Colonization of habitat islands in the deep sea: recruitment to glass sponge stalks

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Abstract

Biogenic structures in the deep sea often act as hard substratum 'islands' for the attachment of encrusting fauna. At an abyssal station in the NE Pacific, stalks of hexactinellid sponges in the genus *Hyalonema* are habitat islands for species-rich epifaunal communities. An experimental study was conducted to (1) determine the colonization rates of artificial *Hyalonema* stalks, (2) compare the species composition and diversity of recruits to newly available substrata to that of the natural communities, and (3) examine the vertical distribution of recruits. Four sets of six artificial sponge stalks, constructed of *Hyalonema* spicules, were deployed at 4100 m depth for 3- to 5-month periods. There was no difference in net colonization or immigration rate among the four deployments. Colonization rates were similar to those reported for other deep-sea, hard substratum recruitment experiments. The taxa that recruited to the artificial stalks were a subset of the taxa found in natural communities. However, several taxa important in structuring natural communities did not recruit to the artificial stalks. The two taxa with the highest invasion rates, a calcareous foraminiferan (*Cibicides lobatulus*) and a serpulid polychaete (*Bathyvermilia* sp.), also were the two taxa with greatest relative abundance in natural communities. Vertical distributions of *Cibicides* and an agglutinated foraminiferan (*Telammina* sp.) were skewed towards the top of the artificial stalks, potentially because of active habitat selection. These results have several implications for natural *Hyalonema* stalk communities. Most importantly, species composition and abundance of individuals in the stalk communities appear to be maintained by frequent recruitment of a few common taxa and infrequent recruitment of many rare taxa. An argument is presented for temporal-mosaic maintenance of diversity in these deep-sea, hard substratum communities. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Artificial substrata; Colonization; Epizoites; Foraminifera; *Hyalonema*; Recruitment; USA; Northeast Pacific

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1. Introduction

A discrete, insular habitat surrounded by an environment that poses difficulties for dispersal can be considered a habitat island (Schoener, 1988; Rosenzweig, 1995). Previously studied marine habitat islands include subtidal rocks (Osman, 1977), experimental fouling panels (e.g. Schoener and Schoener, 1981), and living organisms (e.g. Uebelacker, 1977). Hard substrata in the deep sea are generally in the form of habitat islands. The dispersal barrier for attached organisms is the vast areal extent of soft sediment on the deep-sea floor. Islands in the deep sea encompass those at large scales, such as seamounts (e.g. Mullineaux, 1994; Mullineaux and Mills, 1997) and hydrothermal vents (e.g. Lutz, 1988; Hessler et al., 1988), to those at small scales, such as rock outcrops (Lissner et al., 1991), dropstones (Oschmann, 1990), and manganese nodules (Mullineaux, 1987).

Biogenic structures also act as habitat islands in the deep sea. Structures such as the tubes or stalks of epibenthic organisms protrude from the soft mud floor, providing a hard substratum that elevates suspension feeders into benthic boundary layer flow (Barthel et al., 1991; Levin, 1991; Gooday et al., 1992). At an abyssal station in the NE Pacific (Sta. M), the most conspicuous and dense assemblages of suspension feeders are attached to the stalks of hexactinellid (glass) sponges in the genus *Hyalonema* (Beaulieu, 1998; Beaulieu, submitted). The stalks are the basal columns of spicules that support the sponge bodies tens of centimeters above the sea floor. Because the stalks are siliceous, they persist long after the sponges die (Fig. 1A). In a study of the *Hyalonema* stalk communities at Sta. M, stalks provided hard substrata for a variety of encrusting organisms and refuge for motile cryptofauna. These 'islands' appeared to be distributed randomly across the sea floor and could be centimeters to meters apart (Beaulieu, 1998; Beaulieu, submitted).

The slope of the species-area curve for *Hyalonema* stalk communities sampled from Sta. M was characteristic of islands with low immigration rates ($z = 0.32$; Beaulieu, submitted). Immigration rate can be defined as the number of species that recruit to an island in a given time, as distinguished from colonization rate, which is the number of individuals recruiting per time (Simberloff and Wilson, 1969; Schoener, 1988). A low immigration rate means that, on the time scale of community development, recruitment of propagules of different species to the islands occurs infrequently. Recruitment to the stalks can occur in two main ways: (1) propagules advected through the water column settle and recruit, or (2) juveniles or adults crawl up from the sediment.

The time scale for community development in the deep sea usually is much longer than in shallow waters. With few exceptions (e.g. Desbruyères et al., 1980), colonization experiments in soft-bottom environments in the deep sea led to the conclusion that colonization rates for unenriched sediments were very low relative to shallow water environments and that recovery to species richness of the background community would take years (e.g. Grassle, 1977; Smith and Hessler, 1987). Studies of the recruitment of fauna to hard substrata in the deep sea are few, with recent work conducted at seamounts (Mullineaux and Butman, 1990; Bertram and Cowen, 1999) and hydrothermal vents (Mullineaux et al., 1998). The colonization rates for hard substratum communities also were relatively low, with the exception of wood 'islands' that were colonized by opportunistic wood-boring bivalves (Turner, 1973, 1977).

