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Life on glass houses: sponge stalk communities in the deep sea

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Abstract Photographs of the deep-sea floor often show organisms attached to biogenic structures that protrude from the soft bottom. In particular, the stalks of glass sponges (hexactinellids) provide hard substrata and act as habitat islands for deep-sea fauna. The primary objectives of this study were to determine the abundance of glass sponge “stalks” at an abyssal station in the NE Pacific, to identify the fauna associated with stalks, and to compare the distribution patterns of epifaunal taxa both horizontally and vertically. Densities of stalks and large epifauna were estimated from analysis of ~9 km of photographic transects taken in 1994–1995 at station M (34°45'N; 123°00'W; 4,100 m depth) off California, USA. At least 87% of the stalks were the spicule columns of live or dead hexactinellids in the genus *Hyalonema* (Gray, 1832). Stalks appeared to be distributed randomly across the sea floor (density: 0.13 stalks m⁻²). A colonial zoanthid, *Epizoanthus stellaris* (Hertwig, 1888), inhabited 20% of the stalks and was the most commonly observed epifaunal organism, followed by other suspension feeders that generally were situated at the top of the structures. Thirty-five stalk communities were collected in tube cores in 1994–1995

using the submersible “Alvin”. A total of 139 taxa was associated with these hard-substratum habitats (another five species were observed only in photographs). Although taxon richness was high, the species diversity of these communities was relatively low due to the dominance in percentage abundance of a foraminiferan, *Cibicides lobatulus* (Walker and Jakob, 1798), and a serpulid polychaete, *Bathyvermilia* sp. (Zibrowius, 1973). The relationship between number of taxa and surface area of the stalks yielded a slope (*z*-value) typical of islands with a low rate of immigration. Three-dimensional complexity created by branching epifauna on the stalks provided more surface area and a variety of cryptic microhabitats. Vertical zonation on the stalks appeared to be controlled by biological interactions among species, with solitary fauna and certain functional groups of colonial organisms restricted by sheet-like colonial organisms that appeared to be dominant space competitors.

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Additional documentary material has been deposited in electronic form at and can be obtained from <http://link.springer.de/link/service/journals/00227>.

Introduction

The deep-sea floor, other than hydrothermal vents and seamounts, often is described as a vast expanse of soft sediment, sparsely populated by epibenthic fauna. Space-limited communities would not be considered likely in this habitat. Also in the deep sea, suspension feeders would not be expected to thrive because the two components of advective food flux, flow speed and organic particle concentration, generally are very low. Studies of deep-sea communities usually report that deposit feeding is the dominant trophic mode for abyssal taxa (Gage and Tyler 1991, and references therein). However, photographs of the deep-sea floor in all oceans show dense fauna inhabiting biogenic structures such as the stalks of glass sponges (e.g. Heezen and Hollister 1971; Gutt and Schickan 1998). These structures protrude from the soft mud floor into benthic boundary layer flow and provide hard substrata for suspension feeders.

Epifaunal communities on hard substrata in the deep sea rarely are studied, with the exceptions of hydrothermal vent (e.g. Hessler et al. 1988; Tunnicliffe et al. 1998), seamount (Genin et al. 1986; Kaufmann et al. 1989), manganese nodule (Mullineaux 1987), and foraminiferan tube epifauna (Gooday et al. 1992). Most research on deep-sea benthic community structure has detailed the diversity and distribution of fauna living in and on the sediments. Diversity of deep-sea sediment communities generally is high in terms of species richness and evenness (Hessler and Sanders 1967; Grassle 1989; Grassle and Maciolek 1992; Gage 1996). Biogenic structures that project above the sediment surface have been considered important for generating small-scale heterogeneity for sediment fauna (e.g. Thistle and Eckman 1990; Bett and Rice 1992). However, the organisms that live on these structures are poorly known and are not accounted for in estimates of deep-sea species diversity. The lack of knowledge about deep-sea, hard-substratum communities is due mainly to difficulties in sampling from surface ships using box cores, trawls, or dredges.

My goal in this study was to describe the communities associated with erect biogenic structures, collectively called "stalks" (Lauerma et al. 1996), at an abyssal station in the NE Pacific. I quantified the distribution of stalk-associated fauna across and above the sea floor, focusing on fauna associated with hexactinellid sponges in the genus *Hyalonema* (Fig. 1A). *Hyalonema* spp., also known as glass rope sponges because of their twisted column of basal spicules, have been collected and/or photographed at depths >1,000 m in all of the world's oceans. Faunal associates of other hexactinellids have been observed in the Antarctic (Barthel and Tendal 1994; Kunzmann 1996) and in a bathyal basin off California (Smith and Hamilton 1983). In this study I considered only the organisms associated with the basal root tuft spicules of *Hyalonema* spp., rather than those associated with the living sponge bodies. These spicules, the stalk of the sponge, anchor the sponge and can extend up to 1 m above the sediment surface. The spicules, composed of hydrated silicic acid, persist long after the sponge has died (Fig. 1B, C). These stalks act as habitat islands for attached fauna which typically are stripped from the spicules when collected in dredges or trawls.

Materials and methods

Study area

Station M (34°45'N; 123°00'W; 4,100 m depth) is located ~220 km west of Point Conception, California (see Electronic Appendix 1, <http://link.springer.de/link/service/journals/00227>). The sea floor at stn M has little topographic relief (<100 m over 1,600 km²), and microtopography consists of small mounds, tracks, and pits in the fine-grained, silty-clay sediments. Hard substrata at stn M consist of a few consolidated outcrops, manganese nodules submerged under the sediment surface (not visible in photographs), and biogenic structures. The average near-bottom flow speed is 2.2 cm s⁻¹ (2.5 m above the sea floor; Beaulieu and Baldwin 1998).

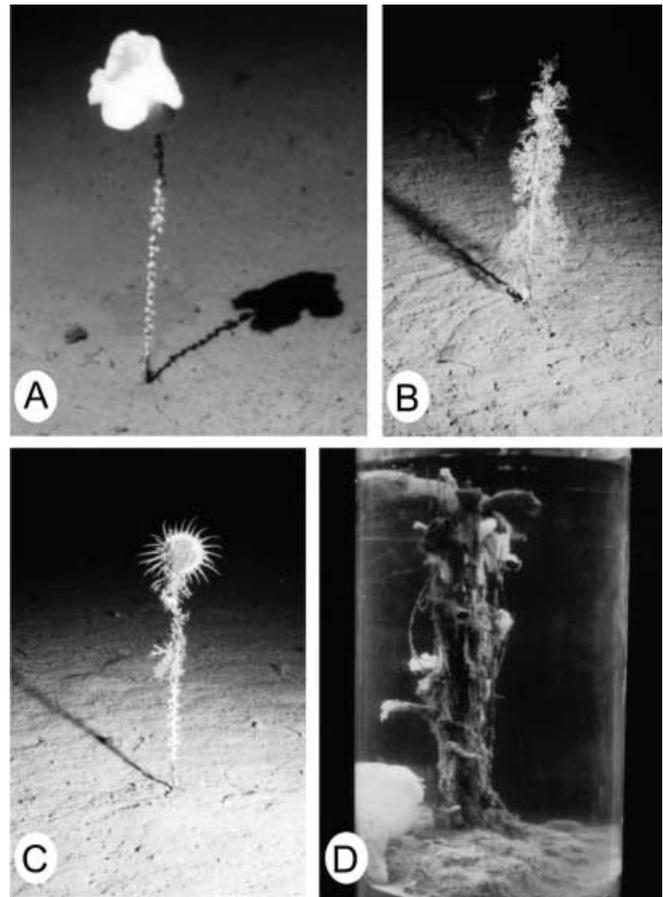


Fig. 1A–D *Hyalonema* spp. stalks in situ at ~4,100 m depth at stn M. Stalks extend 25–50 cm above the sea floor. **A** *Hyalonema* sp. with epizoic zoanthid colony encircling the stalk. **B** Dead *Hyalonema* sp. stalk with hydractiniid colony and other epifauna. A second dead *Hyalonema* sp. stalk, with an anemone at the top, is in the background. **C** Dead *Hyalonema* sp. stalk with an anemone, *Actinauge abyssorum*, at the top (oral disk facing away from camera). **D** Dead *Hyalonema* sp. stalk collected in an "Alvin" tube core (7 cm diam.) and photographed in the laboratory. Scalpellid barnacles (*Verum proximum*) are attached at the top

Analysis of photographic transects

A towed camera sled was used to photograph transects of the sea floor seasonally from 1989 to 1996 as part of a long time-series study of stn M (Smith and Druffel 1998). In order to analyze the spatial distribution of stalks and large epifauna at stn M, I quantitatively examined seven transects made over a 1-year interval (June 1994–June 1995) that included periods of sea floor sampling (Table 1). I determined the location of objects in the oblique photographs by a perspective grid method (Wakefield and Genin 1987). Each photograph was projected with a Beseler enlarger onto a flat surface, and an electronic digitizer (GP-7 GrafBar MARK II, Science Accessories, Conn., USA) interfaced with computer software was used to convert the position of objects in the photograph to sea floor coordinates. I obtained transect lengths by summing the overlap between successive photographs as described by Lauerma et al. (1996). In total, I analyzed an ~9-km swath of sea floor. Because the strobe did not flash for several photographs in the middle of transect 2628, I analyzed it in two segments.

