HARPACTICOID COPEPODS AND BIOGENIC STRUCTURES: IMPLICATIONS FOR DEEP-SEA DIVERSITY MAINTENANCE[1,2]

David Thistle

Florida State University

ABSTRACT

Although several models have been proposed to explain the maintenance of enhanced diversity in the deep sea, the data do not clearly support a particular view. This paper reports a study of the relationship of harpacticoid copepods of the San Diego Trough (1200 m depth) to biogenic environmental structures. Harpacticoid species are shown to be significantly associated with such structures. The associations appear to be weak, but the sign of the correlation coefficient between particular species and individual structural classes is conserved on the average. These results support Jumars' grain-matching model and have implications for several of the other models of diversity maintenance.

INTRODUCTION

Hessler and Sanders (1967) demonstrated that the apparent low diversity of the deep sea (see *Ekman,* 1953; *Marshall,* 1954; *Bruun,* 1957) was a sampling artifact, and that, rather than being a region of few species, the deep sea was among the most diverse marine, soft-bottom areas. This result presented deep-sea workers

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with an apparent paradox because the deep sea did not appear to have characteristics which readily suggested why it should be more diverse than other marine regions.

Several models have been proposed to resolve the paradox of high deep-sea diversity. *Sanders* (1968, 1969), and *Slobodkin and Sanders* (1969) developed the stability-time hypothesis. In this view, the stability of conditions in the deep sea over long periods of time permitted species to become biologically accommodated to each other by evolving highly specialized niches which overlap minimally. In contrast, *Dayton and Hessler* (1972) suggested that, given the constancy of the environment and food resources, there were insufficient independent factors to permit large numbers of species to have non-overlapping niches. Rather, predation and disturbance kept potential competitors sufficiently low in abundance that resources were never limiting. *Grassle and Sanders* (1973) and *Menge and Sutherland* (1976) have presented arguments which incorporate aspects of both models.

Jumars (1975a, b) presents another view. Many mud-bottom organisms create microenvironmental heterogeneity. In physically stable habitats, such heterogeneity persists at least as long as the lifetime of the organism and, therefore, is available to other animals for habitat partitioning. Further, because this hetero-geneity is organism-generated and maintained, it has the same spatial and temporal scales as animal ambits and life spans. Following *Hutchinson's* (1961) arguments, environmental changes on these scales are those most likely to minimize competitive exclu-sion. As a result, Jumars suggests that scale matching between species and biogenic environmental heterogeneity could permit high diversity to be maintained in the deep sea.

Jumars (1975b) supported his model by citing evidence that small-ambit polychaete species as a group were more diverse than large-ambit species, as would be expected if biogenic microenviron-mental heterogeneity regulated community diversity. *Thistle* (1978) analyzed harpacticoid copepod dispersion patterns and found that harpacticoid species were discordant in their abundance patterns in pairs of contiguous 10 x 10 cm samples; and, for some highly aggregated species, there was evidence that the patch size was less than 10 cm in diameter. Thistle suggested that these data supported the grain-matching model because organism-generated environmental heterogeneity was likely to generate patches with scales on the order of centimeters in dimension which corresponded to scales of patchiness observed for harpacticoids.

However, these scale data, at best, indirectly test the grain-matching model. This paper attempts to establish a more direct relationship between organism-generated environmental hetero-geneity and harpacticoid copepod species.

MATERIALS AND METHODS

Locality

The sample site was located in the San Diego Trough (Fig. 1) at 1218.3 to 1223.8 m depth near the base of the Coronado Escarpment (32° 35.75'N, 117° 29.00 W) away from areas of known turbidity channels. *Thistle* (1978) found that the study site can be characterized as having the physical stability typical of the deep sea: granulometric analyses showed no evidence of recent disturbance by turbidity flows; measurements of temperature, salinity, and dissolved oxygen revealed little variability.

