The stability–time hypothesis as a predictor of diversity in deep-sea soft-bottom communities: a test

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Abstract—In a test of Sanders' stability–time hypothesis in the deep sea, I show that the hydrodynamic regime of the HEBBLE site (40°24.0'N, 63°07.4'W) is less stable than that of the San Diego Trough (32°35.75'N, 117°29.00'W) and that this instability is important to the harpacticoid copepod fauna. Contrary to the prediction of the stability–time hypothesis, the harpacticoid diversity of the stable site was not greater than that of the unstable site.

INTRODUCTION

THAT soft-bottom communities in the deep sea are relatively more diverse than those in shallow water was discovered only recently (HESSLER and SANDERS, 1967). Since that time, much of the effort expended in studies of the deep sea has been to clarify diversity patterns and to explain their origin and maintenance (REX, 1981). The beginning of the effort was the seminal series of papers by SANDERS (1968, 1969; SLOBODKIN and SANDERS, 1969) proposing the stability–time hypothesis. The stability–time hypothesis states that diversity should increase with increasing stability of the physical regime governing the habitat (although stable environments may have low diversity if they are new). Sanders exemplified the hypothesis by contrasting two hypothetical, end-point communities. A physically controlled community results when the need to withstand the rigors of the environment is paramount. Few species have adapted to survive under such conditions. "Because the fauna must give adaptive priority to the physical regime the biological interactions are not refined or mutually balanced and competition and predation can be most severe" (SANDERS, 1977). A biologically accommodated community results when the physical environment is relatively benign; many species can survive such conditions. In such communities species adapt to each other's presence. Sanders argued that under such circumstances species should develop specialized niches to minimize biological stress. A physically controlled community tends not to accumulate species because few species are physiologically capable of living there. A biologically controlled community tends to accumulate species because of the lack of physiological barriers and the tendency of existing community members to evolve into specialized niches. Thus, the theory predicts that physically controlled communities should be less diverse than biologically accommodated communities.

SANDERS (1968) used the stability–time hypothesis to explain the increased diversity of polychaetes and bivalves with depth in the deep sea. It has been invoked in other contexts

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(BUZAS and GIBSON, 1969; COULL, 1970; GAGE, 1972). The hypothesis has been criticized on empirical and theoretical grounds (see GRAY, 1974; MENGE and SUTHERLAND, 1976; PETERS, 1976; ABELE and WALTERS, 1979a, b). Below I test the ability of the hypothesis to predict the diversity of the harpacticoid copepod faunas of two deep-sea localities. In the test, I use morphology to infer the life position of some harpacticoid copepod species, and I show that forms expected to be rare under physically controlled conditions are largely absent in one locality and abundant in the other. In this way, I show that the contrast in the physical environments between locations has relevance for the harpacticoid fauna independent of any difference in diversity and thus avoid circularity (PETERS, 1976). I then test for the diversity difference predicted by the stability–time hypothesis.

LOCALITIES

The San Diego Trough is the southernmost basin in the California continental borderland. It is 16 by 80 km with the long axis northwest to southeast. The basin floor has a 0.4% southward slope (SHEPARD and EINSELE, 1962). The sediments are derived from pelagic sedimentation, slumping from the bordering escarpments, and turbidity flows from submarine canyons (SHEPARD and EINSELE, 1962). The sediment consists of 3.0% sand, 52.7% silt, and 44.3% clay (R. R. HESSLER, personal communication). The near-bottom temperature is $3.5 \pm 0.3°C$ and the salinity is $34.53 \pm 0.02 \times 10^{-3}$ (ROKOP, 1975). A study site was selected at 1218.3 to 1223.8-m depth (32°35.75′N, 117°29.00′W) (Fig. 1) away from areas of known turbidite channels (see MOORE, 1969). Granulometric analyses show no evidence of recent turbidity flows (R. R. HESSLER, personal communication).