I recorded the position of each stalk in the photographic transects and categorized each stalk in three ways: (1) vertical or bent; (2) type of substratum (live *Hyalonema* spp., dead *Hyalonema* spp., cladorhizid sponge, pogonophoran tube, or undetermined); and (3)

Table 1 Photographic transects of the sea floor at stn M

Transect no.	Date	No. of photographs	Transect length (m)
2017	17 Jun 1994	822	1,216.6
2108	21 Aug 1994	850	1,340.5
2231	22 Sep 1994	825	1,462.4
2304	22 Oct 1994	785	1,322.4
2404	14 Feb 1995	825	1,536.4
2534	1 May 1995	504	741.8
2628	9 Jun 1995	777 (322 + 455) ^a	1,269.5 (456.6 + 812.9) ^a

^a Number of photographs and lengths of parts 1 and 2 in parentheses

single (compact column) or multiple (separated spicules). For vertical stalks, I also digitized the length of the shadow. I used the length of the shadow, the position of the stalk base, the geometry of the camera angle, and a calculation based on similar triangles to estimate the approximate height of each vertical stalk above the sediment surface. Because it was not possible to determine accurately the absolute height above the sea floor for the epifauna on a photographed stalk, I recorded each organism as located on the top, middle, or base of a stalk. I visually determined the relative positions of epifauna, with the top of the stalk being the uppermost 10% and the base being the lowermost 10%.

To calculate densities [no. per 10⁴ m² (hectare, ha)] of the stalks and epifauna, I analyzed the position data using line transect theory (Lauerman et al. 1996). A histogram of the perpendicular distances of each object type from the center line of the photographs was truncated by 5% and compared to uniform, half-normal, and hazard-rate distributions using the computer program DISTANCE (Laake et al. 1994). The DISTANCE program determined the model that best described a detection function for each object type and returned a value for effective strip width (ESW) that essentially described the distance from the centerline to which all objects of that type were visible in photographs. DISTANCE used the area surveyed for each object type (2 × ESW × transect length) and the number of objects detected to determine density. Generally, 40 is the minimum sample size (total number of objects) for an accurate density estimate for line transect data (Krebs 1989). For the stalk and epifauna types that did not meet this requirement, I quantified abundance by encounter rate (number observed per unit transect length).

I analyzed the spatial distribution of stalks and the most abundant epifauna using the variance-to-mean ratio as an index of dispersion. This index of dispersion is used to compare a distribution of abundances to a Poisson (random) distribution (Ludwig and Reynolds 1988; Krebs 1989) and requires measurements of abundance in at least six quadrats. Quadrats were taken as along-transect segments with lengths increasing in a geometric series from 1 to 128 m. I tested departure from the Poisson distribution at the $\alpha = 0.05$ level (two-tailed) by comparing the index of dispersion with a chi-square statistic divided by $n - 1$ and having $n - 1$ degrees of freedom (where n is the number of quadrats; Kaufmann et al. 1989; Lauerman et al. 1996). At low densities (mean abundance < 5 per quadrat) it is difficult to detect a departure from random. I used Green's index of clumping to compare the magnitude of aggregation or uniformity for significant deviations from a random distribution. Green's index, which is the variance-to-mean ratio normalized to sample size, varies between -1 and 1 (from most uniform to most aggregated; Ludwig and Reynolds 1988).

Collection and examination of stalk communities

Intact stalk communities were collected from the sea floor at stn M using the submersible "Alvin" in August and September 1994 and April 1995. The stalks and underlying sediment were collected in tube cores (40 cm long, 7 cm inner diameter; Fig. 1D). Tube cores

were brought to the surface in an insulated box and immediately transferred to a cold room at 2 °C. I photographed each stalk and measured its height above the sediment surface in the core tube. I then carefully extracted the stalks from the sediment and placed them in individual containers with 10% buffered formalin. Because some stalks were pushed into the sediment during coring, I determined the true height for each vertical stalk by comparing the height above the sediment surface in the tube core to in situ video of the stalk recorded during collection. Generally, an adjustment of several centimeters was required to match the height above the sediment surface measured in the tube core with the height apparent in the in situ videos.

In the laboratory, I removed the stalks from their containers into trays of deionized water. Water from the original containers was poured over a 0.3 mm mesh screen, and any organisms retained on the screen were suspected to have come from sediment that adhered to the bottom of the stalks. Gross measurements of each stalk, including the diameter of the spicule column and the linear extent to which the stalk was covered by colonial organisms, were made before close examination using a dissecting microscope. To the nearest millimeter I measured the height above the sediment surface for each attached organism. To do so, I measured the distance between the mouth of the organism and the top of the stalk and subtracted this value from the stalk's true height. I also noted the surface to which each organism was attached. Then, I detached, measured, wet-weighed, and stored each organism in 70% ethanol. Specimens were sent to taxonomic specialists for identification to the lowest taxonomic level.

I determined similarity between each pair of stalk communities using the Jaccard index for presence/absence data, an index similar to the Bray-Curtis measure for continuous data (Clifford and Stephenson 1975). I chose this index because encrusting foraminifera and colonial organisms were counted as single individuals, yet, when present, they covered a greater area than single, solitary taxa. I performed a cluster analysis of the similarity matrix using unweighted, pair-group average linking, and I used the cluster analysis to examine whether stalks of the same substratum type, similar height, or that were collected in close proximity grouped together in terms of species composition.

I quantified species diversity on the collected stalks using several diversity indices and the rarefaction method of Sanders (1968) modified by Hurlbert (1971). Similarity and diversity indices, rarefaction curves, and species accumulation curves were calculated using BioDiversity Professional software (N. McAlece, Natural History Museum, London, 1998). For species-area curves, the number of taxa was compared to the surface area of primary substratum by making the assumption that each stalk was a cylinder. Because the *Hyalonema* spp. stalks generally were narrow at the top and the spicules flared out at the base, I used the diameter of the spicule column at mid-height in calculations of approximate surface area.

Results

Density and spatial distribution of stalks

Of the 2,418 stalks observed in the photographic transects, 87% were *Hyalonema* spp. stalks, and only 14% of these were alive (Table 2); 46% of all stalks were characterized as vertical, dead *Hyalonema* spp., single column stalks. The mean height for this category of stalks, estimated using shadow lengths, was 17.5 cm (means for the seven individual transects ranged from 14.1 to 25.6 cm). Of all the stalks, 12% were unidentified; most of these were vertical (rather than bent) and potentially were *Hyalonema* spp. stalks that could not be identified

with certainty. Pogonophoran tubes and other sponge stalks only represented 1% of the total counts, although pogonophoran tubes might have been among the unidentified stalks. Densities for stalks determined from the photographic transects ranged between 879 and 1,639 stalks ha⁻¹, with a pooled estimate of 1,305 stalks ha⁻¹ (Table 2). On average *Hyalonema* spp. stalks were encountered every 5 m during the camera-sled transects. Neighboring stalks were observed as close together as 2 cm but not farther than 33 m.

