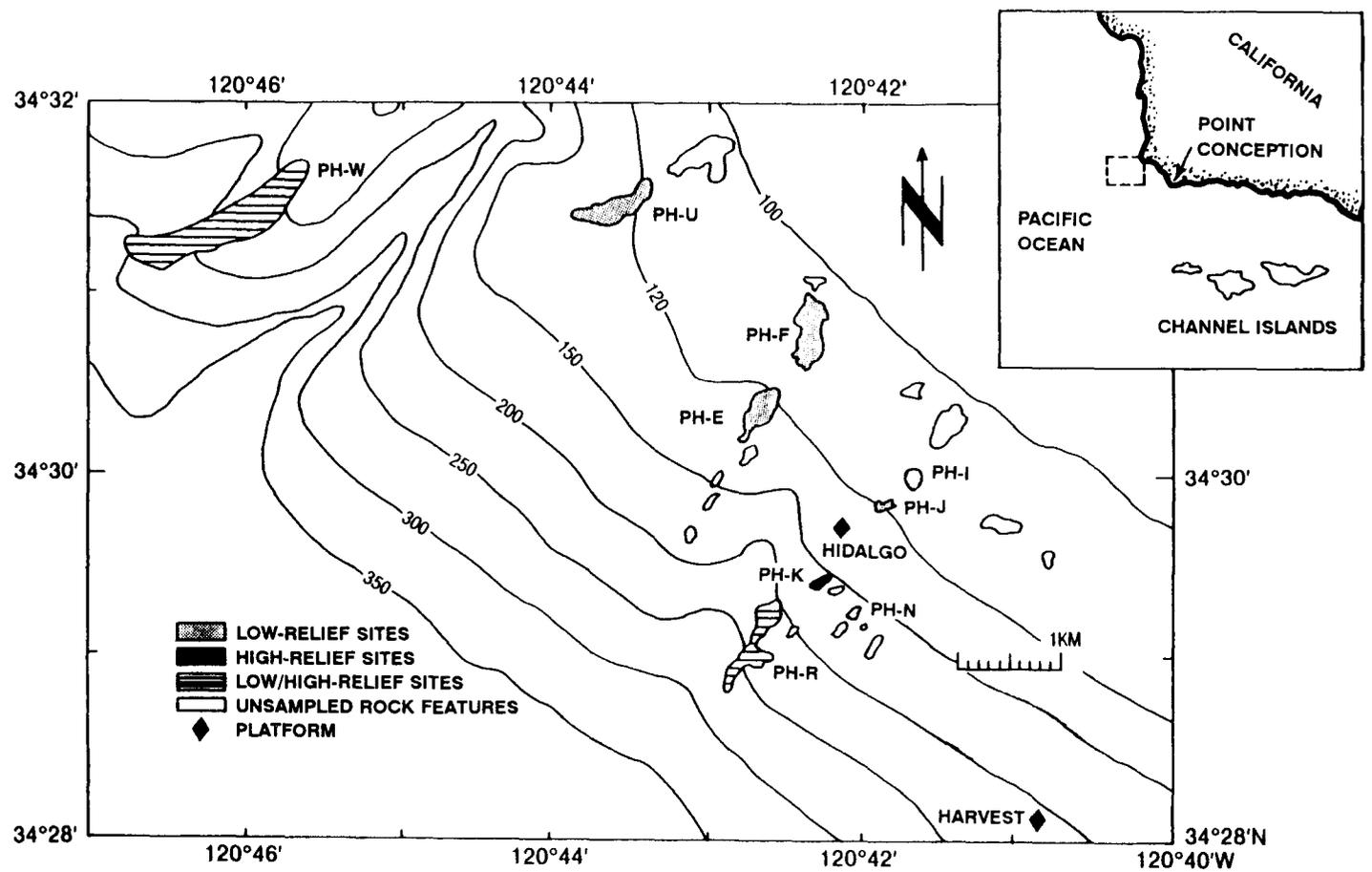


Fig. 1. Hard-bottom features sampled in the Santa Maria Basin, near Point Conception, California (bathymetry in metres).

and a five-function manipulator. The ship's position was determined with an accuracy of  $\pm 3$  m using range data from a series of transponders located at surveyed sites on shore. These data were interfaced with an acoustic navigation system on the ROV, which enabled a position accuracy for the ROV of  $< 5$  m.

The primary sampling device for the hard-bottom assemblages was the 70-mm still camera. The coincidence of the parallel lines of laser images, as seen on the video monitor, indicated the proper distance and angle of incidence between the camera and the seabed (Caimi *et al.*, 1987). Photographs were taken from a distance of 1.4 m, so that the area sampled was 1 m<sup>2</sup>. The mounts for the photographs provide a clear opening of 60 mm on a side, such that the area that was effectively sampled in each replicate was approximately 0.73 m<sup>2</sup>.

Sampling methods at low-relief and high-relief stations differed slightly. Sampling at low-relief stations was accomplished by directing the ROV on a random heading with the cameras pointing down toward the bottom. Since the seabed in these areas is characterized by patchy hard bottom surrounded by soft bottom, all suitable rocks that occurred every 5–10 s were photographed until five to 10 samples had been obtained (depending upon the density of rocks in the area). Another heading was then taken and the process was repeated. At high-relief stations, the ROV took a random heading with the cameras pointed towards the front of the vehicle. When suitable habitat was encountered, the ROV was maneuvered around, and up and down the rock feature, taking nonoverlapping photographs. After a rock feature was sampled, the ROV was directed on another random heading until the next suitable feature was located. The process was then repeated. The ROV position was recorded for every 10th photographic sample, to ensure that the same area of each reef was sampled on successive sampling periods.

Approximately 80 photographic samples were taken at each station to allow 60 samples per station to be analyzed. Some samples were rejected for having too little relief and some were rejected for having less than 30% cover of rock. In all, 3587 photographic samples were analyzed, representing seven samplings of 11 stations.

Epifaunal specimens were collected and identified to aid in the analysis of the photographs. The manipulator on the ROV was used to obtain rocks and to bring them to the surface. The rocks were labeled, placed into buffered 10% formalin, and taken ashore to the laboratory. The epifauna were subsequently removed and identified.

Ancillary measurements were made at each station for later use as correlates in the statistical analyses. The compass heading of the ROV was recorded for each photograph in high-relief habitat to determine if

species distributions vary according to their orientation on high-relief rocks. Sediment traps were also deployed at each station (Parr *et al.*, 1991), and the sediment flux data are used to determine whether organism abundances vary according to concentrations of suspended sediments.

Photographic samples were analyzed by a random point-contact method. Although this method may be inferior to in-situ methods of quantifying abundances in multilayered assemblages (Foster *et al.*, 1991), the inaccessibility of these deep habitats, and the absence of layering, justifies its use in this case. Each photograph was projected, at life size, onto a screen upon which 50 points were randomly distributed. The species or substrate type under each point was noted, and the numbers of individuals of solitary species were counted. Some types of sponges are very consistent in size and were also counted. In addition, all species that showed in a photograph were recorded, regardless of whether they had been contacted by a random point. These species were assigned a default percent cover of 0.5 for calculations of similarity. Default percent-cover values were not added into the total abundances for each taxonomic group.

The percent cover of a species that was contacted by the random points was estimated by dividing the number of contacts by the total number of points. Since this study is focusing on hard-bottom habitat, and because some points fell on deep shadow and could not be read, the denominator in the percent-cover calculations was reduced by the number of dots contacting sediment or shadow. Similarly, the counts of individual organisms were normalized to the visible amount of rock in each photograph by dividing them by the percentage of visible-rock points.

Many of the taxa (e.g., sponges, hydroids, anthozoans, polychaetes, and ectoprocts) observed in the photographs were given descriptive names only, which were assigned to specific morphological forms that could be consistently distinguished from other forms. Such separation of taxa can, however, result in either overestimation or underestimation of the abundance of the correct species. Conversely, because some descriptive taxa may contain several species that cannot be distinguished from one another, an underestimate of the species richness of the group would result.

Several procedures were performed to determine the factors affecting spatial variation in the hard-bottom epifaunal assemblages. Descriptive as well as parametric statistical methods were used. Initially, the affinities among the assemblages at each station and among species were estimated using the Bray–Curtis Similarity Index (Bray & Curtis, 1957). The values from these comparisons were clustered using an unweighted pair/group method (Swartz, 1978). The trends suggested by the similarity comparisons were evaluated using analyses of variance (ANOVA).