The samples were taken as part of Expedition Quagmire (*Thiel and Hessler*, 1974). The project was designed around the capabilities of the Remote Underwater Manipulator, which took cores *in situ* with great deliberateness yielding samples which were essentially undisturbed. In particular, the shock wave which precedes non-deliberate samplers (*McIntyre*, 1971; *Hessler and Jumars*, 1974; *Jumars*, 1975a, b) was eliminated. Sample locations were determined to within a meter.
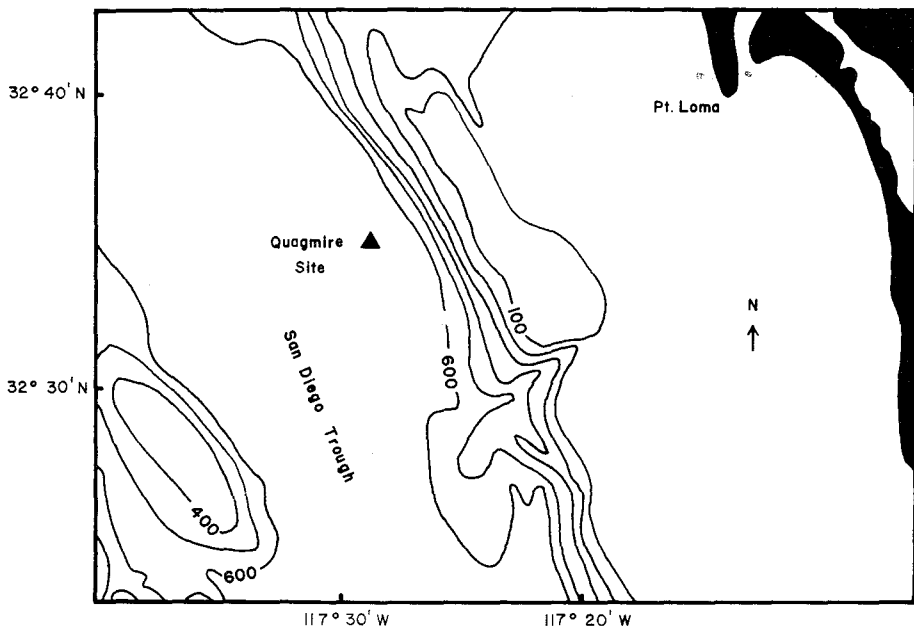

Fig. 1. Chart of sampling area. The filled triangle marks the Quagmire site. Depth contours are in fathoms. Modified from Coast and Geodetic Survey Map N. 5101.

Fifty-eight samples were taken in a stratified random manner from the triangular study site (Fig. 2) using a modified Ekman grab (20 x 20 cm). The grab was partitioned internally into four subcores (10 x 10 cm) which were the units of this study. I analyzed the harpacticoid fauna from fourteen subcores (pairs of subcores from six cores and two single subcores). Figure 2 shows the distribution of samples in the study site; Table 1 gives the intersample distances.

The top 1 cm layer and overlying water for each subcore were formalin fixed at sea. In the laboratory, each sample was screened through sieves of 1.00 mm and 0.062 mm mesh and transferred to ethanol. The 0.062 mm fractions containing the harpacticoids were sorted; adults were identified to species and counted.

The > 1.00 mm fraction was used to quantify the abundance of biogenic structures (e.g. tubes, mud balls). Structures were
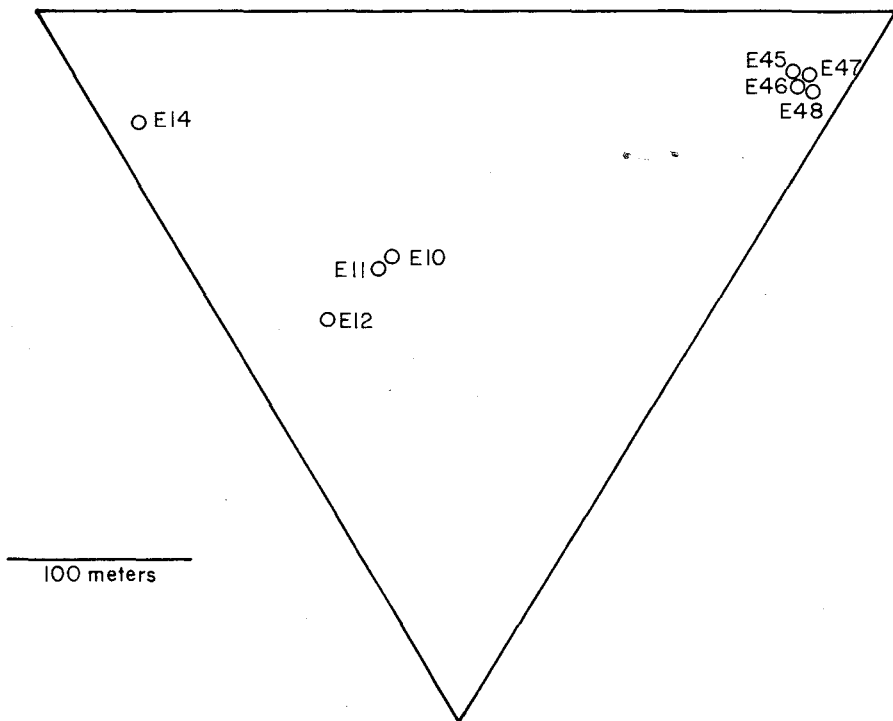
Fig. 2. The Quagmire-site sampling triangle. The Ekman cores treated in this study are indicated by circles.