The HEBBLE (KERR, 1980) samples come from two sites at 4626 m separated by 3 km along the upper part of the Scotia Rise in the abyssal North Atlantic (40°24.0′N, 63°07.4′W; 40°24.3′N, 63°09.6′W) (Fig. 2). The region has <0.5% slope (HOLLISTER, personal communication). The sediment consists of 6.0% sand, 50.6% silt, and 39.3% clay [median of eight determinations on the 0 to 1-cm layer (TUCHOLKE, personal communication)]. Near-bottom *in situ* temperature varies between 2.23 and 2.27°C and salinity varies between 34.89 and 34.90×10^{-3} (WEATHERLY, personal communication).
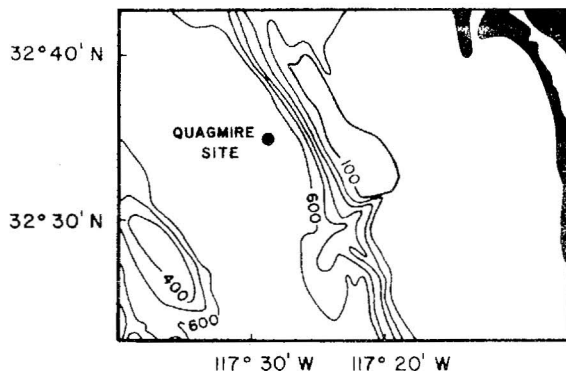

Fig. 1. Chart of the San Diego Trough showing the sampling area (dot). Contours are in fathoms (1 fathom = 1.83 m). Modified from Coast and Geodetic Survey map N.5101.
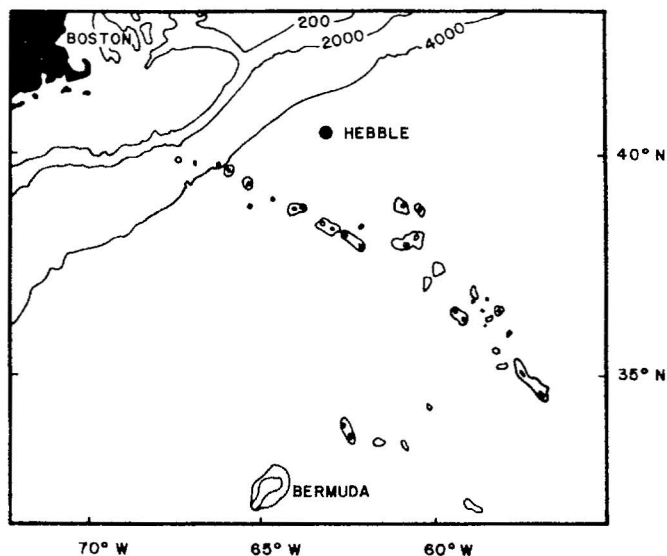
Fig. 2.   Chart showing the HEBBLE sampling area (dot). Contours are in meters. Modified from UCHUPI (1971).

MATERIALS AND METHODS

The samples from the San Diego Trough were taken during Expedition Quagmire (THIEL and HESSLER, 1974). A remote underwater manipulator was used to take 58 randomly located Ekman grabs. Each grab contained four 10 by 10-cm subcores. The harpacticoid fauna from 14 subcores, two from each of six Ekman grabs and one subcore from each of two additional grabs, was analyzed. The subcore(s) within a grab to be analyzed were selected at random. From each subcore, the overlying water and the 0 to 1-cm layer of sediment were fixed with formaldehyde at sea. In the laboratory, each sample was washed on a screen with 0.062-mm apertures, transferred to ethanol, and stained with rose bengal. The harpacticoid copepods were sorted under a dissecting microscope. Adults were determined to species and counted.

The HEBBLE samples were taken on R.V. *Knorr* cruise 78 using a 0.25-m^2 corer (HESSLER and JUMARS, 1974) with the 'Sandia' modifications developed by R. R. HESSLER, P. A. JUMARS, and J. FINGER. This version of the box corer was designed to improve the passage of water through the corer and, thereby, to reduce the bow wave. In particular, the corer top was fitted with doors held open during descent and closed after the sample was taken. The system permitted a larger area of the box corer top to be unobstructed during sampling than previous designs. The core had 25 10 × 10-cm subcores (Fig. 3). Only the inner nine were used because of the expectation that they would be the least biased (JUMARS, 1975). The subcores contained 5 × 5-cm subsubcores (Fig. 3) whose bottom edges were beveled such that a sub-subcore sampled 23 cm^2. The subsubcores were used for sedimentological and microbial measurements (YINGST and ALLER, 1982). The subcores were processed as above with the following differences. Samples were washed on sieves of 0.300 and 0.062-mm apertures. The harpacticoids were picked from the 0.300-mm fraction under a dissecting microscope. The sorting trough described by BARNETT (1968) was used to concentrate the harpacticoids quantitatively from the 0.062-mm fraction before sorting. The Barnett trough procedure was 100% efficient on the samples ($N = 3$).
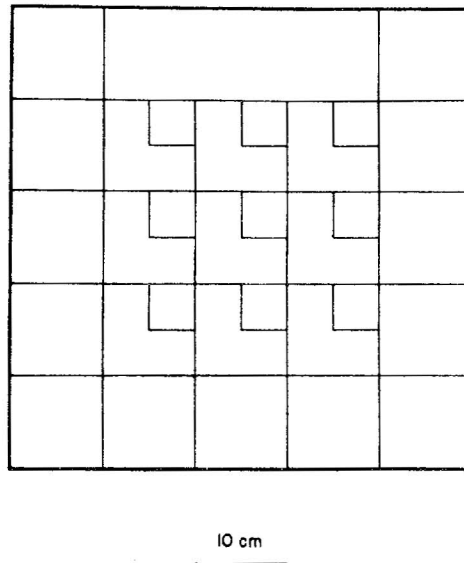
10 cm