The main objective of the experimental study described in this paper was to gain insight into processes responsible for the diversity and vertical distribution of fauna on the *Hyalonema* stalks as hard substratum islands in the deep sea. Goals for the research were to determine the colonization and immigration rates for artificial *Hyalonema* stalks, compare these rates to other deep-sea studies,
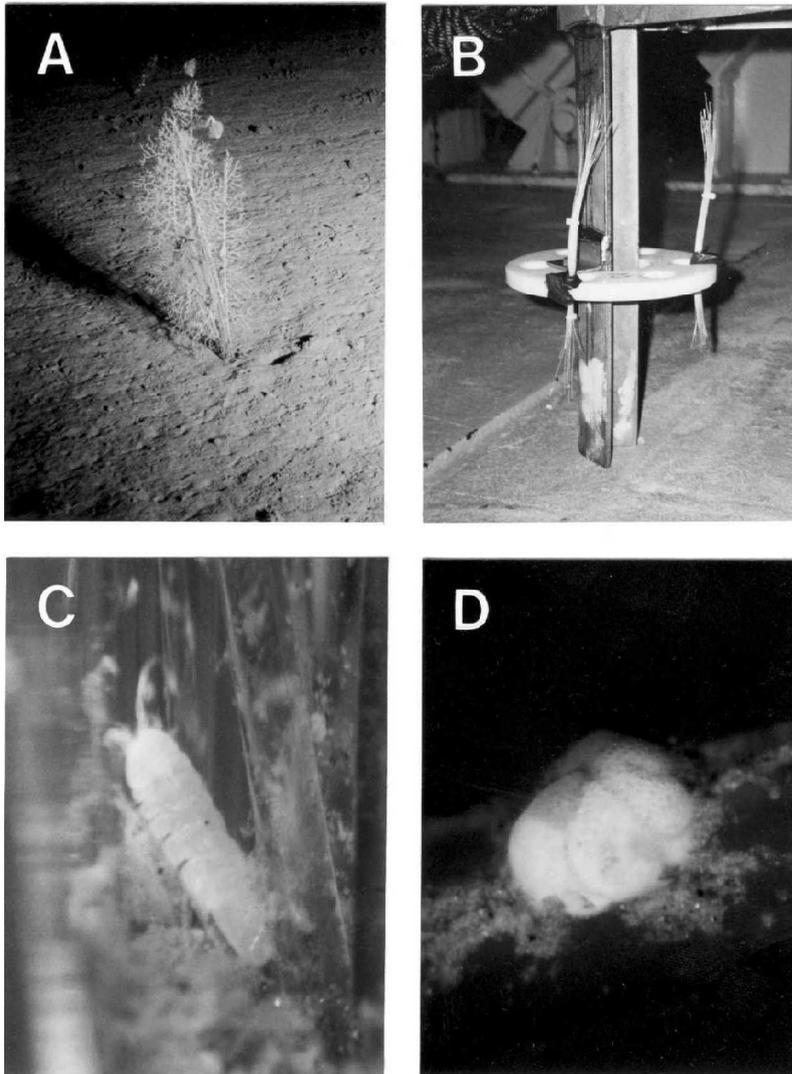
Fig. 1. (A) Dead *Hyalonema* stalk colonized by a hydroid, tunicate, and various other epifauna in situ at 4100 m depth at Sta. M in the NE Pacific (stalk extends ∼ 20 cm above the sea floor). (B) Two artificial *Hyalonema* stalks attached to a foot-pad of the camera tripod (on deck before deployment; each stalk extends ∼ 15 cm above the foot-pad). (C) Isopod (body length 1.7 mm) perched on tube (occupied by phyllodocid polychaete) between spicules of an artificial stalk. (D) A calcareous foraminiferan *Cibicides lobatulus* (∼ 600 μm across test) attached to a spicule of an artificial stalk.

and probe hypotheses concerning the development of communities on hard substrata in the deep sea. Artificial stalks constructed of *Hyalonema* spicules were deployed in situ at the abyssal station (Sta. M) as 'fouling panels'. Data from the recruitment experiments were used to examine whether the species composition and diversity of recruits to newly available substrata differed from those of the natural communities. Data also were used to examine whether recruits to newly available substrata exhibited a skewed distribution with respect to height above the sea floor. The vertical

distribution of recruits often can reveal clues about physical (or biological) mechanisms that supply propagules and whether attachment sites are selected actively.

2. Materials and methods

2.1. Study site

Colonization experiments were conducted at a time-series station in the abyssal NE Pacific (Sta. M, 4100 m depth) about 220 km west of Point Conception, California (34°50′N, 123°00′W). The physical environment is relatively stable, with gentle currents (mean speed 2.19 cm s^{-1} at 2.5 m above bottom in long-term records; Beaulieu and Baldwin, 1998). Flow at 10 cm above bottom, measured in short-term experiments, ranged from 1.34 to 2.75 cm s^{-1} (Beaulieu, 1998). A free-vehicle tripod with a titanium frame ($\sim$ 3 m high with legs $\sim$ 2 m apart; described in Smith et al. (1993)) provided a platform for deployment of the artificial *Hyalonema* stalks. Surveys to determine the distribution of natural stalk communities at Sta. M were conducted $\sim$ 20 km south of the tripod deployments. The density of natural *Hyalonema* stalks, estimated from 9 km of camera sled transects, was 1118 per hectare, corresponding to $\sim$ 1 stalk every 5 m of transect (Beaulieu, submitted).

2.2. Materials

Artificial stalks were constructed of basal root tuft spicules of *Hyalonema* that were collected from otter trawl samples taken seasonally at Sta. M. Spicules $\sim$ 25 cm in length were stripped of all epifaunal organisms and left to dry for several months in the laboratory. To create an artificial stalk, 20–25 spicules were cinched together to a diameter of $\sim$ 5 mm with two small plastic cable ties (the number of spicules and diameter of the spicule bundles were consistent with natural stalks). These bundles of spicules were attached to the foot-pads of the tripod with two additional cable ties and electrical tape (two stalks per leg; see Fig. 1B). A minimal amount of electrical tape was used in order to maximize the surface area of the spicule column available to colonists. Six stalks were attached to the tripod during each of four deployment periods between June 1995 and October 1996. Three additional stalks, created with long (25 cm), thin (1 mm) rods of Pyrex^{TM} glass fused together at the bottom, also were attached to the tripod foot-pads during the fourth deployment period.