The ANOVAs were performed to determine the effects of depth and relief on the abundance of each of the 15 most abundant taxa in each of low-relief and high-relief habitats. Since some taxa are present on both lists, a total of 22 taxa were tested. Stations were pooled into two depth categories: shallow (105 to 119 m) and deep (160 to 212 m). Stations were also categorized as being either low-relief or high-relief. There are significant differences in epifaunal abundances among stations within depth and relief categories, preventing the use of each random photographic sample as an independent replicate. Therefore, unreplicated two-way ANOVAs (time  $\times$  depth and time  $\times$  relief) were used, in which the mean of all photographic samples within each time  $\times$  depth or time  $\times$  relief combination was used as the unreplicated value in each cell. The two-way interaction effects were pooled to provide an estimate of error variance. All tests based upon densities of organisms were run on data transformed by the square root transformation, and all tests based upon percent cover were run on data transformed by the arc sine transformation (Sokal & Rohlf, 1969). Species that failed Bartlett's test for homogeneity of variances were tested with a nonparametric two-way ANOVA. Because our sampling design is unbalanced (Table 1), two separate two-way ANOVAs were run. These included (1) for effects of depth, in low-relief habitat, and (2) for effects of relief, at deep stations.

Correlation coefficients (Pearson product-moment) were calculated to determine the relationships between physical and biological measurements. Correlations were determined among the 22 common taxa to ascertain whether interspecific interactions might be influencing their abundances and distributions. Partial correlations were also determined between the abundances of the 22 common taxa (and the total abundances of porifera, anthozoa, polychaeta, ectoprocta, brachiopoda, and urochordata) and the estimated sediment flux measured with the sediment traps.

The spatial variation of species abundances on high-relief rocks was evaluated with a one-way ANOVA. The percent cover of each of the 22 common taxa was tested in high-relief habitat for differences among eight orientation categories (N, NE, E, SE, S, SW, W, and NW). The reciprocal of the ROV heading, at the time each photograph was taken, was used to determine the orientation for each sample.

## RESULTS

A rich epifaunal assemblage inhabits rocky areas near Platform Hidalgo in the Santa Maria Basin. Over seven sampling periods, there were 263 taxa observed at eight low-relief stations and 222 taxa observed at three high-

relief stations. Total organismal cover on rocks averaged approximately 97.5%. Much of this cover consists of a turf composed of komokoiacea foraminiferans and hydroids. This turf varies in average percent cover from 59.5 at station PH-R(H) to 87.1 at station PH-I(L), covering most of the unsedimented rock surfaces which are not occupied by megafauna.

No other taxon dominates the percent-cover estimates within the study area (Table 2). The 15 most abundant taxa in low-relief habitat total

**TABLE 2**

The 15 Most Abundant Hard-Bottom Taxa in Low-Relief (0.2–0.5 m) and High-Relief (>1.0 m) Habitat near Platform Hidalgo. Percent Cover Averaged over all Stations in each Relief Category and over Seven Sampling Periods from October 1986 through October 1990

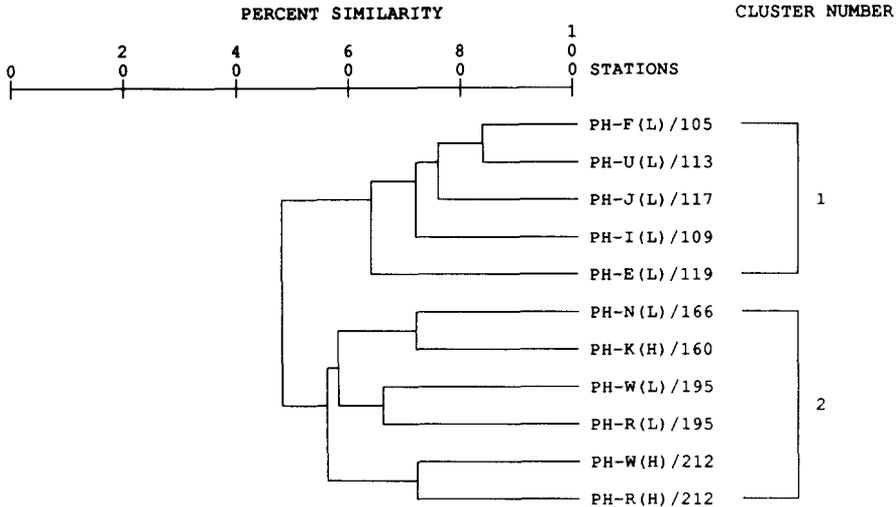
<i>Taxa</i>	<i>Taxon group</i>	<i>Mean percent cover</i>	<i>Standard deviation</i>	<i>Percent frequency of occurrence</i>
<b>Low Relief</b>				
<i>Ophiuroidea</i> , unidentified	Ophiuroidea	5.8	6.4	99.8
<i>Florometra serratissima</i>	Crinoidea	2.7	7.3	26.5
<i>Paracyathus stearnsii</i>	Anthozoa	1.5	2.4	75.2
<i>Metridium giganteum</i>	Anthozoa	1.2	4.9	14.2
Sabellidae, unidentified	Polychaeta	1.1	2.6	51.6
<i>Ophiacantha diplasia</i>	Ophiuroidea	1.1	2.3	51.0
<i>Caryophyllia</i> sp(p).	Anthozoa	1.0	1.5	91.3
<i>Pyura haustor</i>	Urochordata	0.8	1.5	67.5
Terebellidae, unidentified	Polychaeta	0.8	1.7	55.4
Sponge, white encrusting	Porifera	0.7	1.1	84.9
Galatheidae, unidentified	Decapoda	0.6	1.2	61.8
Sponge, tan encrusting	Porifera	0.6	1.0	70.2
<i>Cellaria</i> sp(p).	Ectoprocta	0.5	1.0	59.4
<i>Lophogorgia chilensis</i>	Anthozoa	0.5	1.0	64.7
<i>Halocynthia hilgendorfi igaboja</i>	Urochordata	0.4	1.0	46.7
<b>High Relief</b>				
<i>Amphianthus californicus</i>	Anthozoa	4.6	5.2	97.9
<i>Ophiuroidea</i> , unidentified	Ophiuroidea	3.5	4.0	99.6
Sabellidae, unidentified	Polychaeta	2.4	3.2	93.2
<i>Desmophyllum cristagalli</i>	Anthozoa	2.1	3.4	75.9
Galatheidae, unidentified	Decapoda	1.7	2.0	97.6
<i>Metridium giganteum</i>	Anthozoa	1.7	4.7	28.2
<i>Lophelia californica</i>	Anthozoa	1.6	5.9	23.1
Sponge, white encrusting	Porifera	1.5	2.0	96.5
<i>Stomphia didemon</i>	Anthozoa	1.4	3.1	38.4
<i>Florometra serratissima</i>	Crinoidea	1.3	5.3	14.6
Anemone, tan zoanthid	Anthozoa	1.1	2.8	66.2
Sponge, shelf	Porifera	1.0	2.7	34.6
Amenone, white disc, purple tentacles	Anthozoa	1.0	1.7	65.1
<i>Pyura haustor</i>	Urochordata	0.9	1.6	75.7
Sponge, tan encrusting	Porifera	0.8	1.4	76.1

approximately 19.3% cover, whereas the 15 most abundant taxa in high-relief habitat total approximately 26.6% cover. Although no taxon dominates, seven are common in both low-relief and high-relief habitat. The group of unidentified ophiuroids, the crinoid *Florometra serratissima*, the anemone *Metridium giganteum* (formerly *M. senile*; see Fautin *et al.*, 1989), the group of unidentified sabellids, the solitary urochordate (ascidian) *Pyura haustor*, the white encrusting sponge, and the group of unidentified galatheid crabs are all among the 15 most abundant taxa in both types of habitat. Conversely, the solitary corals *Paracyathus stearnsii* and *Caryophyllia* sp(p), the soft coral *Lophogorgia chilensis*, the unidentified terebellid polychaetes, the ectoproct *Cellaria* sp(p), the ophiuroid *Ophiacantha diplasia*, and the solitary ascidian *Halocynthia hilgendorfi igaboja* are among the 15 most abundant taxa only in low-relief habitat. Similarly, the shelf sponge, four anemones (*Amphianthus californicus*, *Stomphia didemon*, the tan zoanthid, and the anemone with white disc and purple tentacles), the solitary coral *Desmophyllum cristagalli*, and the colonial coral *Lophelia prolifera* are among the most abundant taxa only in high-relief habitat.