Fig. 3.   A schematic representation of a core box showing the *in situ* subsamplers.

The taxonomy of deep-sea harpacticoids is poorly known. In both studies, species were recognized, illustrated, and incorporated into working keys. The working species have been placed in existing families and genera where possible (see THISTLE, 1977, for the San Diego Trough list; the HEBBLE list is available from the author). The description of these rich, new faunas has begun (THISTLE and COULL, 1979; REIDENAUER and THISTLE, submitted). There now appears to be no species that occurs in both the San Diego Trough and the HEBBLE site.

In comparing the harpacticoid diversity of the San Diego Trough and the HEBBLE site, TIPPER (1979) is followed. Tipper recognized that for 'cluster' samples (e.g., box cores) a key assumption of methods of calculating confidence limits about rarefaction curves fails (see also ROUTLEDGE, 1980). In his alternative method, the HURLBERT (1971) rarefaction procedure is used to allow comparisons among samples at a given number of individuals (a 'knot'). The expected numbers of species in the replicate samples from one location are compared to those in a second location using the nonparametric Mann–Whitney U test (TATE and CLELLAND, 1957) at each shared knot.

For the diversity comparisons, the data were manipulated in two ways. In the first, the subcores of each HEBBLE box core were treated as independent samples. The assumption was tested explicitly for each species by a test of the null hypothesis that the abundance of a species in a subcore was independent of its abundance in adjacent subcores, i.e., that no significant spatial autocorrelation was found using the techniques of CLIFF and ORD (1973). The procedure was described in THISTLE (1978) with the exception that only adjacent subcores were joined and Monte Carlo confidence limits were calculated (based on 200 permutations). Significant departures from randomness occurred no more frequently than expected by chance, suggesting that the subcores within a box core can be treated as independent samples. Subcore data were then combined to yield samples that had both equal areas and reasonable numbers of individuals per sample from both sites. For HEBBLE, the faunas from randomly

selected adjacent pairs of subcores from each box core were combined (subject to the constraint that four pairs be formed per box core). For the San Diego Trough, the faunas of paired subcores were combined from each of six Ekman grabs.

In the second analysis, subcores were combined to give samples from the HEBBLE site with the largest possible number of individuals per sample to improve the reliability of the estimates of the diversity of the HEBBLE area. The two HEBBLE box cores were treated as single samples. For the San Diego Trough, eight subcores were used as independent estimates; one subcore was chosen at random from each of the six paired subcores. These subcores plus the two single subcores yielded a total of eight samples.

RESULTS AND DISCUSSION

SANDERS (1969, 1977) stated that the stability–time hypothesis can predict diversity differences. In a demonstration of this ability, he first established a difference in the physical stability of the boreal shallow waters of the east and west coasts of the United States and then found the expected difference in the diversities of the benthic faunas. The harpacticoid copepod faunas of the San Diego Trough and the HEBBLE site are compared in a similar test.

The San Diego Trough and the HEBBLE site differ in their near-bottom hydrodynamics. Photographs of the HEBBLE area reveal current-molded bedforms. It is an area of high mean current velocity (12.2 cm s⁻¹) punctuated by periods of even higher velocities up to 39.2 cm s⁻¹ (both measured at 50 m off the bottom) that are sustained for days. Such velocities are among the highest ever recorded in the deep ocean and can erode surficial sediment (RICHARDSON, WIMBUSH and MAYER, 1981; YINGST and ALLER, 1982). BISCAYE et al. (1980) reported that the concentration of near-bottom suspended particulate matter in the HEBBLE area is extremely high compared to areas of strong nepheloid layers known elsewhere in the world ocean. The current-meter mooring nearest the HEBBLE site was 33.3 km away at 4500 m. The eight-month record (at 10 m off the bottom) shows frequent daily-averaged velocities of 20 to 25 cm s⁻¹ (WEATHERLY, personal communication).