Because the tripod was recovered in surface waters that were much warmer than ambient bottom water and sometimes quite rough, some organisms that were attached to the artificial stalks may have fallen off before the tripod was brought on deck. Immediately after the tripod was secured on deck, the artificial stalks were photographed, removed from the foot-pads, placed into individual plastic tubes, and preserved with 5% buffered formalin. The frame of the tripod was inspected visually for attached fauna.

2.3. Sample processing and data analysis

Within days of collection, each stalk was stained in its tube with Rose Bengal. After one or two days the stained water was poured over a 300 μm screen to retain macrofaunal organisms that became detached during handling. Each stalk was placed into a tray filled with water, and the

spicules were separated by cutting off the plastic cable ties. Each spicule was examined under a dissecting microscope for all attached organisms. The size of each organism was estimated with an ocular micrometer (to the nearest 100 μm), and the location of most organisms in terms of in situ height above the sediment surface was measured with calipers (to the nearest mm). To measure height above the sea floor, the lower cable tie (that had been taped to the top of the tripod foot-pad) was assumed to have rested on the sediment surface. Each organism then was removed from the spicules, stored in 70% ethanol (calcareous foraminifera were stored dry on cardboard slides), and sent to appropriate taxonomic specialists for identification.

Colonization rates to individual stalks were determined by dividing the number of individuals that recruited to each stalk by the approximate surface area of the stalk and the length of time deployed. Surface area was calculated by making the assumption that each stalk was a cylindrical column (with twice the diameter enclosed in the cable ties to account for the spicules flaring at the top). Immigration to individual stalks was calculated as the number of taxa that recruited to each stalk. To determine whether the colonization rates or number of immigrants differed among the deployment periods, one-way analyses of variance were performed with the individual deployments as treatment effects. Levene's test was used to check for homogeneity of variances. Nonparametric Kruskal–Wallis tests were used to check whether sizes of recruits differed among deployment periods (Sprent, 1993).

Similarity in species composition between each pair of artificial stalks was determined using the Jaccard index for presence/absence data. The Jaccard index, similar to the Bray–Curtis index for continuous data (Clifford and Stephenson, 1975), measures the percentage of co-occurring species. This index was chosen because encrusting foraminifera and colonial organisms were counted as single individuals, yet, when present, they covered a greater spatial area than single individuals of solitary taxa. Similarity indices and rarefaction curves were calculated using BioDiversity Professional software (N. McAleece, Natural History Museum, London). A Kruskal–Wallis test also was used to compare the vertical distributions of different taxa, assuming independence of distributions. For the most abundant taxa, sizes of recruits were plotted against height above bottom to check for correlation. ANOVAs, Kruskal–Wallis tests, and tests for the significance of correlations were performed with Statistica 5.0 software.

Results for three natural, dead *Hyalonema* stalks that were similar in diameter and height to the artificial stalks are presented here for comparison (Appendix A). All three stalks were collected at approximately 34°41.7′N, 123°00.0′W at Sta. M. The detailed procedure for collecting and examining natural *Hyalonema* stalk communities is described elsewhere (Beaulieu, 1998; Beaulieu, submitted). Briefly, the natural communities were collected in tube cores using the submersible *Alvin*, and all organisms > 300 μm in size were detached from the stalks and identified to the lowest taxonomic level.

3. Results

3.1. Colonization of artificial stalks

A total of 220 individuals in 19 taxa recruited to the 24 artificial stalks (Table 1). No organisms recruited to the plastic cable ties that held the spicules together or to the electrical tape that held the

spicule bundles to the foot-pad. In all four deployments only three ampharetid polychaetes (*Neosabellides* n. sp.) and two tubulariid hydroids colonized the tripod frame. A total of seven individuals in five taxa recruited to the three Pyrex™ glass stalks deployed the same time as Set 4.

The net colonization rates for artificial stalks from each set, in terms of the number of individuals recruiting to a stalk per unit area per time, are depicted in Fig. 2. Although Set 2 (deployed Nov. 1995–Feb. 1996) had the highest colonization rate (mean 2.3×10^{-3} recruits $\text{cm}^{-2}\,\text{d}^{-1}$), there was no significant difference in colonization rate among the deployment periods ($F = 1.06$; $P = 0.39$). The number of taxa immigrating to the artificial stalks is plotted against deployment length of the four sets in Fig. 3. This figure differs from typical plots for fouling panel experiments in that it does not represent a single set of stalks monitored over time but rather four discrete sets. Approximately five taxa immigrated to each individual stalk; there was no significant difference among the deployment periods in the number of immigrants ($F = 0.07$; $P = 0.98$). Because these data did not meet the assumption of homogeneity of variances, a nonparametric Kruskal–Wallis test was performed, also indicating no difference in immigration among the deployment periods ($H(3, n = 24) = 0.96$; $P = 0.81$). Although both the colonization and immigration rates generally reflect the recruitment of propagules from the water column, three of the individuals (in three taxa) likely recruited from the sediments, based on their size and their mobility. These were a phyllodocid polychaete, a nereid polychaete, and an isopod (Fig. 1C).