Despite the lack of dominance by any one taxon, the 22 taxa comprising the 15 most abundant in each relief category consist mostly of athozoans. Ten of these 22 taxa are anthozoans that cover 4.2% of the low-relief rock surfaces and 13.5% of the high-relief rock surfaces. Three of these 22 taxa are poriferans, which contribute 1.3% and 3.3% cover on low-relief and high-relief rocks, respectively. There are two ophiuroid taxa that cover 6.9% and 3.5% of low-relief and high-relief rocks, respectively. Two polychaete taxa cover 1.9% of low-relief rocks and 2.4% of high-relief rocks. Two urochordates cover 1.2% of low-relief rocks and 0.9% of high-relief rocks. The one decapod taxon covers 0.6% and 1.7% of low-relief and high-relief rocks, respectively; the one ectoproct taxon covers 0.5% of low-relief rocks; and the one crinoid taxon covers 2.7% and 1.3% of low-relief and high-relief rocks, respectively.

The epifaunal distributions contribute to station similarities that cluster according to depth and relief (Fig. 2). Cluster 1 is composed exclusively of shallow low-relief stations. The high similarity between stations PH-F(L) and PH-U(L) are attributable to high densities of the solitary coral *Balanophyllia elegans*. Cluster 2 consists of all the deep stations, with smaller clustered pairs comprising the shallowest two deep stations, PH-N(L) and PH-K(H), and pairs of deeper low-relief stations and high-relief stations.

The ANOVAs also indicate that abundances of the 22 common taxa vary generally according to either depth or habitat relief (Table 3). Nevertheless, no difference between depths was found for *Lophogorgia chilensis*, *Metridium giganteum*, *Florometra serratissima*, *Ophiacantha diplasia*, the



**Fig. 2.** Clusters of similarities (Bray & Curtis, 1957) between hard-bottom stations in the Santa Maria Basin, based on comparisons of mean abundances over seven sampling periods from October 1986 to October 1990. Low and high habitat relief ( $L = 0.2\text{--}0.5$  m,  $H = >1.0$  m) and depth in meters are indicated for each station.

unidentified ophiuroids, *Halocynthia hilgendorfi igaboja*, and *Pyura haustor*. Similarly, no habitat relief preference is displayed by the anemone with white disc and purple tentacles, *L. chilensis*, *Paracyathus stearnsii*, the unidentified sabellids, *Cellaria* sp(p), *F. serratissima*, *O. diplasia*, the unidentified ophiuroids, and *Pyura haustor*. Only *Caryophyllia* sp(p), *P. stearnsii*, *Cellaria* sp(p), and the combined cover of all taxa (including the foraminifera-hydroid turf) are highest at shallow stations. The abundance of 12 taxa and total suspension feeders, and the total number of taxa are highest at deep stations. Highest abundances are found in low-relief habitat only for *Caryophyllia* sp(p), the unidentified terebellids, *H. hilgendorfi igaboja*, and total abundance of all taxa. There are significantly higher abundances for 10 taxa and total suspension feeders, as well as higher numbers of taxa at high-relief stations.

The ANOVA results enable the definition of eight categories of taxa, based upon variations in abundances according to depth and habitat relief (Fig. 3(a-h)). *Paracyathus stearnsii* and *Cellaria* sp(p) are most abundant at shallow stations and do not vary according to depth, whereas the anemone with white disc and purple tentacles and the unidentified sabellids are most abundant at deep stations, regardless of habitat relief (Fig. 3(a, b)). *Caryophyllia* sp(p) is most abundant at shallow stations and in low-relief habitat, and the unidentified terebellids are most abundant at deep stations in low-relief habitats (Fig. 3(c, d)). *Halocynthia hilgendorfi igaboja* was most abundant in low-relief habitat, without regard for depth, and

TABLE 3

Results of ANOVA for Effects of Depth at Low-Relief Stations, and Effects of Relief at Deep Stations

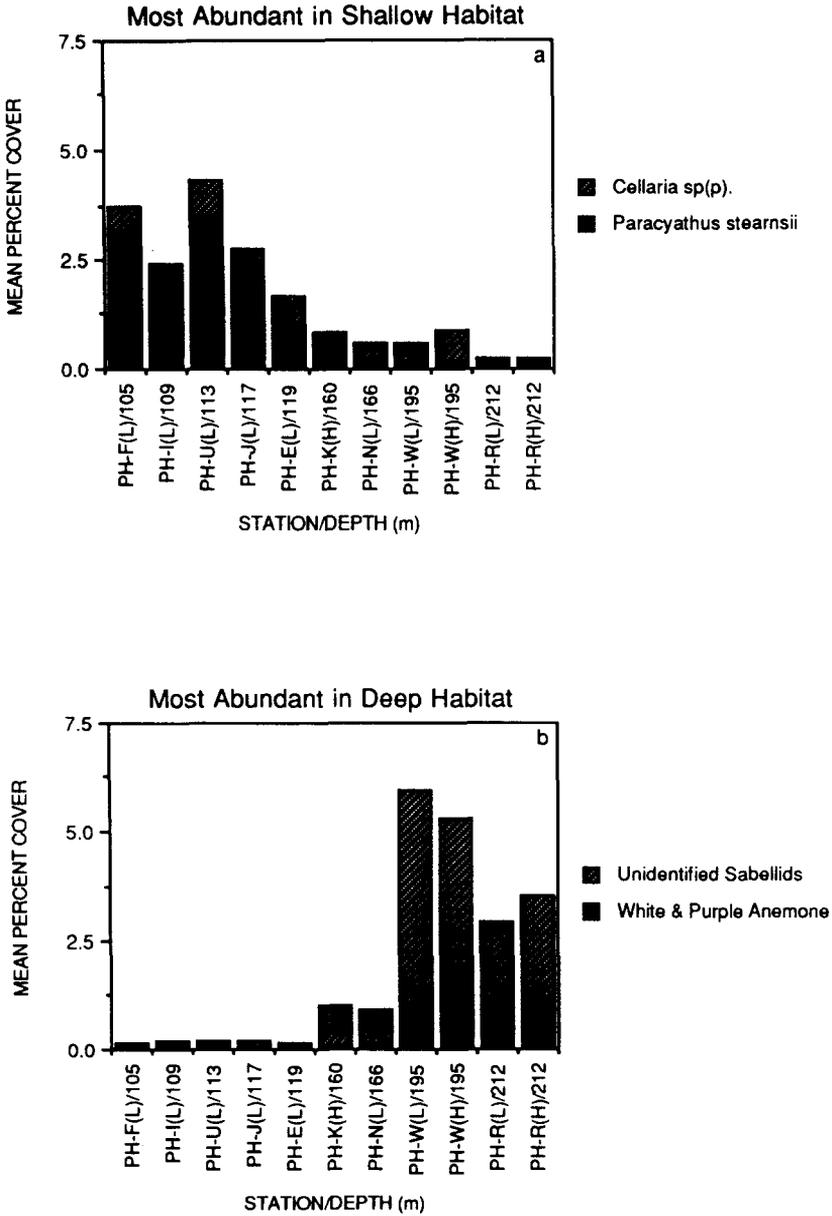
Taxa	Depth		Relief <sup>f</sup>	
	p	Result <sup>a</sup>	p	Result <sup>a</sup>
Sponge, shelf cover	<0.000 1	D	0.000 5 <sup>b</sup>	H
Sponge, tan encrusting cover	0.032 7	D	0.002 2 <sup>b</sup>	H
Sponge, white encrusting cover	<0.000 1 <sup>b</sup>	D	<0.000 1	H
<i>Amphianthus californicus</i> counts	<0.000 1 <sup>b</sup>	D	<0.000 1	H
Anemone, tan zoanthid cover	<0.000 1 <sup>b</sup>	D	0.010 0	H
Anemone, white disc and purple tentacles counts	<0.000 1 <sup>b</sup>	D	0.367 2	—
<i>Caryophyllia</i> sp(p). counts	<0.000 1	S	0.002 7	L
<i>Desmophyllum cristagalli</i> counts	<0.000 1 <sup>b</sup>	D	<0.000 1 <sup>b</sup>	H
<i>Lophelia prolifera</i> cover	<0.000 1	D	<0.000 1 <sup>b</sup>	H
<i>Lophogorgia chilensis</i> cover	0.345 5	—	0.696 2 <sup>b</sup>	—
<i>Metridium giganteum</i> counts	0.170 9	—	0.001 4	H
<i>Paracyathus stearnsii</i> counts	<0.000 1	S	0.460 0	—
<i>Stomphia didemon</i> counts	<0.000 1 <sup>b</sup>	D	0.000 4	H
Sabellidae, unidentified counts	<0.000 1	D	0.640 3 <sup>b</sup>	—
Terebellidae, unidentified counts	<0.000 1 <sup>b</sup>	D	<0.000 1	L
Galatheidae, unidentified counts	<0.000 1	D	<0.000 1	H
<i>Cellaria</i> sp(p). cover	<0.000 1	S	0.067 8 <sup>b</sup>	—
<i>Florometra serratissima</i> counts	0.383 7	—	0.115 3	—
<i>Ophiacantha diplasia</i> counts	0.260 0	—	0.097 2	—
Ophiuroidea, unidentified counts	0.682 2	—	0.054 1	—
<i>Halocynthia hilgendorfi igaboja</i> counts	0.153 2 <sup>b</sup>	—	0.041 3	L
<i>Pyura haustor</i> counts	0.065 7 <sup>b</sup>	—	0.825 3	—
Total suspension feeders cover	<0.000 1 <sup>b</sup>	D	<0.000 1	H
Total abundance cover	<0.000 1	S	0.001 6	L
Total number of species	<0.000 1 <sup>b</sup>	D	<0.000 1	H