TABLE 1. Distances in meters between Ekman cores.

Sample

	E11	E12	E14	E45	E46	E47	E48
E10	6.0	50.5	152.2	239.9	239.8	239.9	242.1
E11		44.6	152.3	244.5	244.5	244.5	246.7
E12			151.5	284.9	284.9	284.8	286.9
E14				356.6	356.9	357.6	359.9
E45					0.1	2.1	3.4
E46						2.0	3.4
E47							2.2

grouped into seven classes: (1) mud balls formed by the cirratulid polychaete *Tharyx luticastellus* (*Jumars*, 1975b, c); (2) smaller mud balls made by a congener, *Tharyx monilaris*, Fig. 3A; (3) all other polychaete tubes; (4) tests of the agglutinating foraminiferan genus *Orictoderma*, Fig. 3A; (5) tube-shaped agglutinating Foraminifera, Fig. 3B; (6) bush-like agglutinating Foraminifera, Fig. 3C; (7) tanaid crustacean tubes. All structures or fragments of structures which exceeded 0.5 mm in minimum axial dimension and were retained on a 1.0 mm sieve were classified. The maximum orthogonal length and width were measured except that the second widest dimension was used for branched forms to represent more accurately the diameter of the volume occupied by the organism. The shape of each class was approximated by a sphere (2, 4 of above), a cylinder (3, 5, 7), or a prolate elipsoid (1, 6) and volumes for each class were calculated (Table 2).

The correlation coefficients cited in *Results* are *Kendall* (1948) rank correlation coefficients. The five percent significance level was used unless stated otherwise.