Both the number and size of individuals of the two most abundant taxa recruiting to the stalks, *Cibicides lobatulus* and *Bathyvermilia* sp. (described below), were not proportional to the length of the deployment periods. In fact, there was a significant difference in the median size of *Cibicides* among the four deployment periods (Kruskal–Wallis $H(3, n = 79) = 21.48$; $P = 0.0001$), and an a posteriori test did not segregate the size for the shortest deployment (75 d) from the size for the longest deployment (167 d). Both *Cibicides* and *Bathyvermilia* had the greatest median size in Set 3 (deployed Feb.–Jun. 1996).
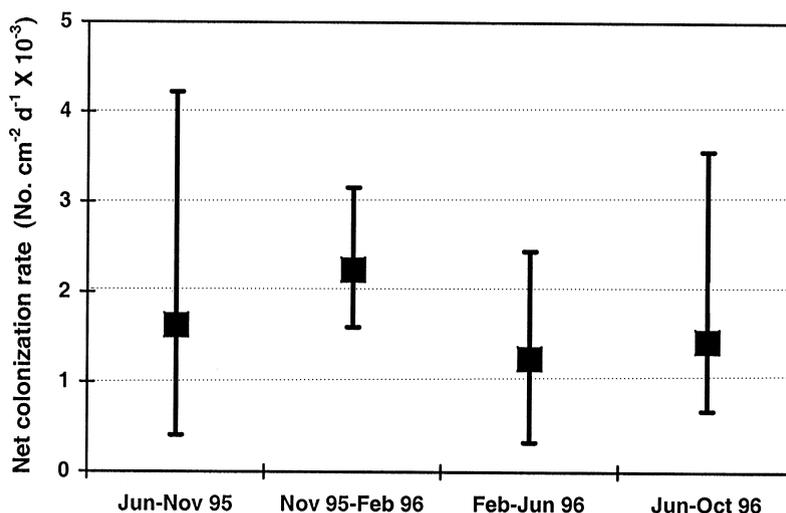

Fig. 2. Approximate colonization rates (number of recruits per unit area per time) for the artificial *Hyalonema* stalks deployed at Sta. M. ■ = mean for each set; bars indicate range for six individual stalks.

Table 1
Abundance of taxa that recruited to artificial *Hyalonema* stalks deployed at Sta. M in the abyssal NE Pacific

Artificial stalk set no.	1						2						3						4						Totals
Location (Lat. N, Long. W)	34°54.5′, 123°13.4′						34°52.8′, 123°14.1′						34°51.5, 123°14.0′						34°55.8′, 123°05.0′						
Date deployed	4 Jun. 95						18 Nov. 95						2 Feb. 96						3 Jun.96						
Date recovered	18 Nov. 95						1 Feb. 96						3 Jun. 96						10 Oct. 96						
No. of days in situ	167						75						121						129						492
Average height above bottom (cm)	14						13						15						18						15
Stalk no.	1-1	1-2	1-3	1-4	1-5	1-6	2-1	2-2	2-3	2-4	2-5	2-6	3-1	3-2	3-3	3-4	3-5	3-6	4-1	4-2	4-3	4-4	4-5	4-6	
Protozoan groups																									
Agglutinated foraminifera																									
Bulbous, thick-walled			2																						2
Telammina sp.		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		21
"Tree" type 1 (hemisphaeramminid)	1	1	3						1	1		1		1	1	1		1	1	1					12
Tubular, flexible (includes *Rhizammina* sp.)				1			1	1					1	1	1	1		1		1	1				9
Tubular, rigid			1										1												1
Calcareous foraminifera																									
Cibicides lobatulus	11	2	5	5	15	4	3	3	6	1	1	3	8	5	1	1	1		19	7	2	3	2		106
Miliolid			1											1						1					2
Other			3		3					1	1	1		1		1	1			1					9
Metazoan taxa																									
Cnidaria - Colonial, thecate hydroid	1	1		1	1					1	1														5
Nematoda																					1				1
Polychaeta																									
Ampharetid — *Egamella* quadribranchiata	2				2	1														1					4
Ampharetid — *Neosabellides* n. sp.										1											1				2
Ampharetid — unidentified			1												1										1
Nereid — *Nereis* sp.			1																						1
Phyllodocid — n. gen. 1		1																							1
Serpulid — *Bathyvermilia* sp.	1				3		1	2	2				1		3			1	3	1	2	5	1		29
Unidentified						1	1					1	1												5
Crustacea — Isopod — Unidentified asellote			1		1																				1
Unidentified					1		1			1	1		1	1	1	1	1		1	1			1		8
Total no. taxa occurring	3	2	7	2	10	4	6	4	5	5	7	5	7	5	5	6	2	4	6	4	5	5	5	4	19
Total no. individuals of all taxa	13	3	11	6	31	8	8	10	5	5	9	5	14	11	5	6	6	4	26	10	6	10	7	5	220

3.2. Diversity of fauna that recruited to artificial stalks

On the artificial and natural stalks, the calcareous foraminiferan *Cibicides lobatulus* was dominant in relative abundance (Fig. 1D). The next most abundant species and the most abundant metazoan on both the artificial and natural stalks was *Bathyvermilia* sp., a serpulid polychaete. Some individuals of both of these genera were too small to be identified to species and simply were assigned to these species labels. The mean length across the test for *Cibicides* on the artificial stalks was significantly less than on the natural stalks (0.31 mm vs. 0.52 mm; one-tailed *t*-test assuming unequal variance: $P < 0.001$). The mean length of *Bathyvermilia* (pulled from their tubes) on artificial stalks was 0.34 mm, much less than the mean size of individuals on natural stalks (2.57 mm). Although most organisms on the artificial stalks were small, one ampharetid polychaete had enough time (< 129 d) to develop into a reproducing adult (one *Egamella quadrabranchiata* was gravid).