<sup>a</sup> S: Highest abundance occurred at shallow stations (105–119 m); D: Highest abundance occurred at deep stations (160–212 m); L: Highest abundance occurred in low-relief habitat (0.2–0.5 m); H: Highest abundance occurred in high-relief habitat (>1.0 m).

<sup>b</sup> Nonparametric ANOVA used because of failure to pass Bartlett's test for homogeneity of variance.

*Metridium giganteum* was most abundant in high relief habitat, without regard for depth (Fig. 3(e, f)). Nine taxa are significantly more abundant at deep stations with high-relief habitat (Fig. 3(g)), and five taxa do not vary according to depth or habitat relief (Fig. 3(h)).

Therefore, clusters of similarities among taxa, based upon their mean percent cover at each station and time (Fig. 4), can be defined in terms of the depth and habitat differences determined by the ANOVA. Cluster 1 contains taxa that do not vary according to depth or habitat relief. Cluster 2



**Fig. 3.** Combined mean abundances for 22 common hard-bottom taxa from 11 stations in the Santa Maria Basin. Taxa are combined according to the ANOVA results shown in Table 3. Means are over seven sampling periods from October 1986 to October 1990. Low and high habitat relief ( $L = 0.2-0.5$  m,  $H = >1.0$  m) are indicated for each station.

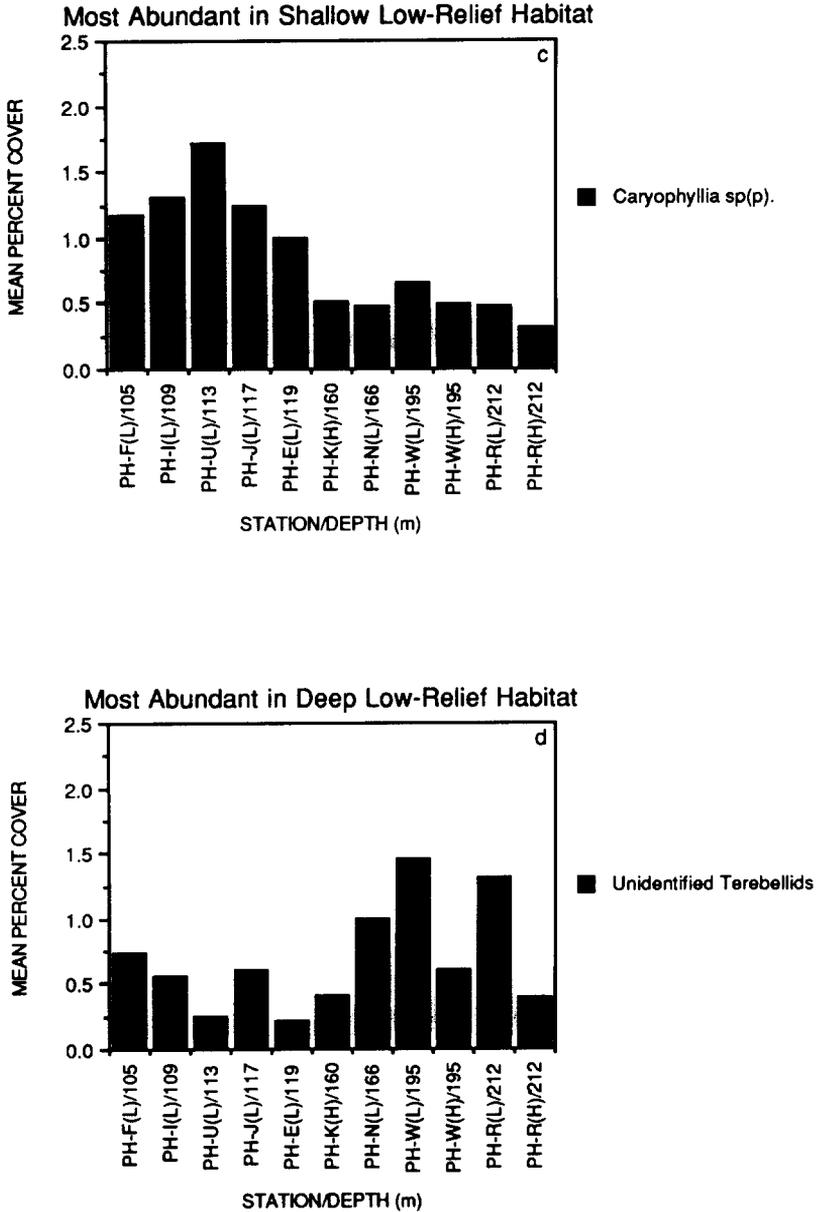


Fig. 3.—contd.

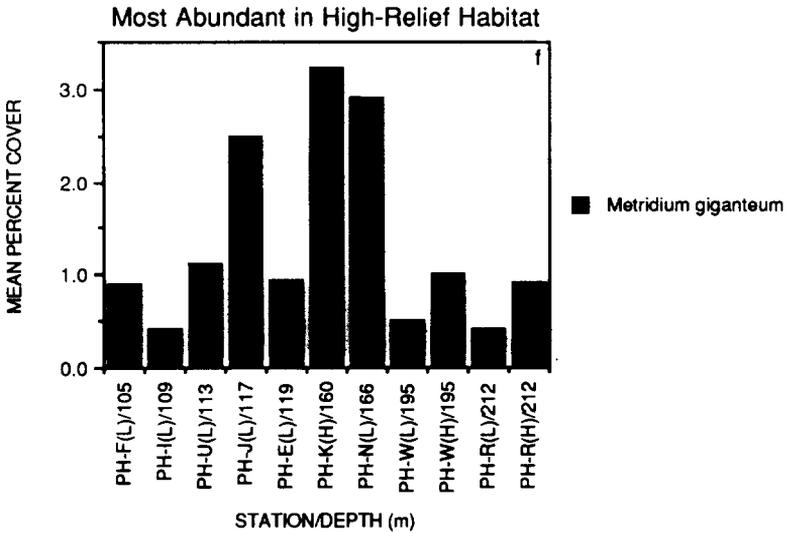
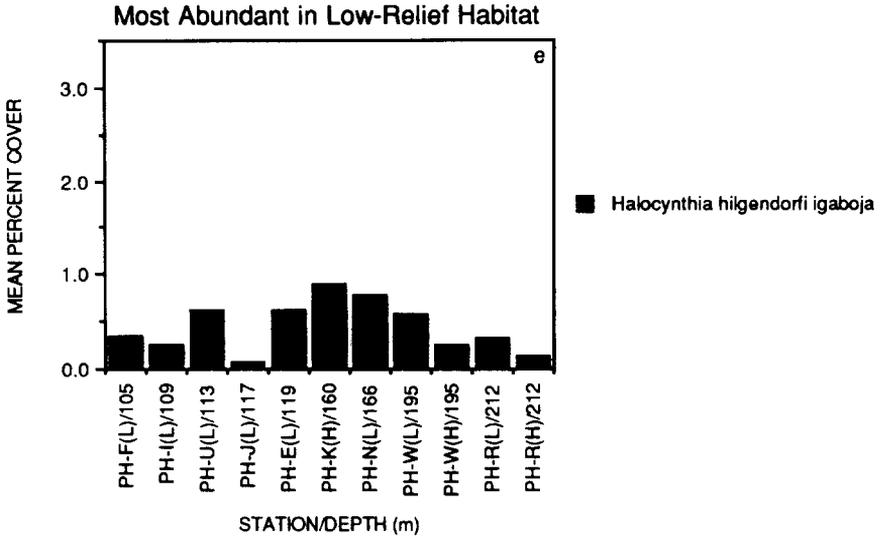