In the San Diego Trough, bottom photographs show no evidence of current-molded bedforms, and observations from submersibles have failed to detect currents of erosive magnitudes (BARHAM, AYER and BOYCE, 1967; LAFOND, 1967). A 5.5-day current-meter record (10 m off the bottom) taken during Expedition Quagmire revealed no velocities exceeding 10 cm s⁻¹ (R. R. HESSLER, personal communication). The HEBBLE area lacks the physical stability of the San Diego Trough in terms of hydrodynamic regime.

For the differences in physical stability between the San Diego Trough and the HEBBLE site to permit a test of the stability–time hypothesis, one needs to show that the lack of physical stability affects organisms independently of changes in their diversity. Therefore, the relative abundances of two morphological groups of harpacticoids in the two faunas for which differences in life positions are inferred will be compared. In the San Diego Trough, there are species of harpacticoids with massive dorsal projections (Fig. 4a). For these species, the inference that they live on the sediment surface seems inescapable because the dorsal projections would seriously interfere with movement through the sediment. In addition, the animals have thick sediment coats anchored on their backs by the dorsal projections. The sediment coats seem to be stabilized (perhaps with mucus, HICKS and GRAHAME, 1979) because the coat cannot be washed away readily but must be picked off the animal. It has been suggested
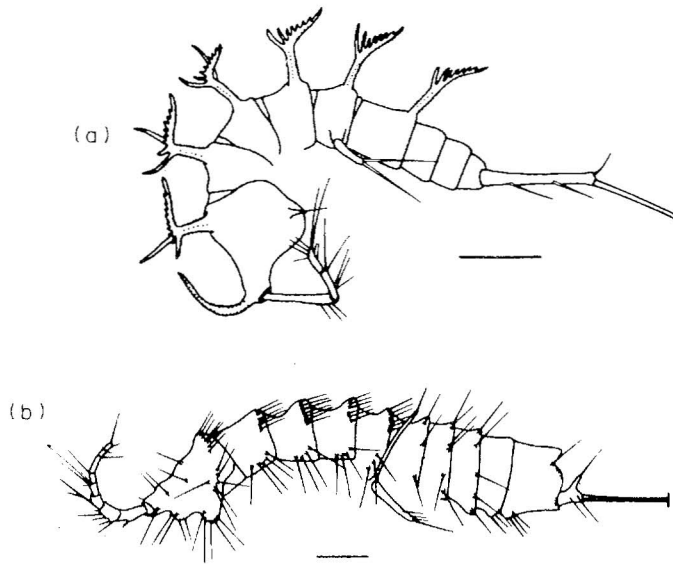
Fig. 4. Lateral views of representatives of the sediment-covered group. Note that the second antenna and the pereopods have been omitted. Scale lines = 0.1 mm.

elsewhere that the sediment coat serves as camouflage (THISTLE, 1982), but whatever its function, it appears to be an additional marker of the surface-dwelling habit. Species of two other families (Fig. 4b) have similar dorsal anchors and sediment coats and are also inferred to be surface dwellers. The argument can be reinforced by the observation that the sediment-covered species as a class are significantly larger than other harpacticoid species (THISTLE, 1982), as might be expected if they moved primarily through the flocculent layer rather than through more consolidated sediment.

The second functional group consists of species that have a second antenna modified for burrowing (Fig. 5). In these species, the normally delicate setae of the second antenna are modified into a stout, spade-like form and arranged around the circumference of the appendage in circles. The effect suggests the pushing foot of *Limulus*.

The proportional representations of the functional groups in the two faunas differ conspicuously (Table 1). In the San Diego Trough, 10.7% of the species and 4.4% of the individuals are sediment-covered (and by inference surface dwellers) vs 1.1 and 0.9%, respectively, for the HEBBLE area. The burrowing group constitutes 3.6% of the species and 3.6% of the individuals in the San Diego Trough vs 6.8 and 5.8% in the HEBBLE samples. Significance levels are given in Table 1. The impoverishment of the HEBBLE fauna in surface-dwelling species seems likely to have resulted because the organisms are at risk in the stormy habitat. The animals must be poor burrowers, so burial by sediments deposited between storm events appears to be a likely source of mortality. Whether the erosion of an individual results in its death or decreased viability is unclear; harpacticoids are routinely found in the water column in shallow water, but their fate is unknown. For the benthic, surface-dwelling harpacticoids at the HEBBLE site, being rolled along the bottom by the current or eroded and transported must disrupt their ordinary feeding activities at the least.