Foraminifera, in general, were the most commonly observed recruits. *Cibicides* and the agglutinated, chain-like foraminiferan *Telammina* sp. were found on almost all of the artificial stalks (22 and 21 of the 24 stalks, respectively). The third most common and abundant foraminiferan, an agglutinated 'tree'-like hemisphaeramminid, was found on stalks from all deployment periods. *Bathyvermilia* was the most common metazoan, colonizing 16 of 24 stalks. When present on a stalk, organisms such as *Telammina*, tubular agglutinated foraminifera, and the colonial hydroid occurred only once (as single, continuous 'colonies').

Seventeen of the 24 artificial stalks had $> 50\%$ similarity with at least one other stalk in terms of presence/absence of taxa. Stalks from separate deployment periods were up to 100% similar in terms of presence/absence of taxa. Accumulated numbers of taxa and individuals for the artificial stalks were plotted in the order in which the samples were examined to show that by the third set of stalks, no new taxa were observed (Fig. 4). Of the 19 taxa that recruited to the artificial stalks, only
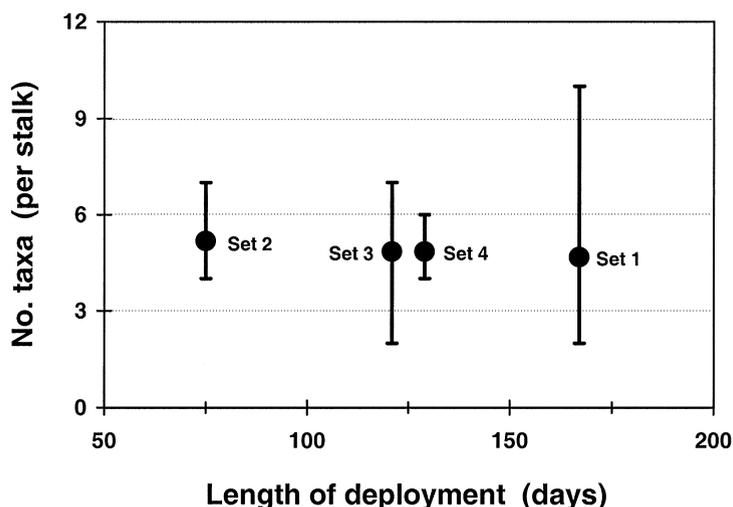

Fig. 3. Immigration of taxa to artificial *Hyalonema* stalks deployed at Sta. M. ■ = mean for each set; bars indicate range for six individual stalks.

five were not found in the three natural stalk communities. Only one of these five was not observed in the survey of 35 natural stalks conducted by Beaulieu (submitted), and this particular taxon, an unidentified metazoan, was potentially the early growth of a bryozoan (*Arachnidium* sp.) that did occur in some natural communities. Diversity of recruits to the artificial stalks was compared to the three natural stalks using rarefaction, which offers a means to compare diversity between sets of samples with different total numbers of individuals (Hurlbert, 1971). The diversity of the artificial stalk recruits appeared to be greater than that of the natural stalks (Fig. 4), with values for the expected number of taxa on the artificial stalks lying above the rarefaction curve for the natural stalks.

3.3. Vertical distribution of recruits

The average height above the sea floor for the artificial stalks was 149 mm (range 116–180 mm). The mean heights of recruits above the sea floor $\pm$ std. dev. (number of measured individuals in parentheses) for three abundant taxa were as follows: *Cibicides* 134 ± 36 mm ($n = 72$), *Bathyvermilia* 115 ± 32 mm ($n = 23$), and foraminiferan 'tree' 132 ± 35 mm ($n = 8$). Because the distribution of *Cibicides* did not meet the assumption of normality for an ANOVA, a nonparametric Kruskal–Wallis test was performed to compare the medians of the three species' distributions. A significant difference was detected among the medians ($H(2, n = 103) = 6.04; P = 0.049$), and an a posteriori test determined that *Cibicides* was located higher than *Bathyvermilia* on the stalks (at the $\alpha = 0.05$ level).

The distribution of individuals in terms of relative location on the artificial stalks is shown in Fig. 5. Overall, only 10% of the recruits were recorded on the bottom half of stalks. Forty-six
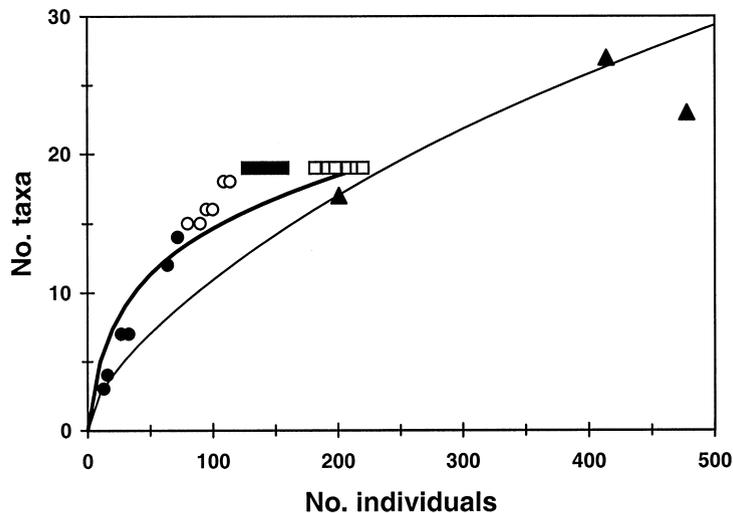