Fig. 3.—contd.

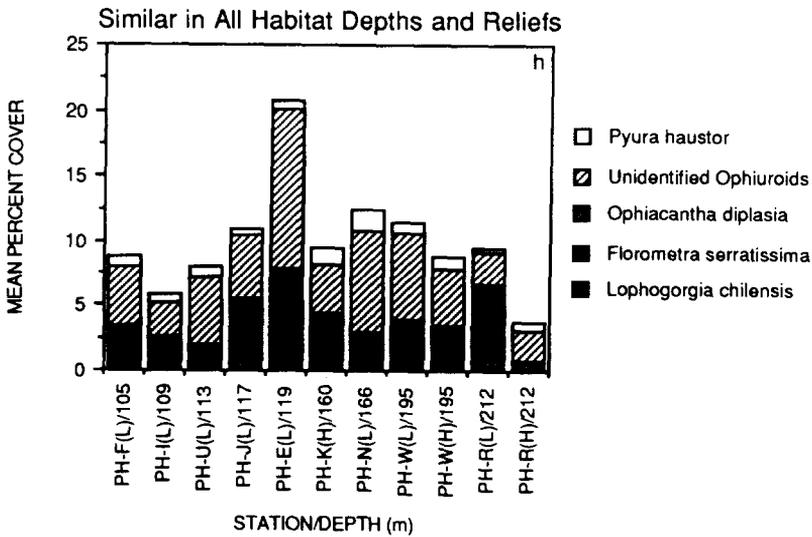
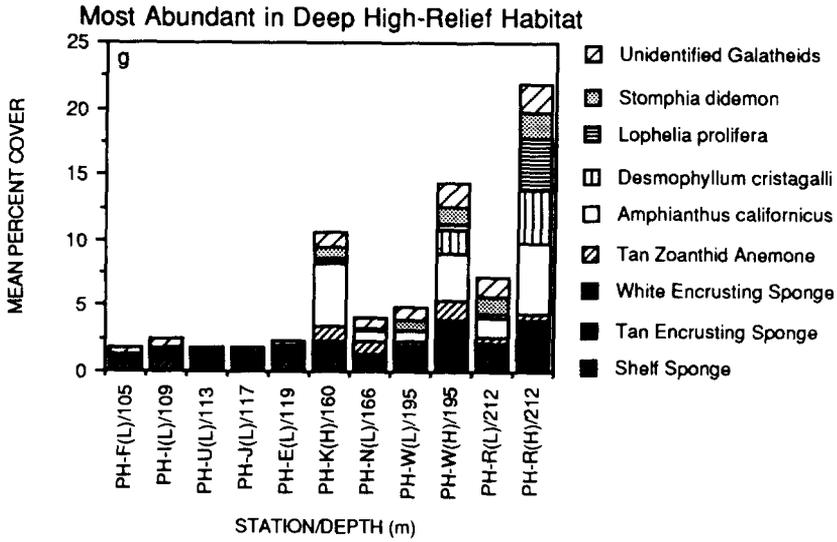


Fig. 3.—contd.

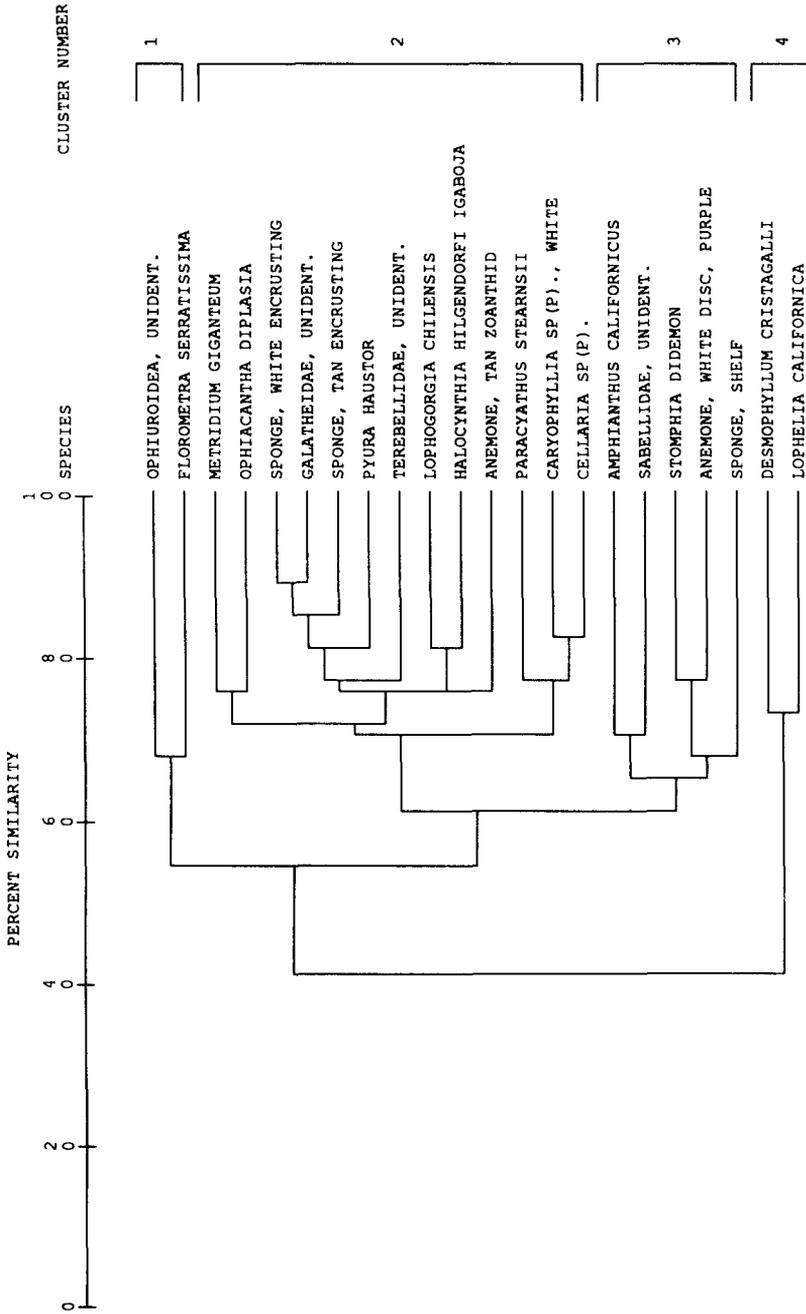


Fig. 4. Clusters of similarities (Bray & Curtis 1957) between hard-bottom taxa over 11 stations in the Santa Maria Basin, based on comparisons of mean abundances over seven sampling periods from October 1986 to October 1990.