RESULTS

The habitat varies locally in the amount of a given structural class present (Table 2). I calculated rank correlation coefficients using all 14 subcores for each harpacticoid species'
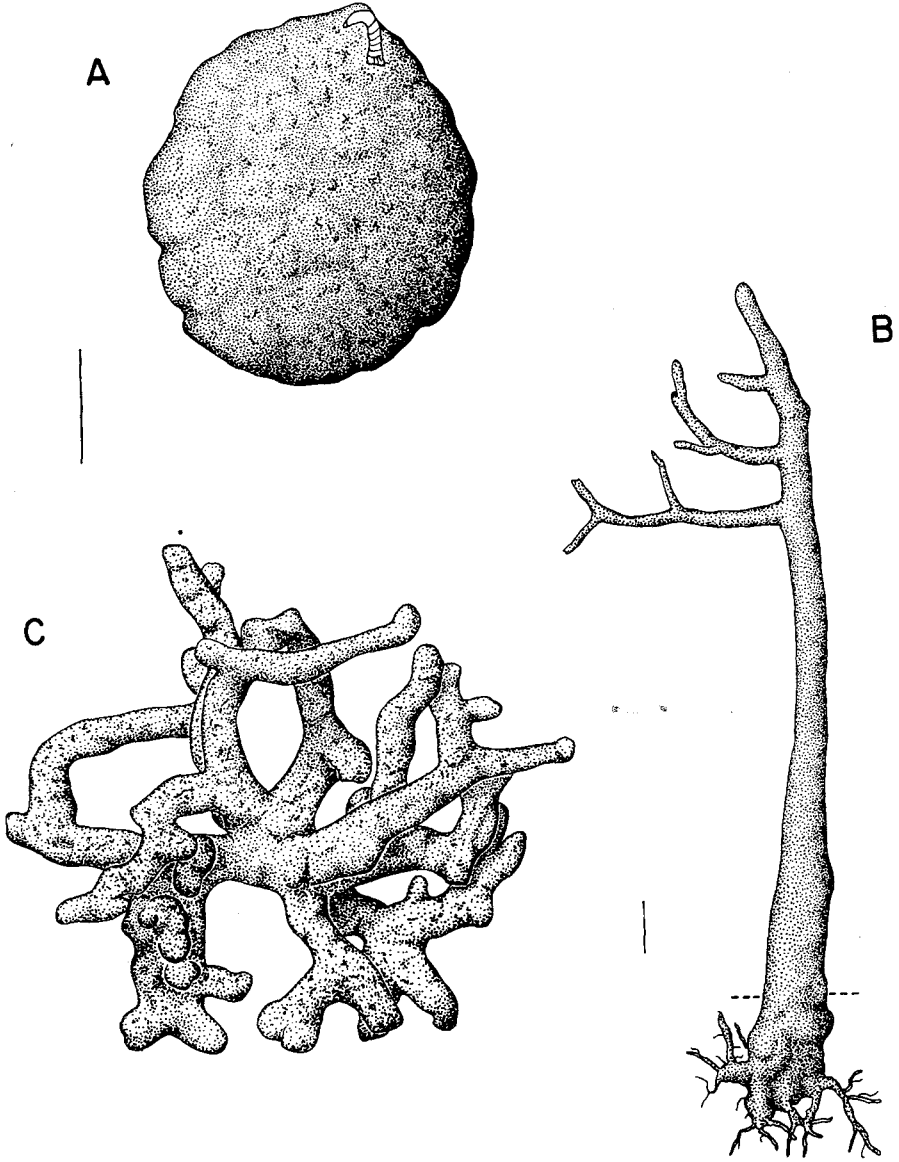
A

B

C

Fig. 3.   Quagmire-site biogenic structures.   A. The empty
test of the foraminiferan *Orictoderma* sp. which, in this instance,
is occupied by the polychaete *Tharyx monilaris*.   B. A tube-shaped
foraminiferan; the dashed line indicates the surface of the sedi-
ment.   C. A bush-like foraminiferan.   The scale lines equal 1.0 mm.

TABLE 2. Volume (mm^3) of biogenic structures by class in 100 cm^2 subcores from the San Diego Trough.

Subcore   Structural Class

	Tharyx luticastellus	*Tharyx monilaris*	Polychaete tubes	*Orictoderma*	Tube-shaped Foraminifera	Bush-like Foraminifera	Tanaid tubes
E10X	0.00	0.00	55.35	37.00	506.30	257.24	7.03
E11X	0.00	0.00	372.75	169.90	717.05	146.58	44.76
E12W	49394.46	38.97	414.03	152.77	1602.39	31.07	34.41
E12Z	668.52	32.78	193.46	21.58	624.47	1243.64	13.19
E14X	5782.00	0.00	267.12	16.34	1270.43	76.10	0.00
E14Y	6423.81	0.00	271.74	0.00	894.61	791.92	0.77
E45X	0.00	203.15	408.91	674.85	1655.34	354.10	2.11
E45Z	3279.22	426.02	543.78	126.24	2375.86	1247.59	31.80
E46Y	13391.23	0.00	770.46	220.16	3638.50	1019.85	23.22
E46Z	3420.61	48.97	156.76	190.17	1976.05	18.75	29.52
E47W	0.00	84.08	257.17	703.14	1684.00	357.07	0.00
E47Z	307.96	28.10	354.33	720.04	771.87	74.79	29.25
E48Y	763.63	113.84	210.48	117.77	1359.26	114.44	7.23
E48Z	10719.57	47.38	508.01	178.36	2629.75	160.13	7.10

abundance with the volume of each structural class. Species which occurred at only one station were omitted because there is no information about species covariance with structure under those circumstances. Of the 868 coefficients calculated, 88 were significant (two-tailed test), significantly more than would be expected by chance alone (chi square 1 d.f. = 48.2455, p less than 0.0005). These significant correlations are distributed among 58 species. Species differ in the class of structure with which they are correlated; among those species correlated with the same class of structure, some are negatively and some positively correlated (Table 3).