Fig. 4. Species diversity of artificial stalk recruits compared to three natural *Hyalonema* stalk communities. Symbols indicate accumulated counts for the artificial stalks (in the order in which they were examined) and counts for individual natural stalks ($\bullet$ = artificial stalk Set 1; $\bigcirc$ = Set 2; $\blacksquare$ = Set 3; $\square$ = Set 4; $\blacktriangle$ = natural stalks). Lines indicate the rarefaction curves for all samples combined (thick line for artificial stalks; thin line for natural stalks). The rarefaction curves plot $E(S_n)$, the expected number of taxa given n individuals, against number of individuals.
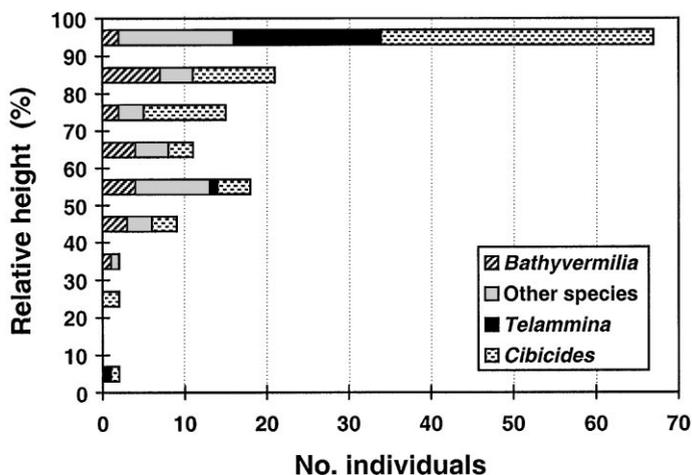
Fig. 5. Vertical distribution of fauna that recruited to the artificial *Hyalonema* stalks. Upper limits are presented for taxa that extended along spicules (*Telammina*, the colonial hydroid, and the unidentified metazoan).

percent of all recruits were found on the top 10% of the stalks. This result mainly reflects the distribution of *Cibicides* and *Telammina*, the most abundant foraminifera. Four of the five ampharetids, grouped in the 'other' category on Fig. 5, were found on the top 10%. In contrast to these very skewed distributions, 9 and 10 *Bathyvermilia* recruits were found in the 50–75% and 75–100% height ranges, respectively.

The size of the *Cibicides* recruits was negatively correlated to both absolute ($n = 51$; $r = -0.55$, $P < 0.001$) and relative ($n = 51$; $r = -0.42$, $P = 0.002$) height above the sea floor, indicating that smaller individuals were found higher up on the stalks. No significant correlation between size and height above the sea floor was observed for *Bathyvermilia* ($n = 21$).

4. Discussion

4.1. Colonization rates in the deep sea

Colonization rates for the artificial *Hyalonema* stalks may be slightly underestimated because of individuals that washed off during ascent and recovery of the tripod. However, the two most abundant taxa, *Cibicides* and *Bathyvermilia*, accounting for 88% of individuals in the three natural stalk communities (Appendix A), generally are firmly attached to spicules. In comparison to hard-substratum recruitment experiments, the average artificial stalk colonization rate (~ 0.2 recruits cm^{-2} in 4 months) was most similar to the rate obtained for mineral-coated plates deployed at Cross Seamount at 1985 m depth (~ 0.1 recruits cm^{-2} in 3 months; Bertram and Cowen, 1999). The artificial stalk colonization rate also was similar to rates reported for experiments with longer deployment periods at hydrothermal vent sites (Van Dover et al., 1988; individuals excluding *Metafolliculina* in Mullineaux et al. (1998)). The artificial stalk colonization rate was higher than that reported for a long-term (19 months) deployment of basalt blocks at Cross Seamount (975 m depth; Verlaan, 1992) and lower than that obtained in short- and

long-term experiments with manganese nodules at 1240 m depth (Mullineaux, 1988) and a short-term (< 2 months) experiment with mineral-coated plates on Cross Seamount at 410 m depth (Mullineaux and Butman, 1990). In general, colonization rates are much higher in shallow temperate and tropical environments, where colonization usually is measured in percentage area covered. For example, glass rods (22 cm² surface area) had 100% coverage after a one month deployment in shallow water at Beaufort, North Carolina (Holm et al., 1997).

Colonization rates for soft sediment studies may not be strictly comparable to rates obtained for hard substratum experiments. In soft sediment recolonization experiments, only a subset of the faunal community (greater than a particular sieve size) is enumerated, and numbers of individuals are expressed per surface area of core samples. Keeping these caveats in mind, the artificial stalk colonization rate was similar to that reported for deep-sea studies using colonization trays flush with the sea floor (Snelgrove et al., 1994; < 2 month deployment in Levin and DiBacco, 1995) and a study in which unfloored sediment mounds were sampled (Kukert and Smith, 1992). In comparison to experiments that used colonization trays raised above the sea floor, the artificial stalk colonization rate was higher than in some studies (Levin and Smith, 1984; tray deployed at 3600 m depth in Grassle and Morse-Porteus (1987)) and lower than in others (Desbruyères et al., 1980).