TABLE 4

The 10 Strongest Positive and 10 Strongest Negative Interspecific Correlations (Pearson Product-Moment) for Hard-Bottom Epifauna near Platform Hidalgo. Correlations are Based upon Replicate Values across Seven Times and 11 Stations. All Correlations are Significant ( $p < 0.0001$ )

	Taxa	r
1	<i>Desmophyllum cristagalli</i> to <i>Amphianthus californicus</i>	0.389
2	<i>Desmophyllum cristagalli</i> to <i>Lophelia prolifera</i>	0.307
3	Anemone (white disc and purple tentacles) to Sabellids	0.256
4	Unidentified ophiuroids to <i>Ophiacantha diplasia</i>	0.245
5	<i>Amphianthus californicus</i> to Galatheids	0.221
6	<i>Desmophyllum cristagalli</i> to Galatheids	0.212
7	<i>Desmophyllum cristagalli</i> to Anemone (white disc and purple tentacles)	0.208
8	<i>Paracyathus stearnsii</i> to <i>Caryophyllia</i> sp(p).	0.195
9	<i>Amphianthus californicus</i> to White encrusting sponge	0.170
10	<i>Amphianthus californicus</i> to Anemone (white disc and purple tentacles)	0.163
1	<i>Paracyathus stearnsii</i> to Sabellids	-0.205
2	<i>Paracyathus stearnsii</i> to <i>Amphianthus californicus</i>	-0.191
3	<i>Paracyathus stearnsii</i> to Galatheids	-0.178
4	<i>Paracyathus stearnsii</i> to Anemone (white disc and purple tentacles)	-0.160
5	Galatheids to Unidentified ophiuroids	-0.154
6	<i>Amphianthus californicus</i> to Unidentified ophiuroids	-0.151
7	<i>Paracyathus stearnsii</i> to <i>Desmophyllum cristagalli</i>	-0.136
8	<i>Desmophyllum cristagalli</i> to Unidentified ophiuroids	-0.127
9	<i>Caryophyllia</i> sp(p). to Sabellids	-0.116
10	<i>Paracyathus stearnsii</i> to <i>Stomphia didemon</i>	-0.115

consists of all the taxa that are most abundant in low-relief habitat, without regard to depth, along with others that are widespread, but that may or may not vary according to depth or habitat relief. Cluster 3 contains only species with greatest abundances at deep stations, some of which are also most abundant in high-relief habitat. Cluster 4 contains two taxa that are almost exclusively restricted to deep stations with high-relief habitat.

Correlations among the 22 common taxa (Table 4) also suggest that the clusters of taxa similarities are due to abundance differences related to habitat variation, and not to obligate associations among taxa. Although these correlations are very low, many are highly significant due to the large number of photographic samples analyzed. Seven of the most positive correlations include at least one taxon that prefers deep high-relief habitat. Among these, numbers 1, 2, 5, 6, and 9 are between taxa, both of which are most abundant in deep high-relief habitat. Conversely, only positive correlations 4 and 8 are between taxa that either have no depth or habitat preference, or that prefer shallow or low-relief habitat. The remaining

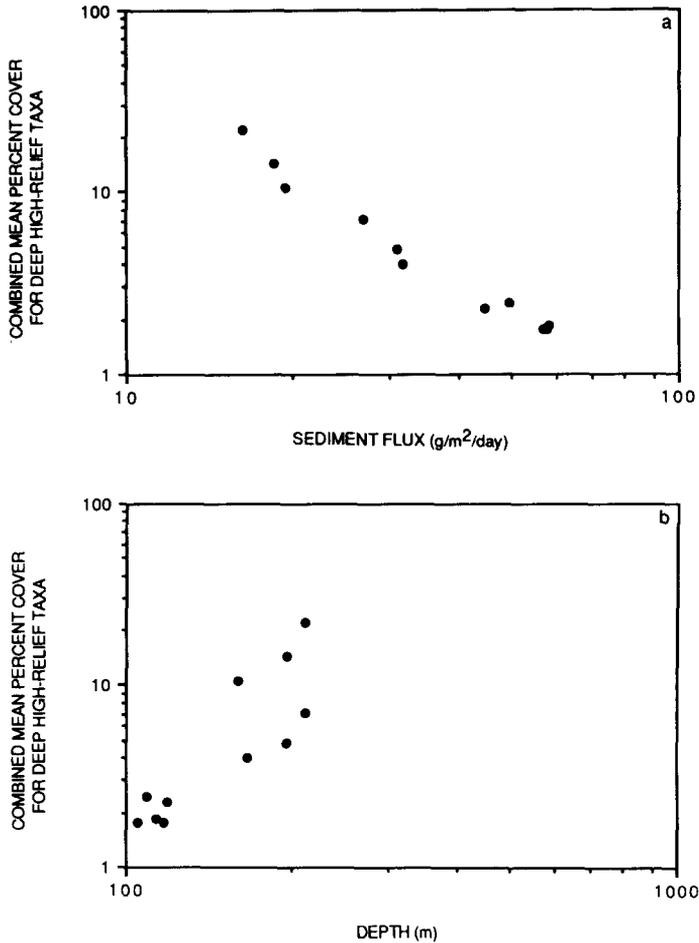
positive interspecific correlation (number 3) is between taxa that are most abundant at deep stations, without regard to habitat relief.

The most negative interspecific correlations probably also reflect abundance differences related to habitat variation, although antagonistic effects cannot be ruled out. Seven of the most negative correlations are between taxa, one of which is most abundant at shallow stations, with or without regard to habitat relief, and the other of which is most abundant at deep stations, with or without regard to habitat relief. Among these, numbers 2, 3, 7, and 10 are between *Paracyathus stearnsii* and one of several taxa which are most abundant in deep high-relief habitat. None of the most negative correlations are between taxa with the same pattern of distribution among depths and habitat reliefs.

The consistently positive correlations between taxa that are most abundant in deep high-relief habitat, and the consistently negative correlations between these taxa and those that are most abundant in shallow habitat suggest that these two groups have very different habitat requirements. Moreover, the requirements of the deep high-relief taxa appear to be especially strong, applying to many (41%) of the 22 most common taxa.

The distributions of the nine deep high-relief taxa are apparently not related to differences in the abundances of predators. There were only four significant correlations between mean abundances of predator groups and deep high-relief taxa. These were: positive correlations between gastropods and the shelf sponge ( $r = 0.692$ ), the tan encrusting sponge ( $r = 0.676$ ), the white encrusting sponge ( $r = 0.714$ ), and the unidentified galatheids ( $r = 0.640$ ). Positive correlations suggest that the adult sponges and galatheids are not more abundant in deep high-relief habitat because it provides a refuge from predation, although predator effects on juveniles in low-relief habitat cannot be ruled out. None of the other correlations between any of the deep high-relief taxa and the separate or combined mean abundances of gastropods, asteroids, or rock fishes was significant.

The strong habitat association displayed by the nine deep high-relief taxa may be related to the physical attributes of deep high-relief habitat. Parr *et al.* (1991) report a strong negative correlation between water depth and sediment flux, based upon sediment-trap measurements made at the nine reefs comprising our 11 stations. The effects of depth and sediment flux may be confounding, because depth can affect sediment flux through the attenuation of orbital water velocities caused by surface waves, and through the generally stronger currents at shallower depths (Savoie *et al.*, 1991). Nevertheless, the combined abundance of the nine deep high-relief taxa is more strongly correlated with sediment flux (Fig. 5(a)), log-log comparison,  $r = -0.988$ ) than it is with depth (Fig. 5(b)), log-log comparison,  $r = 0.869$ ).



**Fig. 5.** Log-log plots of combined mean abundances for nine taxa with highest abundances in deep high-relief habitat in the Santa Maria Basin versus sediment flux and depth at 11 stations. Sediment flux was measured over 18 months with sediment traps 1 m from the seabed at low-relief (0.2–0.5 m) stations, represented by the eight points farthest to the right in Fig. 5(a). Sediment flux for high-relief (>1.0 m) stations, represented by the three points farthest to the left in Fig. 5(a), was estimated using the intermediate wave model run of Glenn and Grant (1987).