To estimate the strength of individual species-structure correlations, I divided the data into two equal stratified-random subsets. In subset A, I calculated all possible rank correlation coefficients between species and structural classes. Among those species which occurred in more than one subcore in both subset A and subset B, forty-eight significant correlations were observed in subset A (alpha less than or equal to 0.10, two-tailed test). These forty-eight correlations were used to predict specific species-structure relationships for testing in subset B. Of these 48 predicted relationships, only two were significant at the 10% level. Table 4 is a contingency table

TABLE 3.   Summary of the significant correlations between harpacticoid species and biogenic structural classes found in the San Diego Trough.

Structural Class	Number of Significant Positive Correlations	Number of Significant Negative Correlations
Tharyx luticastellus	17	4
Tharyx monilaris	6	5
Polychaete tubes	8	2
Orictoderma	7	7
Tube-shaped Foraminifera	9	7
Bush-like Foraminifera	1	6
Tanaid tubes	3	6

TABLE 4.   Number of correlation coefficients predicted to be
            significant or nonsignificant and the number observed
            to be significant or nonsignificant in data subset B.

		OBSERVED	
		Significant	Nonsignificant
	Significant	2	46
PREDICTED			
	Nonsignificant	37	494

which was used to test whether specific correlations predicted
to be significant in subset B actually were significant more
frequently than expected by chance. They were not (chi square
1 d.f. = 0.169). In summary, when 14 subcores are used to
calculate correlation coefficients, a species-structure correla-
tion is detected; when 7 subcores are used, one is not.

The question of whether weak species-structure interactions
exist can be pursued further using this two-data subset approach.
If there is a weak but real association of a species with a
structural class, the signs of the correlations should be the
same in the two subsets. If there is no real association, then
the signs of the correlations should, on the average, differ as
often as they are the same. Table 5 gives the results of a test
of this hypothesis. The significant total chi square means that
the null hypothesis of no association between species and
structural classes can be rejected (there is no evidence of
significant heterogeneity in the results for the various
structural classes, chi square heterogeneity 6 d.f. = 7.7038,
p greater than 0.30). The chi square values for each structural
class show that *Tharyx monilaris*, *Tharyx luticastellus*, tube-
shaped Foraminifera, and tanaid tubes are responsible for the
effect.

In each of the six pairs of subcores, more individuals
occur in the more highly structured subcore (binomial p = 0.032,
two-tailed test). This effect results in large part because of
the behavior of the individually aggregated species. In each
pair of replicate subcores, the index of dispersion detects
aggregated species. For those species one subcore contains
many more individuals than the other. Table 6 shows that
these species are more abundant in the more highly structured
subcore (binomial p = 0.0025, two-tailed, *a posteriori* test).

TABLE 5.   The chi-square values resulting from testing the
           observed versus expected proportion of matching to
           mismatching in signs of correlation coefficients
           between harpacticoid species abundances and struc-
           tural class volumes in the two data subsets.

Structural Class	Chi Square	Degrees of Freedom	Probability
Tharyx luticastellus	5.1282	1	<0.025
Tharyx monilaris	6.6952	1	<0.010
Polychaete tubes	0.0127	1	>0.050
Orictoderma	0.1084	1	>0.050
Tube-shaped Foraminifera	4.3784	1	<0.050
Bush-like Foraminifera	1.2821	1	>0.050
Tanaid tubes	3.4000	1	>0.050
Total	21.0060	7	<0.005

However, this result cannot be extended to a general relationship
between harpacticoid abundance and habitat-structure abundance
(rank correlation coefficient = 0.0).