The relatively few pogonophoran tubes were observed in distinct clusters. This was not the case for the many *Hyalonema* spp. stalks, although sometimes two or three *Hyalonema* spp. were observed in the same photograph. In general, stalks appeared to be distributed randomly at all spatial scales (1–128 m quadrat length; Electronic Appendix 2, <http://link.springer.de/link/service/journals/00227>). For live *Hyalonema* spp., the strongest deviation from a random distribution (indicated by the magnitude of Green's index) was actually a uniform distribution at the 128 m scale. Dispersion could not be estimated for live *Hyalonema* spp. in two transects due to low number of observations.

Fauna observed in photographic transects

All of the stalk epifauna identified in photographs were considered to be (at least facultative) suspension feeders, based on their morphology and known feeding modes of related species in shallow water. The most frequently observed organism attached to the stalks was the colonial zoanthid *Epizoanthus stellaris* (on 20% of stalks), followed by the stalked tunicate *Pyura* spp., ophiuroids, and anemones. Abundance estimates for ten stalk-associated taxa enumerated in photographic transects are given in Table 3. The range in encounter rate for *E. stellaris* (mean: ~1 colony every 20 m) was the same as determined for nine other camera-sled transects in 1990–1991 at stn M (L. Lauerman, unpublished data). The shortest distance between neighboring *E. stellaris* colonies was 12 cm, and the farthest, 128 m. Dispersion analysis for the zoanthid colonies indicated that the spatial distribution did not differ from random at all scales, with the exception of the 1 and 2 m scales in a single transect. All other epifauna were observed too rarely to analyze dispersion. Two species, the anemone *Actinauge abyssorum* and a hydractiniid hydroid, were

Table 2 Abundance of stalks at stn M in seven photographic transects over an ~9-km swath of sea floor. Each substratum type had an effective strip half-width > 1 m. Pooled density estimates are weighted means; confidence intervals are log-based (Buckland et al. 1993)

Substratum type	Total no. observed in combined transects	Pooled density estimate (no. per 10 ⁴ m ²) and 95% confidence interval	Range in density estimates (no. per 10 ⁴ m ²) for individual transects	Range in encounter rate (no. m ⁻¹) for individual transects
All stalks	2,418	1,305.4 1,060.1 – 1,607.4	879.2 – 1,638.8	0.18 – 0.33
Live and dead <i>Hyalonema</i> spp.	2,105	1,117.8 892.8 – 1,399.5	709.8 – 1,426.6	0.14 – 0.29
Live <i>Hyalonema</i> spp.	295	123.7 94.7–161.7	72.6 – 180.8	0.02 – 0.05

Table 3 Epifauna of stalks in seven photographic transects at stn M (nd not determined due to low number of counts)

Species name (group)	Percent of stalks on which observed	Range in encounter rate (no. km ⁻¹) for individual transects	Pooled density estimate (no. per 10 ⁴ m ²) and 95% confidence interval
<i>Epizoanthus stellaris</i> (zoanthid)	19.64	35.4 – 68.4	223.1 175.8 – 283.1
<i>Pyura</i> spp. (tunicate) ^a	4.92	6.1 – 18.5	79.4 54.6 – 115.5
Ophiuroids (all species) ^a	4.80	2.7 – 20.5	88.4 59.5 – 131.3
Anemones (all species) ^a	3.80	1.4 – 21.4	61.0 29.4 – 126.7
Hydractiniid sp. (hydroid)	2.73	5.2 – 9.5	41.2 34.1 – 49.8
<i>Actinauge abyssorum</i> (anemone)	2.56	0.7 – 14.2	41.5 19.4 – 88.9
<i>Striatodoma dorothea</i> (bryozoan)	2.27	3.8 – 9.1	55.2 36.8 – 82.8
Hexactinellids (all species) ^a	0.87	0 – 6.7	nd
Unidentified “benthic ctenophore”	0.62	0.8 – 2.3	nd
<i>Fariometra parvula</i> (crinoid)	0.45	0 – 2.6	nd

^a This taxon also was observed on the sediment surface or attached to other substrata, so encounter rates and densities are underestimates of true abundance

observed solely on dead *Hyalonema* spp. stalks (see Electronic Appendix 3, <http://link.springer.de/link/service/journals/00227>). *A. abyssorum* was aggregated in the sense that it was very rare in some transects but abundant in others, and hydractiniid colonies often were observed in close proximity to each other.

Species diversity

I examined a total of 35 stalk communities, 25 of which were intact samples. Nineteen of the complete stalks were vertical, dead *Hyalonema* spp., single-column stalks. One live *Hyalonema* sp. was collected and identified as *H. bianchoratum* var. *typica* (Wilson, 1904). The other five complete stalks consisted of a demosponge (*Cladorhiza* sp.), one live and two dead pogonophorans (*Unibrachium* sp.), and a dead stalked tunicate (*Pyura* sp.). A total of 139 taxa in 13 phyla was identified from 8,580 individuals in the 35 stalk samples. Five other species were observed in photographs and collected in trawls, yielding a total of 144 stalk-associated taxa (Table 4). Seventeen percent of the species were new to science. Many foraminifera were morphologically similar and were grouped in the data analyses. At least 31 additional metazoan species were found in samples, but were assumed to have inhabited the sediment at the base of stalks and were excluded from analyses. Excluding fauna not adequately retained by a 0.3 mm mesh screen (foraminifera, nematodes, harpacticoids, and ostracods) in order to make direct comparisons to other reports of deep-sea diversity, a total of 104 species was identified from 1,933 individuals. Polychaetes represented 76% of these macrofaunal individuals, peracarids 10%, and mollusks only 1%.

Only the data for the 25 complete stalks, which had a total of 6,846 individuals in 124 taxa, were analyzed for species diversity. Dominant taxa in terms of relative abundance included the calcareous foraminiferan *Cibicides lobatulus* (62% of total individuals; occurred on 100% of stalks) followed by the most abundant metazoan, the serpulid polychaete *Bathypermilia* sp. (14% of total individuals; occurred on 76% of stalks). On individual stalks, however, other metazoans such as nematodes, a sabellid polychaete (*Fabrisabella similis*), and an isopod (*Haplomunna* sp.) were sometimes more abundant than *Bathypermilia* sp. (Table 5).

Several other taxa, including two agglutinated foraminifera (tubular, flexible type and *Telammmina* sp.), the hydroid *Lafoea dumosa*, and the zoanthid *Epizoanthus stellaris*, also were common, each occurring on $\geq 60\%$ of stalks. However, I counted these protozoans and colonial organisms as single individuals even though they covered a relatively large area of the stalk. With the exception of the tubular foraminifera, when these colonial organisms were present on a stalk, I observed only one, continuous colony. *E. stellaris* and hydractiniid colonies completely ensheathed *Hyalonema* spp. stalks, covering 37.5–95.6% (mean: 70.5%; $n = 16$) and 46.4–

91.7% ($n = 2$) of the primary surface area, respectively. Mainly because of the 15 colonial taxa, I determined similarity between the stalk communities using the Jaccard index. Stalk communities were at most 50% similar. Neither stalks collected just a few meters apart nor stalks of similar height grouped together in the cluster analysis (Fig. 2). The first group to cluster as dissimilar from the rest included four non-*Hyalonema* spp. stalks.

The number of taxa in the complete stalk communities ranged from 4 to 44 per stalk (mean no. taxa: 22; mean no. individuals: 272). Considering only the macrofauna, the mean Shannon–Wiener diversity index H' (log base e) was 1.53 (range 0.86–2.51). The H' index indicates how difficult it would be to predict the species of the next individual sampled from a community. Maximum uncertainty (H'_{\max}) occurs when all species have the same relative abundance. The mean equitability (evenness) index (H'/H'_{\max}) for stalk communities was 0.69 and was lower when I included foraminifera in the analysis (mean: 0.47), due to the dominance of *Cibicides lobatulus* in relative abundance. Considering all of the taxa, the mean log series α was 6.31 (range: 1.21–12.47). The log series α index can be considered a number close to the number of taxa within a community expected to be represented by a single individual (Hayek and Buzas 1997).