The orientation of several taxa on high-relief rocks may also be related to physical factors. The abundances of eight taxa and the total cover of suspension feeders display significant abundance differences among eight categories of orientation on high-relief rocks (Table 5). The anemone with white disc and purple tentacles, *Desmophyllum cristagalli*, *Lophelia prolifera*, and all suspension feeders combined are all significantly more abundant on the northwest, north, or northeast sides of high-relief rocks than they are on the east sides of rocks. Conversely, the abundances of

TABLE 5

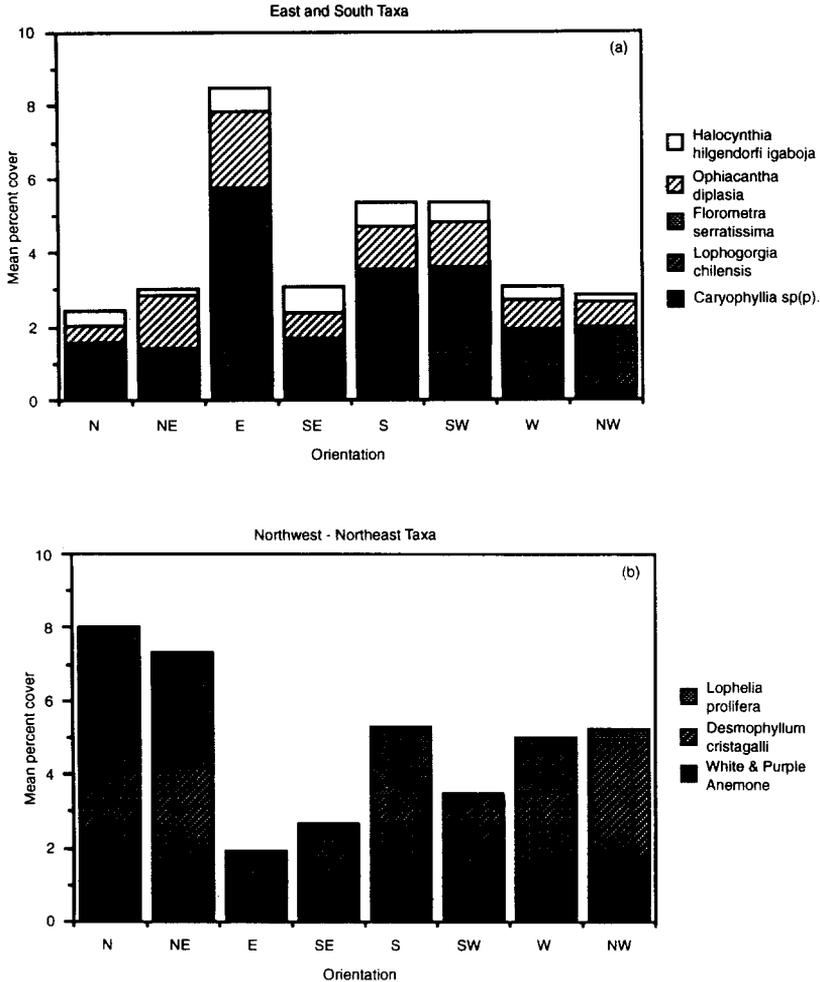
Results of ANOVA for Abundance Differences among Orientation Categories (N, NE, E, SE, S, SW, W, NW) on High-Relief Rocks. Taxa Tested are the 15 most Abundant in each of Low-relief and High-relief Habitat, listed Phylogenetically

Taxa	ANOVA-p	Duncans <sup>a</sup>
Sponge, shelf cover	0.5611	<u>E N NW W S SW SE NE</u>
Sponge, tan encrusting cover	0.4357	<u>NE W S SW N E NW SE</u>
Sponge, white encrusting cover	0.8186	<u>NW W E N S NE SW SE</u>
<i>Amphianthus californicus</i> counts	0.1205	<u>NW N SE SW NE E S W</u>
Anemone, tan zoanthid cover	0.8595	<u>E W SE N S NE SW NE</u>
Anemone, white disc and purple tentacles counts	0.0055	<u>N NW S W NE SE SW E</u>
<i>Caryophyllia</i> sp(p). counts	0.0282	<u>S SW SE E W NE NW N</u>
<i>Desmophyllum cristagalli</i> counts	0.0109	<u>NW NE N W SW S SE E</u>
<i>Lophelia prolifera</i> cover	0.0163	<u>N NE S W SE NW E SW</u>
<i>Lophogorgia chilensis</i> cover	0.0001	<u>E S SW W NE N SE NW</u>
<i>Metridium giganteum</i> counts	0.1528	<u>E SW S W NE SE N NW</u>
<i>Paracyathus stearnsii</i> counts	0.2022	<u>W E S SW N SE NE NW</u>
<i>Stomphia didemon</i> counts	0.0590	<u>N NE SE NW SW W S E</u>
Sabellidae, unidentified counts	0.9194	<u>NE N W NW SE S SW E</u>
Terebellidae, unidentified counts	0.3619	<u>W NE SW S SE NE N E</u>
Galatheidae, unidentified counts	0.1528	<u>NW W S SE NE SW N E</u>
<i>Cellaria</i> sp(p). cover	0.5557	<u>E SE W SW S N NW NE</u>
<i>Florometra serratissima</i> counts	0.0039	<u>E SW S NW W SE N NE</u>
<i>Ophiacantha diplasia</i> counts	0.0220	<u>E NE S SW W SE NW N</u>
<i>Ophiuroidea</i> , unidentified counts	0.1510	<u>E S SW W NE SE NW N</u>
<i>Halocynthia hilgendorfi igaboja</i> counts	0.0035	<u>E SE S SW W N NE NW</u>
<i>Pyura haustor</i> counts	0.8019	<u>NW NE N SE W SW E S</u>
Total suspension feeders cover	0.0265	<u>NE N W NW S SW SE E</u>
Total abundance cover	0.7507	<u>SE S E SW N NE W NW</u>
Total number of species	0.8125	<u>E SW NW S NE SE W N</u>

<sup>a</sup> Duncans Multiple Range Test; categories underlined by a common line are not significantly different; highest mean on left, lowest mean on right.

*Caryophyllia* sp(p)., *Lophogorgia chilensis*, *Florometra serratissima*, *Ophiacantha diplasia*, and *Halocynthia hilgendorfi igaboja* are significantly greater on the east or south sides of high-relief rocks than they are on the north or northeast sides.

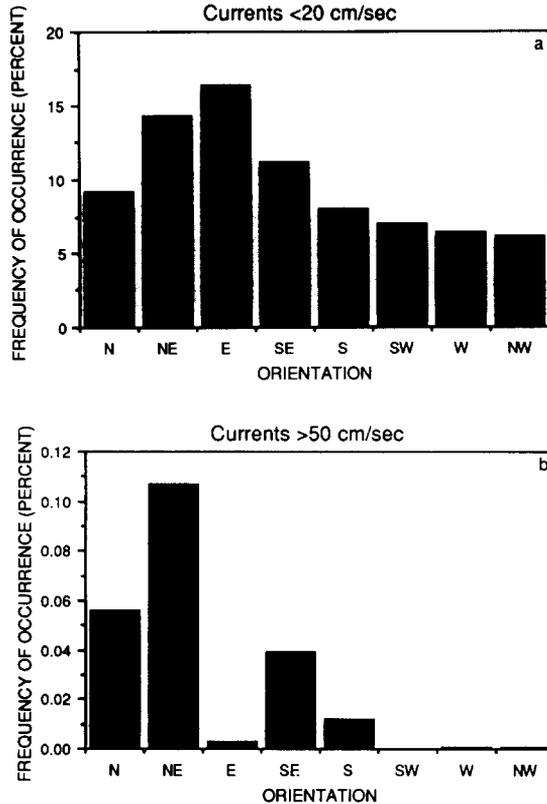
The reciprocal nature of these two orientation patterns is apparent (Fig. 6). Moreover, the habitat distributions of these two groups of taxa are distinct. The taxa which have higher abundances on the northwest, north, or northeast sides of high-relief rocks are characteristic of either deep high-relief habitat (*Desmophyllum cristagalli* and *Lophelia prolifera*),



**Fig. 6.** Combined mean abundance for hard-bottom taxa that have highest abundances on the east or south sides of high-relief (>1.0 m) rocks or on the northwest-northeast sides of high-relief rocks. Abundances are means from three high-relief stations, 160–212 m deep, sampled during seven sampling periods from October 1986 to October 1990.

or deep stations without regard to habitat relief (the white and purple anemone) (Table 3). The taxa with highest abundances on the east or south sides of high-relief rocks are characteristic of either shallow low-relief habitat (*Caryophyllia* sp(p)), or low-relief habitat (*Halocynthia hilgendorfi igaboja*), or do not vary according to habitat (*Lophogorgia chilensis*, *Florometra serratissima*, and *Ophiacantha diplasia*) (Table 3).