The current regime in the HEBBLE region appears to have molded the harpacticoid fauna, indicating that the physical regime is less stable in the HEBBLE area in a way relevant to
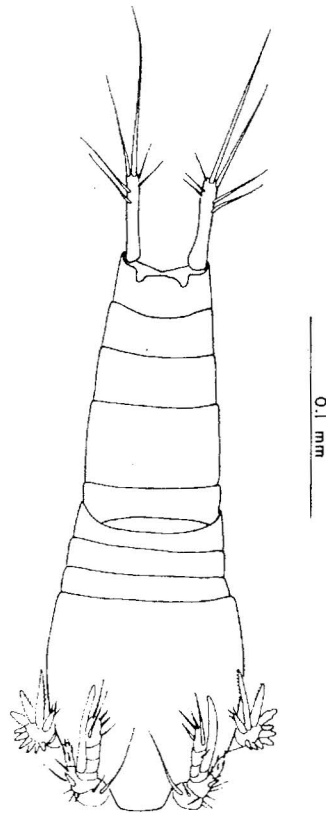
Fig. 5. A burrowing harpacticoid from the San Diego Trough in dorsal view. Scale line = 0.1 mm.

harpacticoids. Given this contrast between a relatively physically controlled and a relatively biologically accommodated community, the stability–time hypothesis predicts that the latter (San Diego Trough) should have the higher diversity.

Before testing the stability–time hypothesis based on the difference in harpacticoid-relevant physical stability, one must decide if sampling bias could explain the proportional representations of the two functional groups. The San Diego Trough samples were taken by an unmanned submersible; the HEBBLE samples were taken with a box corer from a ship. It is possible that the two functional groups are approximately equally represented in the two faunas but that the bow wave of the box corer blew away the surface-living fauna of the HEBBLE site.

Table 1. *A comparison of the proportional contributions of sediment-covered species and burrowing species to the harpacticoid copepod faunas of the San Diego Trough (SDT) and the HEBBLE site. P values are for a two-tailed test*

| | Species (%) | | | Individuals (%) | | |
	SDT	HEBBLE	P	SDT	HEBBLE	P
Sediment-covered	10.7	1.1	<0.01	4.4	0.9	<0.005
Burrowing	3.6	6.8	>0.05	3.6	5.8	<0.05

However, the circumstance seems unlikely because a light, flocculent layer of sediment that would be blown aside by the bow wave of a box corer is unlikely to be present in the HEBBLE area. Further, the water overlying the recovered core was clear; there was no reason to suspect that sediment had been suspended on impact. In particular, several delicate pteropod shells were lying on the surfaces of the cores. JUMARS (1975), in his test for box corer bow-wave bias, compared the inner 9 to the outer 16 subcores. In a similar comparison here, there was no reason to reject the null hypothesis of no difference in harpacticoid numbers between the central subcore and the surrounding eight subcores for either of the two HEBBLE cores. The one surface-living species from HEBBLE was found in only one box core; when subcores from the core were ranked from least to greatest harpacticoid abundance, the species occurred in subcores ranked one and five of nine. Although sampling differences cannot be totally dismissed as contributors to the effect, there is no evidence that they have affected the results.

The diversity comparison was made using the nonparametric procedure described by TIPPER (1979). In the first analysis, the smallest sample contained 16 individuals (Fig. 6). The rarefied values for the San Diego Trough and HEBBLE were compared at knots 2 to 16. None of the tests was significant. There was no reason to reject the null hypothesis that the samples were drawn from communities with the same median diversity.