Due to the dominance of *C. lobatulus* when all taxa are considered, the rarefaction curve for “all taxa” is lower than the curve for “macrofauna only” (Fig. 3). Rarefaction curves for the combined stalk communities did not reach an asymptote; however, as shown by the species accumulation curves (Fig. 4), after about 15 samples only one or two new species were added to the faunal list for each additional stalk community sampled. Jackknife estimation methods, which calculate estimated species accumulation curves based on the observed frequency of rare species (Krebs 1989), predicted that ~ 40 more species would be discovered with more intensive sampling at stn M.

The species–area curve ($S = cA^z$) for the complete stalk communities as replicate samples from stn M had slope $z = 0.32$ (SE = 0.06; Fig. 5). This slope lies within the range for typical island curves (0.25–0.33; Rosenzweig 1995). Log c describes the intercept of the species–area curve in log-log space (Rosenzweig 1995). The variance in surface area of the primary substratum accounted for 52% of the variance in number of taxa, as indicated by the coefficient of determination for the species–area relationship. The number of taxa was correlated significantly with the area of substratum ($r = 0.72$, $P < 0.01$). The mean surface area for primary substratum on each stalk was ~ 43.4 cm².

Vertical distribution of fauna

The correlation between number of taxa and stalk height above the sea floor for the 19 vertical, dead *Hyalonema* spp. stalks was not significant ($r = 0.41$, $P = 0.077$). The

Table 4 All taxa observed in stalk communities at stn M. Relative locations and attachment surfaces for individuals sorted from the 35 collected stalks are listed in order of frequency (most frequent first). Total no. stalk-associated taxa (including all foraminiferan species) = 144; total no. taxon groups collected on 35 stalks and used in data analysis = 130 (total of 8,580 individuals). Voucher specimens are deposited at the Natural History Museum of Los Angeles County and the Benthic Invertebrate Collection at Scripps Institution of Oceanography [for relative location on stalks: *T*, top; *M*, middle; *B*, base; up to five attachment surfaces are listed for each taxon: *Amph*, amphipod tube; *Amptr*, Amphitritinae tube;

Ar, *Arachnidium* sp.; *Brn*, barnacle (*Verum proximum*); *Cau*, *Caulophacus* sp.; *Cl*, *Cladhorhiza* sp.; *Cne*, *Cnemidocarpa* sp.; *Hyd*, hydractiniid exterior surface; *L*, *Lafoea dumosa*; *Muc*, mucus; *na*, data not available; *Neo*, *Neosabellides* sp. tube; *PT*, unidentified polychaete tube; *Py*, *Pyura* sp. stalk; *Sab*, sabellid tube; *Sed(uz)*, sediment package under zoanthid coenenchyme; *Serp*, serpulid tube; *S*, *Hyalonema* sp. spicule; *S(uz)*, spicules under zoanthid coenenchyme; *Stri*, *Striatodoma dorothea*; *Th*, *Thelepus* sp. tube; *U*, *Unibrachium* sp. tube; *Z*, zoanthid exterior surface; *?(uz)*, either from sediment package or loose under zoanthid coenenchyme]

Taxa	Total no. collected	Relative location on stalks	Attachment surface
Protozoan groups			
Agglutinated foraminifera			
Allogromiid and soft-shelled saccamminid	5	M, B	Serp
“Soft-bodied” sphere with stercomata (similar to allogromiid)	50	T, M	L, Py, S, Cau
<i>Thurammina papillata</i>	66	M	Cau, S(uz), Serp
Other bulbous, thin-walled	34	M, B	Cau, S, Ar, Serp
<i>Veleroninoides scitulus</i>	15	T, M	Th
Other bulbous, thick-walled ^a	91	M, B, T	S, Th, U, Sab, Muc
Other multilocular spp. (includes <i>Eggerella</i> sp.)	2	T, M	Th
“Streamer” (similar to <i>Linea simplex</i>)	10	T, M, B	S, L, Cl, Stri, Th
Tubular, flexible (includes <i>Rhizammina algaeformis</i>)	29	M, B, T	L, S, Cau, Th, Py
<i>Bathysiphon</i> spp. (includes <i>B. filiformis</i> , <i>flavidus</i> , and <i>rufescens</i>)	9	M, B	S(uz), Th, Cau
Other tubular, rigid (includes <i>Hyperammina</i> , <i>Rhabdammina</i> , <i>Saccorhiza</i> sp.)	16	M, B	Th, Cau, Sed(uz), Brn
<i>Telammina</i> sp.	22	M, B, T	L, S, U, Serp, Th
Encrusting (similar to <i>Chondrodapis</i> sp. or <i>Tumidotubus</i> sp.)	8	B, M	S, Th, U
“Flattened dome” (similar to <i>Crithionina</i> sp.)	13	M, T	L, PT
“Tree” type 1 (Hemisphaeramminidae)	443	M, T, B	L, Cau, S, Serp, Py
“Tree” type 2	18	M, B	Brn, Muc, Cau, PT, Sab
Calcareous foraminifera			
<i>Cibicides lobatulus</i>	5,581	M, T, B	L, S, Py, Sed(uz), Serp
Miliolid: <i>Pyrgo</i> sp.	11	M	Cau, Amph
Miliolid: other spp.	37	T, M, B	L, S, Py, Muc, PT
Unidentified spp.	45	M, B, T	Sed(uz), L, Muc, Th
Metazoan taxa			
Porifera			
Demospongiae			
<i>Chondrocladia</i> sp.	1	B, M	S
Hexactinellida			
<i>Bathydorus laevis</i> ssp. <i>spinus</i>	14	M, B, T	S, Serp, Cau
<i>Caulophacus schulzei</i>	4	M, B	S
Unidentified sp.	1	na	S
Cnidaria			
Actiniaria			
<i>Actinauge abyssorum</i>	Trawl ^b	T	S
<i>Amphianthus bathybium</i>	Trawl ^b	na	S
Zoanthidea			
<i>Epizoanthus stellaris</i>	22	T, M	S
Hydroida			
<i>Cryptolarella abyssicola</i>	3	T, M, B	S, U, Py
<i>Filellum serratum</i>	4	B, T, M	S, L
Hydractiniid sp.	3	T, M	S
<i>Lafoea dumosa</i>	24	M, T	S, Serp, Th, Py, U
<i>Opercularella</i> sp.	3	B, T	Serp, S
Pandeid sp.	2	M, B	Cau
Tubulariid sp.	3	M	S(uz)
Athecate: colonial: unidentified sp.	1	M	Stri
Thecate: colonial: unidentified sp.	3	M, T, B	Py, U, Cl
Platyhelminthes			
Turbellarian (similar to Fecampiidae)	1	T	na