Although the four sets of artificial stalks were deployed in four different locations during four different time periods, net colonization rate did not differ among deployments. Grassle and Morse-Porteus (1987) also reported that the season or year their sediment trays were deployed had no effect on colonization. These results for deep-sea colonization are in great contrast to shallow water studies of fouling communities that found strong evidence for temporal and spatial variation in recruitment (e.g. Sutherland and Karlson, 1977; Osman, 1977; Bingham, 1992). Seasonal variation in recruitment might be expected at Sta. M if there is a reproductive response by the benthic community to the strong seasonal input of organic matter (Baldwin et al., 1998). A longer time-series study, with more replicate stalks, is required to better examine temporal variability in colonization rate.

4.2. Immigration of species to the artificial stalks

The time and location of deployment appeared to have no effect on the taxa that immigrated to the artificial stalks over the 1.3 yr combined deployment period. Stalks from different deployments were up to 100% similar in species composition, and no new taxa were identified in Sets 3 or 4 (Fig. 4). The number of taxa that recruited to the artificial stalks was the same for the 75 d deployment as for the 167 d deployment (Fig. 3). Interestingly, the taxa that most commonly recruited to the artificial stalks also recruited to Pyrex™ glass rods that were fashioned into *Hyalonema*-like stalks.

The time scale of the recruitment experiments was too long to resolve the immigration curve for rapidly colonizing taxa and too short to resolve the curve for rare taxa. The steepest part of an immigration curve (to be fitted to Fig. 3) must have a rate > 5 taxa per 75 d, and immigration for the rare taxa must be < 1 taxon per 92 (= 167–75) days. Given this low immigration rate for rare taxa, it is likely that it would take years to accumulate the number of taxa observed on natural stalks (average 22 for the three stalks in Appendix A). Even if only the firmly-attached taxa are included in the faunal list in Appendix A (average 16 taxa per stalk), the time scale to accumulate 16

taxa on the artificial stalks still would be very long compared to immigration to shallow water fouling panels. For example, the background number of species was reached in approximately ten weeks on fouling panels deployed in Puget Sound (Schoener and Schoener, 1981) and in 1 to $1\frac{1}{2}$ yr in a study at Beaufort, North Carolina (Sutherland and Karlson, 1977).

Invasion rate is defined as the number of individuals recruiting per time for a particular taxon (Simberloff and Wilson, 1969). Invasion rates usually are high for opportunistic species, characterized as species with high reproductive rates, good dispersal ability, short generation time, and low competitive ability (e.g. Grassle and Sanders, 1973). The most common taxa recruiting to the artificial stalks can be considered opportunistic, and five of these taxa were foraminifera. Foraminifera often are considered opportunistic (Lipps, 1983; Kaminski et al., 1988). Size evidence suggests that the invasion rates of *Cibicides* and *Bathyvermilia* were not constant for the artificial stalk sets. Both the number and size of individuals of these taxa were not proportional to the length of the deployment periods. Bertram and Cowen (1999) also found that colonization rates of calcareous foraminifera were not constant in a deep-sea recruitment experiment. An alternative explanation for the observed size differences among deployment periods is that growth rate was not constant.

4.3. Implications for the diversity of natural communities

The taxa that recruited to the artificial stalks were a subset of the taxa found in natural communities and were similar in relative abundance. Given the colonization and immigration rates obtained in this study, it appears that the relative abundance of fauna inhabiting stalks is maintained by the frequent recruitment of a few common, opportunistic taxa and the rare recruitment of many taxa. The slightly higher diversity of the artificial stalk recruits, as indicated by rarefaction curves (Fig. 4), was likely due to greater dominance of *Cibicides* in the natural stalk communities (82 vs. 48% of the total number of individuals). Diversity of artificial stalk recruits would be even higher if motile taxa such as polychaetes and crustacea washed off the stalks during ascent and recovery of the tripod. Some types of attached taxa were *not* found on the artificial stalks; none of the three taxa that were space-dominators in natural stalk communities (a colonial zoanthid, the athecate hydroid shown in Fig. 1A, and a hexactinellid; Beaulieu, 1998; Beaulieu, submitted) was attached to the artificial stalks. These taxa are important in the natural communities in that the colonial cnidarians reduce the amount of area available to recruits while the epifaunal hexactinellid provides a secondary substratum, increasing the area available to recruits (Beaulieu, 1998; Beaulieu, submitted).

In shallow water studies of habitat islands, Osman (1977) proposed that physical disturbance and the history of a substratum in terms of colonization events were most important in maintaining diversity and structuring epifaunal communities. For deep-sea, soft sediment habitats, where biological rather than physical disturbance is more prevalent, current theory holds that diversity is maintained by a spatial mosaic of patches in different stages of succession (contemporaneous disequilibrium theory proposed by Grassle and Sanders (1973), tested by Kukert and Smith (1992)). Different responses to disturbances in time and space by different taxa are necessary for the patch mosaic theory to hold (Snelgrove et al., 1994). In this artificial stalk recruitment study, different taxa colonized new space at different rates. Just

as in the sediment communities, the *Hyalonema* stalk communities are a spatial and temporal mosaic of patches created by biological disturbance. The most extreme disturbance, when the sponge dies and the body falls off the top of the stalk, makes several centimeters of space available for recruitment of epifauna. Disturbance also results from the creation of new secondary substrata after a rare recruitment event of an epizoic hexactinellid or the frequent recruitment events of tube-building polychaetes or thecate hydroids. Other disturbance results from space-dominating colonial cnidarians overgrowing other organisms. Also, cropping of fauna attached at the base of stalks by infaunal or mobile epibenthic fauna can be considered disturbance (Dayton and Hessler, 1972). This mosaic of primary and secondary substrata in various stages of colonization is important in maintaining the community composition of the hard substratum islands.