In the second analysis, the rarefied values for the two localities were compared at knots 2 to 144. None of the tests was significant. Table 2 gives expected numbers of species at two representative knots. Again, there was no reason to reject the null hypothesis that the samples were drawn from communities with the same median diversity. As an aside, the technique was able to show that the median diversity of the San Diego Trough fauna was greater than that of a shallow-subtidal soft-bottom fauna from the northern Gulf of Mexico ($n_1 = 8$, $n_2 = 4$, U statistic significant at knots 2 to 47).
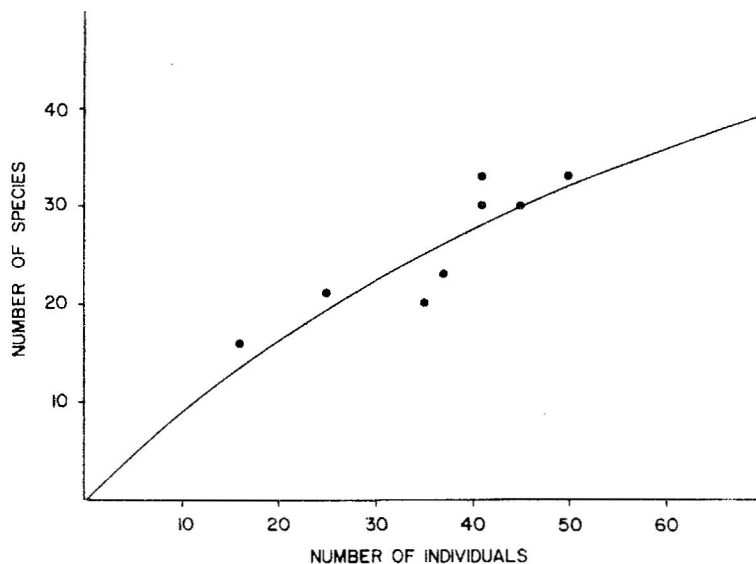

Fig. 6.   The curve is the mean of the expected number of species for the San Diego Trough samples in the first analysis. The HEBBLE samples are plotted as dots. The figure is provided for heuristic purposes and is not involved in the statistical test.

Table 2. For the two sites, the number of individuals included in the rarefaction calculation for each sample is given together with the expected number of species at two knots, 100 individuals, and the largest knot where a comparison among all samples can be made, 144 individuals

Site	Number of individuals	Expected number of species at 100 individuals	Expected number of species at 144 individuals
HEBBLE	182	43.39	52.64
	144	50.84	61.00
San Diego Trough	239	47.17	56.69
	241	45.15	53.20
	236	46.82	55.34
	295	48.51	58.35
	346	47.55	56.15
	288	43.88	52.29
	309	48.36	57.46
	325	46.63	55.41

The stability—time hypothesis predicts a difference in diversity between the two locations. The magnitude of the difference is not predicted, but given the arguments upon which the hypothesis is based and the apparent impact of the current regime on the harpacticoid fauna at the HEBBLE site, it seems reasonable to expect that the difference would be marked. Under such circumstances, the lack of a detectable difference suggests that the stability—time hypothesis is inadequate as a predictor of harpacticoid copepod diversity in the deep sea. GIBSON and BUZAS (1973) and LAGOE (1976) found a similar result for deep-sea foraminiferan diversity.

The data could be interpreted in another way. It could be argued that the frequency and intensity of the erosion—deposition cycle at the HEBBLE site affects only the interface and upper few millimeters of sediment so that only the surface-living-group species experience a physically controlled environment. The rest of the harpacticoids live below the physically controlled zone and experience conditions stable in Sanders' sense. Under such circumstances, the stability—time hypothesis predicts that the diversity of the surface-living group should be low and that that of the remainder of the fauna could be high, as observed.

The above argument could be countered by a demonstration that the non-surface-living-group animals experience a physically unstable regime. Given the surface-living-group result and the presence of 70.3% of the harpacticoid fauna in the 0 to 1-cm layer of those in the upper 3 cm (median of six observations), the assertion that the harpacticoid fauna is molded by the physically unstable HEBBLE environment seems reasonable.

For deep-sea workers, diversity has served as a surrogate variable, of interest because of the difficulty of studying deep-sea communities. By describing diversity differences, we document the existence of deep-sea communities that appear to be organized differently. It is the organization that is at the heart of our interest, as witness the plethora of attempts to model diversity maintenance in the deep sea (e.g., DAYTON and HESSLER, 1972; GRASSLE and SANDERS, 1973; JUMARS, 1975, 1976). It seems likely that gradients in factors that have a proximal effect on community organization such as disturbance (DAYTON and HESSLER, 1972), predation (REX, 1976), and habitat structural complexity (JUMARS, 1976) will eventually be shown, in their sum, to generate the observed geographic patterns in diversity.

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