Table 4 Continued

Taxa	Total no. collected	Relative location on stalks	Attachment surface
Nemertea			
Unidentified spp.	15	M, T	Cau, Cl
Nematoda			
Unidentified spp.	134	M, B	Sed(uz), Muc in Th
Annelida			
Polychaeta			
Ampharetid: <i>Asabellides</i> sp.	11	na	Serp, Amptr, Py
Ampharetid: <i>Egamella quadribanchiata</i>	3	na	na
Ampharetid: <i>Neosabellides</i> sp.	57	M, T, B	S, Th, L, U, Py
Ampharetid: sp. 1	1	na	na
Ampharetid: other unidentified spp.	37	M, T, B	L, Cl, Th, Amph
Aphroditid: <i>Aphrodita</i> sp.	1	na	na
Arabellid: unidentified sp.	1	na	na
Cirratulid: unidentified (“paddle end”) sp.	9	na	na
Cirratulid: other unidentified spp.	32	B, M	Muc, Cau
Dorvilleid: unidentified sp.	2	T	Cl
Flabelligerid: <i>Flabelligera</i> sp.	1	na	L
Nereid: <i>Neanthes mexicana</i>	7	M, B	Inside Th, S under Cne
Nereid: <i>Nereis</i> sp.	1	M	S
Nereid: unidentified sp.	2	na	na
Onuphid: <i>Anchinothria</i> sp.	Trawl ^b	na	S
Orbiniid: unidentified sp.	2	M or B	na
Paraonid: <i>Paraonella cedroensis</i>	1	M or B	na
Paraonid: unidentified spp.	6	na	na
Phyllodocid: <i>Sige brunnea</i>	3	M, B	Cau, S, inside Serp
Phyllodocid: sp. 1	2	na	na
Phyllodocid: sp. 2	5	M	S(uz)
Phyllodocid: other unidentified spp.	7	M or B	na
Polynoid: Macellicephaloidinae sp.	18	T, M	Z, L
Sabellarid: unidentified sp.	1	na	na
Sabellid: <i>Fabrisabella similis</i>	126	M, T	S, S(uz), Cau, Py
Sabellid: unidentified spp.	41	M	Cau, Th, U, S
Serpulid: <i>Bathyvermilia</i> sp.	1,013	M, B, T	S, Serp, Cau, Sab, Th
Serpulid: <i>Hyalopomatus mironovi</i>	12	M	Serp, Stri, S, Th
Syllid: unidentified sp.	18	na	na
Terebellid: Amphitritinae sp.	1	na	Hyd
Terebellid: Thelepininae sp.	1	na	na
Terebellid: <i>Thelepus</i> sp.	10	M, B, T	S, U
Terebellid: unidentified sp.	7	T, M	L, Cau
Unidentified: small, brown-tubed	30	M, T	Th, Cau, Serp
Other unidentified spp.	8	na	na
Sipuncula			
Sipunculan: unidentified sp.	1	M	na
Arthropoda			
Pycnogonida			
<i>Colossendeis</i> sp.	1	M	na
Ammonotheidae? sp.	2	M	na
Crustacea			
Cirripedia			
<i>Verum proximum</i>	20	M, B	S, U, Serp, Cau
Copepoda			
Calanoida			
Calanoid: unidentified sp.	1	na	na
Harpacticoida			
Amereid: unidentified sp.	4	na	na
Cerviniid: <i>Pontostratiotes</i> sp.	1	T	Cl
Poecilostomatoida			
Clausiid: unidentified sp.	2	na	na
Corycaeid: unidentified sp.	1	na	na
Nereicolid: unidentified sp.	2	M	Inside Serp, inside Neo
Serpulidicolid: unidentified sp.	12	M, B	Inside Serp
Poecilostomatoid: sp. 1	4	M	Sab
Other unidentified spp.	17	na	Inside Serp

Table 4 Continued

Taxa	Total no. collected	Relative location on stalks	Attachment surface
Siphonostomatoida			
Asterocherid: unidentified sp.	3	T, M	Cl, Cau
Dinopontiid: unidentified sp.	1	na	na
Unidentified (“Arrowhead”) sp.	18	na	na
Unidentified (“Bulbous”) sp.	9	na	L
Unidentified (“Horseshoe”) sp.	3	na	na
Unidentified (“Vermiform”) sp.	11	na	na
Ostracoda			
<i>Kritha</i> sp.	1	M	?(uz)
<i>Pseudocythere</i> sp. or <i>Paradoxostoma</i> sp.	1	M	?(uz)
Myodocopid: unidentified sp.	1	M	?(uz)
Amphipoda			
Caprellid sp.	1	M	S
Lysianassid: <i>Valettiopsis</i> sp.	1	na	na
Lysianassid: <i>Lepidepcreella</i> sp.	1	na	na
Eusirid: sp. 1	2	na	na
Eusirid: sp. 2	14	T	<i>Hyalonema</i> sp. body
Corophiid (similar to <i>Bonnierella</i> sp.)	11	M, T	Tube on S, Th, U, L, Brn
Melphiddipid: unidentified sp.	2	na	na
Stenothoid: sp. 1 (similar to <i>Meitopa</i> sp.) and sp. 2	48	T, M	L, Cau
Unidentified sp.	2	T	Cl
Isopoda			
Eurycopid: <i>Disconectes</i> sp.	10	M	Amph, Muc
Haplomiscid: unidentified sp.	2	B	Muc
Janirid: <i>Acanthaspida</i> sp.	1	na	na
Nannoniscid (similar to <i>Hebefustis</i> sp.)	2	T	Cl
Haplomunnid: <i>Haplomunna</i> sp.	64	M, B	Cau, S
Epicaridean: unidentified spp.	2	na	na
Arcturid: <i>Arcturus</i> sp.	10	M, B	U, S, Stri, Z
Unidentified spp.	4	B	S
Tanaidacea			
<i>Pseudotanaia</i> sp.	8	M	Tube on Hyd, Z
Anarthruridae sp.	2	M	na
Mollusca			
Aplacophora			
<i>Nematomenia</i> sp.	9	T, M	L, Cau
<i>Neomeniomorpha</i> sp.	2	na	na
Prochaetodermatid: unidentified sp.	1	na	na
Unidentified sp.	4	na	L
Gastropoda			
Skeneid sp.	2	na	na
Rissoid sp.	3	na	Egg sacs on U
Ectoprocta			
<i>Striatodoma dorothea</i>	7	M	S, U, Th, Serp
<i>Arachnidium hippothoides</i>	2	M, T	S
Echinodermata			
Crinoidea			
<i>Fariometra parvula</i>	1	T	S, Py
Holothuroidea			
<i>Abyssocucumis abyssorum</i>	Trawl ^b		
Ophiuroidea			
<i>Ophiacantha cosmica</i>	1	na	na
<i>Ophiacantha</i> sp. B	2	T, M	S
<i>Ophiacantha</i> sp. C (similar to <i>O. adiaphora</i>)	5	T, M	S
<i>Ophiacantha</i> : unidentified sp.	4	B, T	S
Other unidentified spp.	5	B	S
Urochordata			
<i>Cnemidocarpa</i> sp.	2	B	S, Th, Serp
<i>Pyura</i> spp.	6	M, T	S, U
Unidentified: “siphonophore”	1	T	Cl
Unidentified: “benthic ctenophore”	Photos ^b	T	S

^a Species include: *Cribrostomoides subglobosa*, *Hormosira globulifera*, *Recurvodes* sp., *Sorosphaera* sp., and *Storthosphaera alba*^b Taxa collected only in otter trawls or observed in photographs

Table 5 Most abundant of 124 taxa in 25 complete stalk communities. The number of times each taxon ranked first, second, or third in relative abundance for the individual stalk communities is listed

Taxa in order of rank	Percent abundance of total fauna	No. of rankings for individual samples as:		
		First	Second	Third
<i>Cibicides lobatulus</i> (calcareous foraminiferan)	62.08	22 + 1 tie	2	
<i>Bathyvermilia</i> sp. (serpulid polychaete)	13.77	2 + 1 tie	8 + 2 ties	3
Foraminiferan "tree" type 1 (agglutinated foraminiferan)	5.48		7 + 2 ties	5 + 1 tie
Nematode (unidentified spp.)	1.84		1	2
<i>Fabrisabella similis</i> (sabellid polychaete)	1.58			1 + 1 tie
Agglutinated, bulbous, thick-walled foraminiferan	1.11		2	1 + 1 tie
<i>Haplomunna</i> sp. (isopod)	0.80		1	
<i>Neosabellides</i> sp. (ampharetid polychaete)	0.77			1 + 1 tie

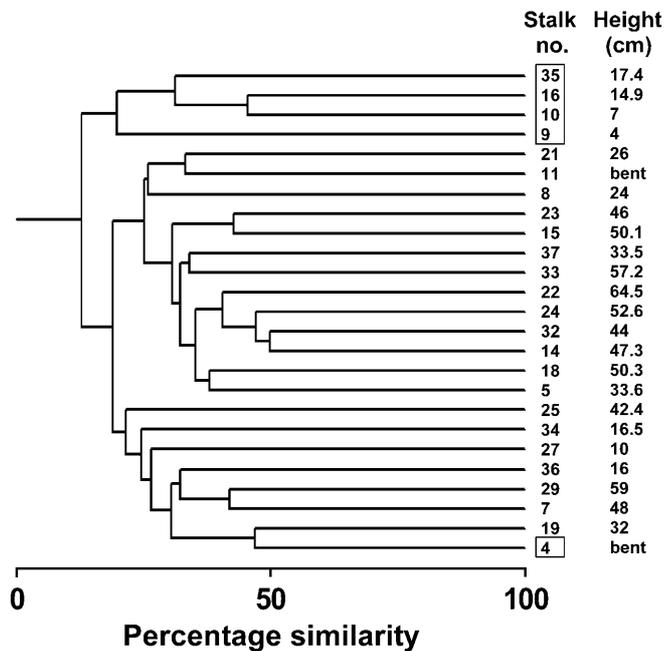


Fig. 2 Cluster analysis for 25 complete stalk communities using the Jaccard index to create the similarity matrix. Clustering was performed by unweighted, group-average linking. Sample numbers are boxed for stalks that were not *Hyalonema* spp. spicules. Height above sediment surface is listed for vertical stalks

average height of the collected vertical stalks was 35 cm, twice the average height of stalks estimated from shadow lengths in the photographic transects.