4.4. Vertical distribution of recruits

Recruits to the artificial stalks were not distributed evenly with respect to height above the sea floor (Fig. 5). The fact that very few individuals recruited to the lower 20% of the artificial stalks (Fig. 5) suggests that the foot-pads of the camera tripod were driven a few centimeters down into the sediment. In fact, on several occasions sediment was stuck between the spicules above the lower cable tie (which was designated as the sediment surface level for height measurements). An alternative explanation for the lack of recruits to the lower portion of the stalks could be predation from sediment dwellers; however, in natural stalk communities, organisms including *Cibicides* and *Bathyvermilia* were attached to spicules all the way down to the sediment surface (Beaulieu, submitted).

Selectivity of larvae during settlement often has been implicated in determining the distribution of epifaunal species (Osman, 1977; Underwood and Denley, 1984; Mullineaux and Butman, 1990). Active attachment site selection by *Cibicides* most likely explains the difference in vertical distribution between *Cibicides* and *Bathyvermilia* on the artificial stalks. The serpulids had limited (if any) movement along the substratum and likely settled where they landed on the stalks. However, the *Cibicides*, which can be motile prior to attachment (Nyholm, 1961; Zumwalt and DeLaca, 1980), could have moved along the substratum until they 'chose' an appropriate environment near the top. A behavioral explanation also may be proposed for the distribution of *Telammina* (*Telammina* may have grown towards the top).

Potentially, the foraminifera responded to the vertical gradient in flow velocity above the sea floor, assuming a suspension-feeding lifestyle at the top of the artificial stalks. In the natural stalk communities, large mobile suspension-feeding organisms such as anemones, crinoids, and ophiuroids were observed most often at the very top of stalks (Beaulieu, 1998; Beaulieu, submitted). Studies of *Cibicides* spp. epizoic on other organisms (Zumwalt and DeLaca, 1980; Lipps, 1983; Alexander and DeLaca, 1987; Lutze and Thiel, 1989; Svavarsson and Davidsdottir, 1995) indicated that foraminifera in elevated habitats are suspension feeding. The strong negative correlation between size and height above the sea floor for *Cibicides* also suggests that juvenile *Cibicides* actively selected sites of attachment elevated above the sea floor. An alternative hypothesis for the skewed vertical distribution of the foraminifera is that more recruitment occurred at the top of the stalks because propagule supply (concentration × flow rate) was greater. However, in a previous study of colonization of deep-sea hard substrata, recruitment of foraminifera to a two-tiered array

of manganese nodules was much greater just above the sediment surface than at 20 cm above the sea floor (Mullineaux, 1988).

Appendix A

Abundance of taxa on the three natural, dead *Hyalonema* stalks that were similar in height to the artificial stalks are provided in this appendix (Table A1).

Table A1

	27	34	36
Stalk no.			
Approximate height above bottom (cm)	10	16.5	16
Protozoan groups			
Agglutinated foraminifera			
Bathysiphon flavidus		1	
Bulbous, thick-walled[a]	2	8	
Encrusting			1
"Soft-bodied" (similar to allogromiid)	1	3	1
"Streamer" (similar to *Linea simplex*)		2	1
Telammina sp.[a]	1	1	
"Tree" type 1 (hemisphaeramminid)[a]	4	15	11
"Tree" type 2	4		
Tubular, flexible (includes *Rhizammina* sp.)[a]		1	1
Tubular, rigid (not *Bathysiphon* sp.)[a]		1	
Veleroninoides scitulus	1		
Calcareous foraminifera			
Cibicides lobatulus[a]	381	337	173
Miliolid — *Pyrgo* sp.	2		1
Miliolid (not *Pyrgo* sp.)[a]	1		
Other[a]	1	1	

Table A1 (*continued*)

Metazoan taxa			
Hexactinellida		1	
Cnidaria — Colonial, thecate hydroid[a]			
Filellum serratum			1
Lafoea dumosa	1		1
Platyhelminthes — Turbellarian	1		
Nemertea			1
Polychaeta			
Ampharetid — *Neosabellides* n. sp.[a]		5	2
Ampharetid — unidentified[a]	1	4	1
Aphroditid — *Aphrodita* sp.	1		
Cirratulid — unidentified		2	
Nereid — *Neanthes mexicana*	1		
Paraonid — unidentified	1		
Phyllodocid — n. gen. 1[a]		1	
Sabellid — *Fabrisabella similis*		1	
Sabellid — unidentified		2	
Serpulid — *Bathyvermilia* sp.[a]	58	12	
Unidentified[a]	2	5	
Mollusca — Rissoid gastropod		1	
Crustacea			
Amphipod — Caprellid		1	
Amphipod — *Bonnieriella* sp.	6		2
Amphipod — Melphidippid		2	
Cirriped — *Verum proximum*	5	2	1
Copepod — Poecilostomatoida - Nereicolid		2	
Copepod — Siphonostomatoida - Asterocherid	1		
Copepod — Siphonostomatoida - unidentified		1	
Isopod — *Arcturus* n. sp.			1
Isopod — *Haplomunna* n. sp.			1
Isopod — Nannoniscid (similar to *Hebefustis* sp.)	1		
Ectoprocta — Ctenostomata - *Arachnidium* sp.		1	
Echinodermata			
Ophiuroid — *Ophiacantha* sp. C	1		1
Ophiuroid — *Ophiacantha* - unidentified		1	
Total no. taxa occurring	23	27	17
Total no. individuals of all taxa	478	414	201

[a]Taxa that also recruited to the artificial stalks.

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