DISCUSSION AND CONCLUSIONS

     Jumars (1975a, b) in his grain-matching model of deep-sea
diversity maintenance argues that biogenic structures can create
small-scale environmental heterogeneity.   Because this hetero-
geneity has space and time scales which correspond to the
spatial and temporal scales of species' ambits and life spans,
it creates a patch structure which permits large numbers of
similar species to co-occur.   The model predicts that the
abundance of species of taxa which show enhanced diversity
in the deep sea should vary nonrandomly with variation in abun-
dance of biogenic structures.   Jumars presents data showing the
impact of mud balls made by a cirratulid polychaete on species
of the family Paraonidae (*Jumars*, 1975b) and the substantial
difference in the species composition of a bathyal polychaete

TABLE 6.   The effect of biogenic structure on individually
            aggregated species at the centimeter scale.   The
            table shows the number of individually aggregated
            species in a pair of subcores which have their
            greater abundance in either the more highly struc-
            tured or the less highly structured subcore.

Core	Subcore with Greater Structural Volume	Subcore with Lesser Structural Volume
E12	6	0
E14	1	0
E45	1	0
E46	4	0
E47	2	2
E48	3	1
Total	17	3

assemblage associated with the remains of a glass sponge (*Jumars*,
1974).

        This paper further tests the grain-matching model.   *Thistle*
(1978) showed the enhanced deep-sea diversity of harpacticoid
copepods in the San Diego Trough.   The present results document
a statistically significant association of harpacticoid species'
abundances with seven classes of biogenic structure as predicted
by the model.   However, the associations between individual
species and particular classes of biogenic structure are weak
on the average; significant correlations in one data subset do
not predict significant correlations in a second subset.   This
apparent weakness could arise because of a poor measure of struc-
ture or because of an inappropriate sample scale.   Given that
the 10 x 10 cm sampler is large relative to the size of the
biogenic structures, other sources of variance are likely to
have been included which could obscure a strong species-structure
correlation.   Whatever the true strength of such associations,
they are almost certainly real because the direction of the
correlation is maintained between data sets more often than one
would expect by chance.   Further, the most aggregated species

between pairs of subcores have been shown to be more abundant in
the more highly structured subcore of a pair. These results
support the grain-matching model of deep-sea diversity maintenance
because they show that the species of a diverse deep-sea taxon
are perceiving biogenic structures as sources of environmental
heterogeneity.

The species-structure interaction results have implications
for certain of the other models of deep-sea diversity maintenance.
If the correlation of species with biogenic structures results
from competitive microhabitat partitioning, then *Sanders'* (1968)
stability-time hypothesis is supported. Moreover, it weakens
Dayton and Hessler's (1972) criticism of Sanders' model because
food resources need provide fewer niches if a portion of the
niche partitioning occurs in terms of microhabitat specialization.

Dayton and Hessler (1972) emphasize food specialization to
the neglect of other potential niche axes. *Jumars* (1975b)
criticizes this imbalance in their view using evidence of
habitat specialization in some deep-sea polychaetes. If the
correlation of harpacticoid species with biogenic structures
indicates habitat separation among potential competitors, then
their model is weakened because it predicts that such partition-
ing should not occur.

Menge and Sutherland's (1976) model of diversity maintenance
by predation on low trophic levels has been supported by *Rex*
(1976, 1977). In terms of the harpacticoid results, if the
covariance between harpacticoid species and biogenic structures
indicates competitive microhabitat partitioning among harpacti-
coids, then their model would be weakened because it suggests
that harpacticoids, as low trophic level species, should be
primarily under predator control.

The results suggest a possible explanation for the higher
harpacticoid diversity in the deep sea than in other environments.
Harpacticoid species appear to display microhabitat partitioning
in terms of biogenic environmental structures. These structures
are relatively delicate mud aggregations. In the stable physical
conditions of the deep sea, such structures persist long enough
to serve as a niche axis for harpacticoids. As *Jumars* (1976)
has argued, in the higher energy situation of less stable,
shallower environments, such structures are likely to be too
short lived to serve in this way. Without this niche dimension,
it seems reasonable to expect that these communities would be
able to accommodate fewer species. This consequence of the
physical stability appears to be one reason that the deep-sea
benthos has higher diversity than that observed in shallow-water
soft bottoms.

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