The relative positions of large suspension feeders on stalks in the photographic transects were skewed towards the top, with the exception of ophiuroids and the holothuroid *Abyssocucumis abyssorum* (Table 6). An unidentified organism resembling a ctenophore, the anemone *Actinauge abyssorum* (Fig. 1C), and the comatulid crinoid *Fariometra parvula* appeared to specialize in living at the tops of stalks. *Epizoanthus stellaris* and hydractiniid colonies generally extended from the top down to just a few centimeters above the sediment surface. *Pyura* spp., even when attached at the middle of a stalk, could extend above the top because their own stalks are ~10 cm long. *Abyssocucumis abyssorum*, which I occasionally observed hanging on

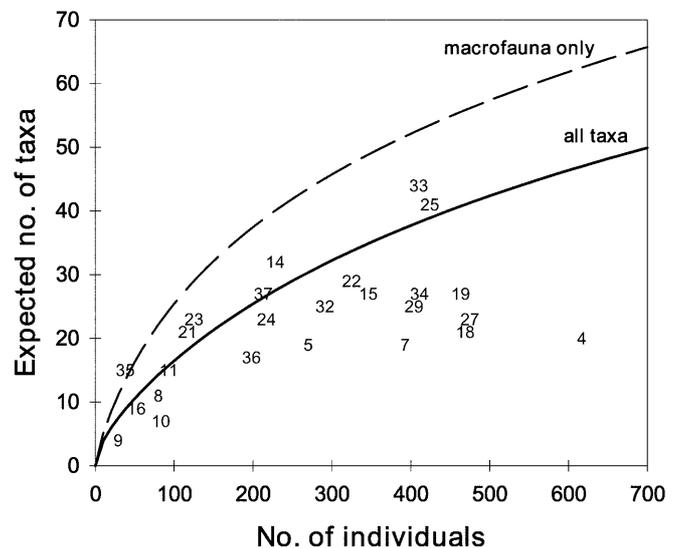


Fig. 3 Rarefaction curves based on the total number of individuals of each taxon summed over 25 complete stalk samples. Data for each stalk sample are plotted for comparison to the curve for all taxa (solid line). Dashed line is expected number of species when foraminifera, nematodes, harpacticoids, and ostracods are excluded. Curves have been truncated at 700 individuals

sponge stalks, generally is considered a mobile deposit feeder.

Distributions in absolute height above the sea floor for common taxa attached to the collected stalks are shown in Fig. 6. Each of these taxa had more than ten measurements of absolute height, and none had a large percentage of individuals sorted from the same stalk. I used values for the tops of the *Lafoea dumosa* and *E. stellaris* colonies in analyses. Some of the heights for *Cibicides lobatulus* and *Bathyvermilia* sp. were <0 (below the sediment surface), most likely because some stalks were pushed down into the sediment upon collection.

Because data for the vertical distributions did not meet two main assumptions for ANOVA (homogeneity of variances and normal distributions), I used a non-parametric Kruskal–Wallis ANOVA to test the hypothesis that taxa were drawn from distributions with the same median height above the sea floor (Sprenst 1993). The Kruskal–Wallis test was very significant ($P <$

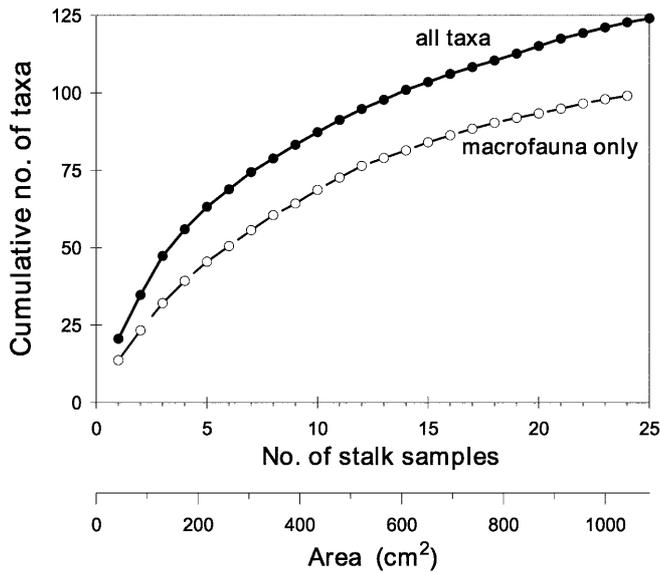


Fig. 4 Species accumulation curves for 25 complete stalks. Curves were calculated using 50 random re-orderings of the samples. The curve for macrofauna only (dashed line, open circle) has one less data point because no taxa other than foraminifera were found on stalk 9. The endpoint for accumulated area is 1,086.5 cm²

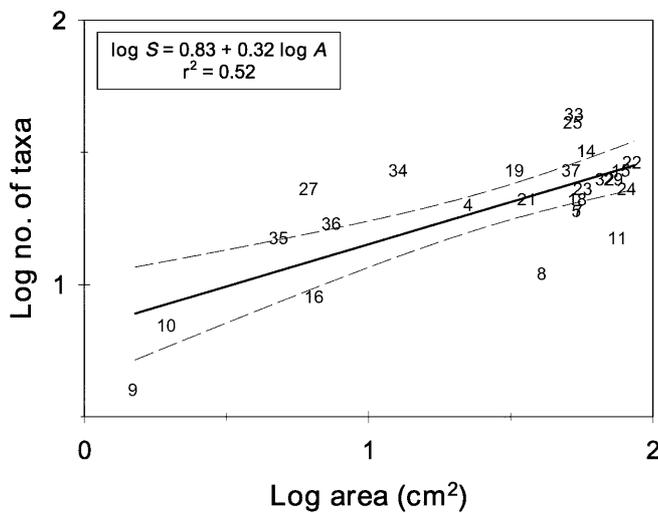


Fig. 5 Species-area curve for 25 complete stalks. Stalk sample numbers are used as data points. The solid line represents the linear regression, and dashed lines indicate the 95% confidence interval for the regression. In the equation for the linear regression S no. taxa; A area of primary substratum

0.0001), thus an a posteriori test similar to the Tukey test was used to check which distributions differed from each other. Due to the large variance in absolute height, only two groups were significantly different at the $\alpha = 0.05$ level: a top group that included *L. dumosa* and *E. stellaris* and a base group that included all other taxa. I also conducted a specific *t*-test assuming unequal variances to compare the vertical distributions of the two most common suspension-feeding polychaetes, *Fabrisabella similis* and *Bathyvermilia* sp. *F. similis* occurred significantly higher on stalks (mean height: 13.8 cm) than the serpulids (8.8 cm; $P < 0.001$).

Discussion

Density and distribution of stalks

Values for the density of stalks at stn M in 1990–1991 were slightly higher than reported here (Lauerman et al. 1996), but those stalks included foraminiferan tubes and antipatharians, which I did not enumerate because they did not support epifauna visible in photographs. The siliceous *Hyalonema* spp. stalks are likely to be long-term features of the sea floor (they remain long after the sponge dies) and are not expected to change in density over a several-year time period. The density of live *Hyalonema* spp. at stn M ($\sim 124 \text{ ha}^{-1}$) was higher than densities reported for hexactinellids in most deep-sea areas. For example, the density of *Hyalonema* spp. at Horizon Guyot in the North Pacific was only 5 ha^{-1} (Kaufmann et al. 1989), and the density of hexactinellids in Santa Catalina Basin off California was only 20 ha^{-1} (Smith and Hamilton 1983). Much higher densities were reported for the hexactinellid *Phoronema carpenteri* in the bathyal NE Atlantic (maximum $15,000 \text{ ha}^{-1}$; Rice et al. 1990); however, those values were calculated for very restricted spatial scales. *Hyalonema* spp. and other hexactinellids apparently are abundant in the abyssal Venezuela Basin in the NW Atlantic, contributing a large percentage of the biomass of trawl samples (Briggs et al. 1996).