Current meter records from the study site (Savoie *et al.*, 1991) indicate that strong and weak currents do not have the same frequency of occurrence in all directions, and that strong and weak currents are each usually



**Fig. 7.** The frequency of occurrence of low (<20 cm/s) and high (>50 cm/s) current speeds directed toward eight orientations on high-relief rocks. Data were obtained from a current meter moored near the seabed at 126 m near Platform Hidalgo in the Santa Maria Basin from October 1986 to October 1990 (after Savoie *ete al.*, 1991).

directed toward a different side of high-relief rocks (Fig. 7). Although strong currents (>50 cm/s) account for only 0.2% of all current records, they represent 8.2% of the kinetic energy in currents (current speed squared). Conversely, weak currents (<20 cm/s) represent 78.6% of all current records, but provide only 41.1% of the kinetic energy in currents.

The orientation of some taxa on high-relief rocks is correlated with current energy. Although correlations between the combined percent cover of the three northwest–northeast taxa (Fig. 6) and the kinetic energy represented by currents >50 cm/s are not significant ( $r = 0.683$ ,  $p = 0.07$ ), *Lophelia prolifera* is significantly correlated with the energy in currents >50 cm/s ( $r = 0.764$ ). The combined percent cover of these three taxa are negatively correlated with weak currents, although not significantly ( $r = -0.332$ ). The combined percent cover of the east and south taxa (Fig. 6) are negatively correlated ( $r = -0.381$ ) with currents >50cm/s and positively

correlated ( $r = 0.539$ ) with currents  $<20$  cm/s, although neither correlation is significant. Among the east and south taxa, only *Ophiacantha diplasia* is nearly significantly correlated with the kinetic energy in currents  $<20$  cm/s ( $r = 0.677$ ,  $p = 0.07$ ). Therefore, the deep high-relief taxa that vary according to their orientation on high-relief rocks tend to face into the highest-energy currents, and the low-relief and shallow low-relief taxa that vary according to their orientation on high-relief rocks tend to face into low-energy currents.

## DISCUSSION

We have described a rich epifauna in hard-bottom habitats of the Santa Maria Basin, with many of these organisms varying according to depth and habitat relief. The effects of habitat relief occur over gradients of as little as 1 to 2 m. The effects of depth and habitat relief on organism abundances were detected despite the possible effects of the platform discharges (Hyland *et al.*, 1994). Hyland *et al.* (1994) report variation consistent with discharge effects for sabellids in deep low-relief habitat, for *Caryophyllia* sp(p) in deep low-relief and deep high-relief habitat, for galatheids in deep low-relief habitat, and for *Halocynthia hilgendorfi igaboja* in deep low-relief habitat. Therefore, although the distributions of these four taxa may have been affected by the platform discharges, the patterns we describe for the remaining 18 taxa are probably associated with factors that are not related to the platform. Since most of the most common taxa are suspension feeders, explanations for the observed distribution patterns may be related to this mode of feeding.

The combined percent cover of suspension feeders was significantly greater in deep high-relief habitat (Table 3). Moreover, among the 22 common taxa, all of those with highest abundances in deep high-relief habitat, except for the unidentified galatheids, are suspension feeders. The five anthozoans are passive suspension feeders that capture small food items as the water sweeps them past their tentacles. The three sponges are active suspension feeders that capture food items from water which is pumped through the animals by ciliary action. In either mode of suspension feeding, decreased feeding efficiency can be assumed when the concentration of inorganic sediments increases in the water relative to the concentration of food items. We know of no behavioral or morphological adaptations possessed by these eight taxa which would allow them to effectively exclude high concentrations of suspended sediments from their feeding apparatus.

Most of the nine taxa that were most abundant at either shallow stations, or in shallow low-relief habitat, or in low-relief habitat, or

which did not vary according to depth or habitat relief, are also assumed to be suspension feeders (except for the ophiuroids). Nevertheless, in this group of taxa, *Cellaria* sp(p), *Halocynthia hilgendorfi igaboja*, and *Pyura haustor* are able to either withdraw their feeding appendages into an enclosed space or close their incurrent and excurrent siphons for short periods of time to exclude high concentrations of suspended sediments. Two others of these taxa, *Lophogorgia chilensis* and *Florometra serratissima*, grow to be more than 30 cm tall, thus extending their feeding apparatus above the highest concentrations of suspended sediment near the bottom. Therefore, many of the suspension feeders that do frequently occur in low-relief habitat may have ways of mitigating the effects of suspended sediments, although this topic requires further investigation.

High abundances of suspension feeders have previously been reported in locations that are elevated from the surrounding seabed (Pequegnat, 1964; Genin *et al.*, 1986; Mullineaux, 1989). In particular, *Lophelia proliфера* has been observed high on the up-current edge of high-relief features along the western edge of Little Bahama Bank (Messing *et al.*, 1990). It has often been assumed that the increased abundances of suspension feeders on high-relief rocks are related to the acceleration of currents as water is forced up and over the rocks (for example Genin *et al.*, 1986). Acceleration of currents over high-relief rocks would increase the flux of both larvae and food items in these areas. The assumed effects of current flow and food flux upon suspension feeders has been supported by studies relating the distribution of benthic fauna to current patterns in McMurdo Sound, Antarctica (Dayton *et al.*, 1982; Barry & Dayton, 1986, 1988).

The significant correlation between *Lophelia proliфера* on high-relief rocks and currents >50 cm/s also indicates the importance of strong currents for at least some deep high-relief taxa in the Santa Maria Basin. Nevertheless, it is unlikely that the distribution of such large organisms (colonies may exceed 2 m in width) depends solely on events that occur less than 0.2% of the time. Moreover, there is evidence suggesting that near-bottom current speeds are greater at shallower depths in our study area. Unpublished data from current meters placed on sediment traps (Parr *et al.*, 1991), within 1 m of the seabed, show that the frequency of current speeds >40 cm/s was 5.6% at a depth of 170 m during May and October 1988, whereas the frequency of currents >40 cm/s was 11.8% at a depth of 118 m during May and October 1989. Although this higher frequency of fast currents at the shallower depth may have been due to temporal variation in current speeds, examination of records from a current meter that was moored near the seabed at 126 m during both periods indicates that maximum current speeds were actually lower during the May and October 1989 period. The increased frequency of faster

currents at shallower depths suggests that if suspension feeders, particularly the deep high-relief taxa, were responding solely to current speed, they should be more abundant at shallower depths. Therefore, while the importance of current speed and food flux to suspension feeders is undeniable, other considerations are necessary to explain the distributions of deep high-relief taxa in our study area.

There are clear gradients in the concentrations of suspended sediments in our study area that are related to depth and habitat relief (Parr *et al.*, 1991). Mean fluxes of suspended sediments within 1 m of the seabed ranged from 44.62 to 58.34 g/m<sup>2</sup>/day at our shallow stations (105–119 m) and from 27.03 to 31.75 g/m<sup>2</sup>/day at our deep stations (160–212 m) over 18 months. Estimates of sediment flux at 2 m off the seabed (using the intermediate wave model run from Glenn and Grant, 1987) ranged from 16.22 to 19.42 g/m<sup>2</sup>/day for deep high-relief stations. These spatial patterns in suspended sediment closely parallel those for the abundances of deep high-relief taxa (Fig. 5(a)).

We suggest that suspended sediments and sedimentation are important factors associated with the large-scale spatial patterns of hard-bottom epifaunal assemblages in the Santa Maria Basin. *De facto*, those taxa that are most abundant at shallow stations, those that are most abundant in low-relief habitat, those whose abundances did not vary according to depth or habitat, and especially those that are most abundant in shallow low-relief habitat must be tolerant of sedimentation and high suspended sediment concentrations. Conversely, we propose that those taxa with highest abundances at deep stations, and especially those that characterize deep high-relief habitat, may be relatively intolerant of sedimentation and high suspended sediment concentrations. If the positive influence of current speeds and food flux on suspension feeders is accepted, along with the probable negative influences of suspended sediments, it is likely that the rich assemblages that characterize high-relief habitat from 160 to 212 m in the Santa Maria Basin are associated with a balance between these two factors. Whether these distribution patterns arise as the result of selective larval settlement or over a long period as the result of competition, predation, growth, or mortality remains to be determined.

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