Stalks, including live *Hyalonema* spp., appeared to be dispersed randomly. The random distribution of *Hyalonema* spp. stalks across the sea floor suggests that the soft sediment habitat is homogeneous for *Hyalonema* spp. at stn M. Grassle et al. (1975) came to a similar conclusion for epibenthic megafauna in the deep Atlantic. Although some of the taxa attached to stalks appeared to have aggregated distributions, longer transect lengths are required to obtain sample sizes sufficient for pattern analysis of the epifaunal distributions. All of the organisms attached to stalks that were readily visible in photographs can be considered suspension feeders. Similarly, in a study of the perimeter of Horizon Guyot, almost all (99%) megafauna observed in photographic transects were suspension feeders, and their abundance was correlated with the amount of rock substrata (Kaufmann et al. 1989).

Diversity of stalk communities

A closer look at the stalks revealed that many trophic modes were represented. Observers noticed during “Alvin” dives that the stalks accumulated sinking particles like trees collecting snow on their branches. Pockets of sedimented detritus could support macrofaunal detritivores such as copepods and polychaetes. Also, mobile predators that may feed on the cnidarian colonies (including stenothoid amphipods and aplacophorans) or on the detritivores (including phyllodocid polychaetes) were found in the stalk communities.

Table 6 Relative position of large, suspension-feeding epifauna on all stalks in seven photographic transects at stn M. Taxa are listed in order of percentage of occurrences at the top of stalks. Percentages add to > 100 because colonies could extend over most of a stalk

Taxon	Total no. observed	Percentage of occurrences at:		
		Top	Middle	Base
<i>Epizoanthus stellaris</i> (zoanthid)	492	94	93	2
Unidentified "benthic ctenophore"	15	93	7	0
<i>Actinauge abyssorum</i> (anemone)	62	92	8	0
Hydractiniid sp. (hydroid)	67	91	90	0
Anemones (all species)	92	84	13	3
<i>Fariometra parvula</i> (crinoid)	11	73	27	0
<i>Pyura</i> spp. (tunicate)	119	45	54	1
Ophiuroids (all species)	116	27	39	34
<i>Abyssocucumis abyssorum</i> (holothuroid)	5	20	20	60
Hexactinellids (all species)	21	19	76	5
<i>Striatodoma dorothea</i> (bryozoan)	57	18	75	7

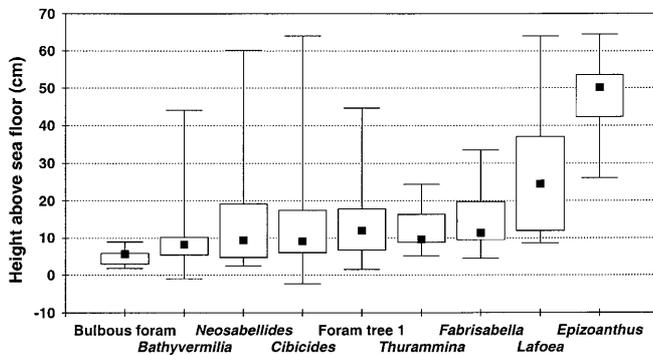


Fig. 6 Vertical distribution of several common taxa attached to stalks. Filled square indicates median height above bottom, box indicates lower and upper quartiles, and whiskers indicate range for all measurements for each taxon. Taxa are listed from left to right in order of mean rank in the Kruskal–Wallis ANOVA. Full names for all taxa are listed in the Table 4 (*Bulbous foram* agglutinated, bulbous, thick-walled foraminiferan)

None of the macrofauna found on the stalks at stn M (Table 4) have been reported from other deep-sea, hard-substratum communities (hydrothermal vents: Tunnicliffe et al. 1998; manganese nodules: Mullineaux 1987; whale bones: Bennett et al. 1994 and A. Baco-Taylor, personal communication). The stalk communities exhibited higher species richness than manganese nodule epifauna (Mullineaux 1987) and whale bone epifauna (Bennett et al. 1994; Table 7). However, the dominance in terms of relative abundance of individuals of the protozoan *Cibicides lobatulus* and the metazoan *Bathyvermilia* sp. was very unusual for abyssal samples, which usually exhibit evenness (Gage and Tyler 1991). *Cibicides* species are known to dominate foraminiferan assemblages on other biotic substrata (e.g. Alexander and DeLaca 1987).

Also unusual for the deep sea was the dominance of colonial organisms in terms of substratum covered. Some *Hyalonema* spp. stalks were covered almost entirely by a hydroid or zoanthid colony (see Fig. 1A, B). For example, stalks 8 and 11 lie below the species–area curve (Fig. 5), because a hydractiniid and zoanthid colony, respectively, covered ~90% of the primary substratum area. Although colonial organisms covered

so much area, the stalk communities exhibited a greater number of taxa and individuals per unit area (species density and faunal density, respectively) than other deep-sea, hard-substratum communities (Table 7). In terms of percentage of stalk substratum covered, only the one cladorhizid sponge, collected as stalk 35, was sparsely colonized by epifauna. In contrast, only 40% of the surfaces of manganese nodules were covered by epifauna (Mullineaux 1987). In a soft-bottom area at 1,800 m depth in the NW Atlantic, rocks were noted as attachment surfaces for sessile suspension feeders; however, most rock surfaces were bare (Grassle et al. 1975).

In addition to the importance of primary substratum area in determining the number of taxa found on a stalk, secondary substrata provided by attached organisms contributed to the 48% of the variance in number of taxa not explained by the species–area curve. For example, the two stalks harboring a large epizoid hexactinellid (*Caulophacus schulzei*) had the greatest number of taxa and the highest α and H' diversity indices among the 25 complete stalk communities. These two stalks, stalks 25 and 33, lie above the species–area curve (Fig. 5) likely because the amount of area in the stalk communities was increased by *C. schulzei* with its thick outstretched branches. *C. schulzei* encases the *Hyalonema* sp. stalk yet differs from the colonial cnidarians in that it provides an inert surface for attachment of epifauna. Organisms might not settle on the cnidarians due to chemical inhibition, the mucus surface, or due to the polyps feeding on settling larvae (e.g. Jackson 1977). The only taxon associated with the exterior surface of *Epizoanthus stellaris* was a polynoid polychaete.

Stalks as habitat islands

Sponges have been considered islands for cryptofaunal associates in shallow and deep water (Long 1968; Schoener 1974; Wendt et al. 1985; Ilan et al. 1994). The slope (z -value) determined for the species–area relationship for the stalk communities was greater than for cryptofauna associated with a coral reef sponge (compare $z = 0.32$ to $z = 0.27$ in Uebelacker 1977) and at the

Table 7 Comparison of species richness, species density, and density of individuals in deep-sea samples of three hard substrate types. Values for “macrofauna only” exclude foraminifera, nematodes, harpacticoids, and ostracods (organisms not sampled adequately with a 0.3 mm screen) (*na* species density was not reported for individual samples)

Substrate	Sample location, depth (citation)	All samples combined		Per sampling unit	
		Area examined (cm ²)	No. of taxa	Species density (no. taxa cm ⁻²)	Faunal density (no. individuals cm ⁻²)
			All taxa	All taxa	All taxa
Glass sponge stalks ^a	NE Pacific, 4,100 m (present study)	1.1 × 10 ³	124	1.1	13.2
Manganese nodules ^b	Eq. N Pacific, 4,500 m (Mullineux 1987)	1.1 × 10 ³	~90	na	1.8
Whale vertebrae ^c	Santa Catalina Basin, 1,240 m (Bennett et al. 1994)	7.4 × 10 ³	36	0.01	0.3

^aData reported for 25 complete samples in this study

^bSpecies richness determined from Fig. 1 and faunal density calculated from Fig. 2 (Mullineux 1987)

^cValues from Table 3 for three samples with surface area quantified in Table 1 (Bennett et al. 1994)

high end of the range for island curves, suggesting that it is difficult for fauna to disperse between stalks on the time scale of community development (Rosenzweig 1995). Recruitment to stalk habitats was examined in relatively short-term (3–5 months) deployments of artificial *Hyalonema* spp. stalks at stn M (Beaulieu, in press). Results suggested that species composition and abundance of individuals in the stalk communities are maintained by frequent recruitment of a few common taxa (including *Cibicides lobatulus* and *Bathymvermilia* sp.) and infrequent recruitment of most taxa.

Cluster analysis separated the communities on *Hyalonema* spp. stalks from four of the five non-*Hyalonema* spp. stalks; however, this may have been due to substratum complexity and not type. Those four stalks (Fig. 2) were only a single, thin column rather than the interwoven spicule columns of *Hyalonema* spp. stalks. All of the taxa found on the live and dead pogonophoran tubes were found in the *Hyalonema* spp. stalk communities. A few metazoan taxa that attach to manganese nodules at stn M, for example brachiopods, were not found in the stalk communities. However, brachiopods have been collected on *Hyalonema* spp. from other areas (Briggs et al. 1996), and the absence of brachiopods on the 35 stalks could be due to limited sample size. Among the stalk-associated epifauna evident in photographs, several species also were attached to other surfaces, such as *Paradiopatra* sp. polychaete tubes which extended ~10 cm above the sediment. Only *Epizoanthus stellaris*, the hydractiniid, and the unidentified “benthic ctenophore” appeared to be restricted to the *Hyalonema* spp. stalks.

Levin (1991) proposed that biogenic structures in the deep sea act as microhabitats for social interactions such as mate location and refuges for young. On the stalks, many of the metazoan taxa were aggregated. For example, the isopod *Haplomunna* sp. was represented by 51 individuals on one stalk but no more than 8 on any other, and tubicolous amphipods (*Bonniertiella* sp.) clustered in multistoried “apartment complexes” on some stalks. Aggregation of *Bathymvermilia* sp. and the cirriped *Verum proximum* probably was enhanced by gregarious settlement. Juveniles of many taxa, including ampharetid and serpulid polychaetes, amphipods, tanaids, and pycnogonids, lived on the stalks. Adults of many taxa, including copepods and polychaetes, were gravid. Egg cases of motile fauna such as gastropods were attached to stalks; Gooday et al. (1992) also found gastropod egg cases on foraminiferan tubes that protrude from the deep-sea floor.

Vertical zonation above the sea floor

In photographs the most conspicuous zonation of organisms on stalks was that of the large suspension feeders living at the top, including cnidarian colonies that extended from the top down to a few centimeters above the sediment surface. Below these colonies, the

stalks were “shaggy” with the tubes of polychaetes and branches of hydroids and sponges. The base of the stalks, within a centimeter or two of the sediment surface, generally supported smaller, solitary epifauna and encrusting foraminifera. Such conspicuous zonation of species or groups of species with similar feeding modes usually reflects a gradient in the environment, such as the increase in flow velocity with increasing distance from the sea floor. Stalks offer vertical living space, extending several tens of centimeters above the sediment surface into turbulent benthic boundary layer flow. The gradient in flow is such that organisms living at 50 cm above the sea floor would experience flow, on average, twice as great as organisms at 5 cm height (Beaulieu 1998). However, as in much of the abyssal ocean, the physical environment at stn M is very calm (Beaulieu and Baldwin 1998), and the flow measured within the bottom 50 cm on six occasions at stn M was $< 5 \text{ cm s}^{-1}$ (Beaulieu 1998).

With a paucity of physical stress in the environment, biological interactions are expected to be most important in determining the structure of hard-substratum communities (Nybakken 1997, and references therein). At the upper parts of stalks, spatial competition is likely to result from passive suspension feeders benefiting from elevation into the boundary layer flow. On many stalks the upper surface area was covered by colonial suspension feeders. At the lower parts of stalks, flow speeds are weakest and the greatest biological pressure may come from predatory infauna and epibenthic megafauna (“croppers” sensu Dayton and Hessler 1972) in and on the sediments. Quite possibly, the colonial cnidarians do not extend down to the base of stalks due to predation from sediment fauna.

Connell (1975) and Menge (1976) suggested the role of local “escapes” from predation in producing patterns of community structure. One example of a pattern in the stalk communities that may be produced by a species escaping predation is that of the sabellid *Fabrisabella similis* living at greater heights above the sea floor than the serpulid *Bathypermilia* sp. (Fig. 6). The sabellids typically grew tubes that attached to *Hyalonema* spp. spicules underneath *Epizoanthus stellaris* and appeared capable of withdrawing back into their tubes (under the zoanthid coenenchyme) when disturbed. Serpulid tubes, however, were attached to spicules below the zoanthids, closer to the sediment surface. Taxa other than *F. similis* also appeared to maintain a commensal relationship with *E. stellaris*, potentially using the sheath of the colony for protection from epibenthic predators. Nereid and phyllodocid polychaetes were found under *E. stellaris* sheaths as were nematodes, ostracods, and, in large numbers, *Cibicides lobatulus*.

Colonial organisms as dominant space competitors

E. stellaris and hydractiniid colonies, when present, covered much of the primary substratum area of the

Hyalonema spp. stalks. Many functional groups of colonial organisms (sensu Jackson 1979) could be identified among the stalk-associated taxa. *E. stellaris* has a sheet-like form. The hydractiniid and the sponge *Caulophacus schulzei* can be considered “mounds” that encase the *Hyalonema* spp. spicules. The bryozoan *Striatodoma dorothea*, with limited attachment to the *Hyalonema* spp. spicules, has a plate-like form. Vine-like forms include the hydroids *Lafoea dumosa* and *Cryptolarella abyssicola*, and “runners” include the agglutinated foraminifera *Telammina* sp. and *Rhizammina algaeformis*.

Jackson (1979) ranked functional groups in terms of successful spatial competition in environments with little physical disturbance and with unlimited food resources as follows: sheets and mounds \geq vines \geq plates and trees $>$ runners. This ranking appears to hold true for the stalk communities. When *Hyalonema* spp. die, the sponge body falls off the top but a central column of spicules remains, leaving several centimeters of new substratum available for colonization. Opportunistic species, which appear to include foraminifera, *L. dumosa*, and other hydroids (Beaulieu, in press), recruit to this area. I found evidence for the superiority of *E. stellaris* in overgrowing opportunists through lateral growth at the top of 10 of the 27 dead *Hyalonema* spp. stalks sampled from stn M. *L. dumosa* branches at the top sometimes protruded from holes surrounded by the zoanthid colony. Solitary organisms such as sabellid and terebellid polychaetes, that generally were located below zoanthid colonies, were found at the tops of some stalks with their tubes covered by zoanthid coenenchyme.

Zoanthids, in fact, are very common epizootes of *Hyalonema* spp. around the world; expedition reports typically label *Hyalonema* spp. specimens as with or without zoanthids (Schulze 1887; Ijima and Okada 1926). At stn M zoanthids inhabited 30% of the live *Hyalonema* spp. stalks and typically extended up to the base of the sponge body. On some dead *Hyalonema* spp. stalks the mound-like hydractiniid dominated, overgrowing *Bathypermilia* sp. tubes, *C. schulzei*, and *Striatodoma dorothea*. Unlike *E. stellaris*, the hydractiniid sometimes inhabited stalks with separated spicules. Because the hydractiniid and zoanthid were never observed on the same stalk and *E. stellaris* apparently is associated with live *Hyalonema* spp., I propose that the hydractiniid is last in a successional sequence. However, we are left to wonder about the time scale for succession in the stalk communities. The life span of *Hyalonema* spp. could, quite possibly, be measured in centuries.

Conclusions

In this study, epifaunal communities on biogenic structures (mainly glass sponge stalks) collected at an abyssal station were species-rich and densely packed with organisms covering the primary substratum and attached to secondary substrata provided by other epifaunal or-

ganisms. The stalks provided hard substrata for passive suspension feeders above the soft sea floor and provided refuge and gathering sites for motile cryptozoa. Processes structuring shallow-water, hard-substratum communities may be important for these deep-sea communities. Spatial competition may determine community structure at elevated positions on the stalks, with sheet- and mound-like colonial organisms exhibiting spatial dominance. Predation potentially is important at the base of stalks, where low flow prohibits a suspension-feeding lifestyle and organisms in the stalk communities would be exposed to epibenthic predators.

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