

## References and Notes

1. J. Mering and A. Oberlin, *Clays Clay Miner.* **15**, 3 (1967); in *Electron-Optical Investigations of Clays*, J. A. Gard, Ed. (Monograph 3, Mineralogical Society, London, 1971), p. 208.
2. H. E. Roberson and K. M. Towe, *Science* **176**, 908 (1972).
3. J. M. Cowley and A. Goswami, *Acta Crystallogr.* **14**, 1071 (1961).
4. I thank Dr. R. E. Grim of the University of Illinois for the samples of bentonites from his invaluable collection.
5. This mixture has a pH of about 11, which considerably reduces aggregation of particles as shown by J. L. McAtee, Jr., and W. Henslee [*Amer. Mineral.* **54**, 869 (1969)].
6. The term "turbostratic" was suggested by J. Biscoe and B. E. Warren [*J. Appl. Phys.* **13**, 370 (1942)] for superposition of layers with a completely random orientation about the layer normal. A turbostratic sequence is then expected to give uniform diffraction rings on the SAD pattern. Stacking of layers with definite orientations (such as multiples of 60° about the layer normal) but with a random sequence will give a spot pattern like that of a single crystal, although the lattice is still two-dimensional. Therefore, the observation of spot pattern with SAD does not necessarily indicate the presence of single montmorillonite layers, as assumed by Roberson and Towe (2).
7. N. Güven, *Clays Clay Miner.*, in press.

15 March 1973; revised 16 July 1973

## Deep-Sea Species Diversity: Decreased Gastropod Diversity at Abyssal Depths

**Abstract.** *Gastropod species diversity is low on the continental shelf, high on the continental slope and abyssal rise, and then decreases with increasing distance out onto the abyssal plain. Increased diversity below the continental shelf has been attributed to increased environmental stability. Decreased diversity on the abyss may result from extremely low productivity.*

The continental slope (about 200 to 2000 m in depth) and abyssal rise (about 2000 to 4000 m in depth) are known to support very diverse deep-sea benthic communities (1). But there has been no detailed comparative study of macroinvertebrate species diversity on the abyssal plain (below 4000 m), which is the deepest and most extensive benthic region. In this report, benthic gastropod diversity is analyzed for 24 stations situated along the Gay Head (Massachusetts)–Bermuda transect (2) from 70 to 4970 m in depth (Fig. 1).

The samples were collected with an epibenthic sled (3) except for stations 171 and 173 on the continental shelf, which were sampled with an anchor dredge (2). All the samples came from soft oozes similar in particle size (2), so that the faunal comparisons made are probably "within habitat" (4). The total gastropod sample from the 24 stations comprised 136 species distributed among 9034 individuals. Only

specimens taken alive were used in the analysis.

Several methods were used to compare species diversity among the samples. In the first, individual samples were treated by rarefaction methodology (5) to reduce sample sizes to a common number of individuals, and then the Shannon-Wiener information function was applied to the rarefied samples. The information function is expressed as

$$H' = - \sum_{i=1}^s p_i \log p_i$$

where  $p_i$  is the proportion of species  $i$  and  $s$  is the number of species in a sample. The function  $H'$  is influenced by both the number of species in the sample and the evenness of their distribution among the individuals in the sample. Evenness was measured as  $J' = H'/H_{\max}$ , where  $H_{\max} = \log s$  is the maximum value of  $H'$ , which occurs when all species in the sample are equally distributed among the individuals (6).

The spectrum of diversity with increasing depth among the 24 samples, all rarefied to 68 individuals, is presented in Fig. 2. (Sixty-eight individuals was the smallest number that included all of the sample sizes.) The pattern of diversity depicted in Fig. 2 obtains for all rarefied sample sizes between 68 individuals and the total sample size.  $H'$  at 68 individuals is correlated with

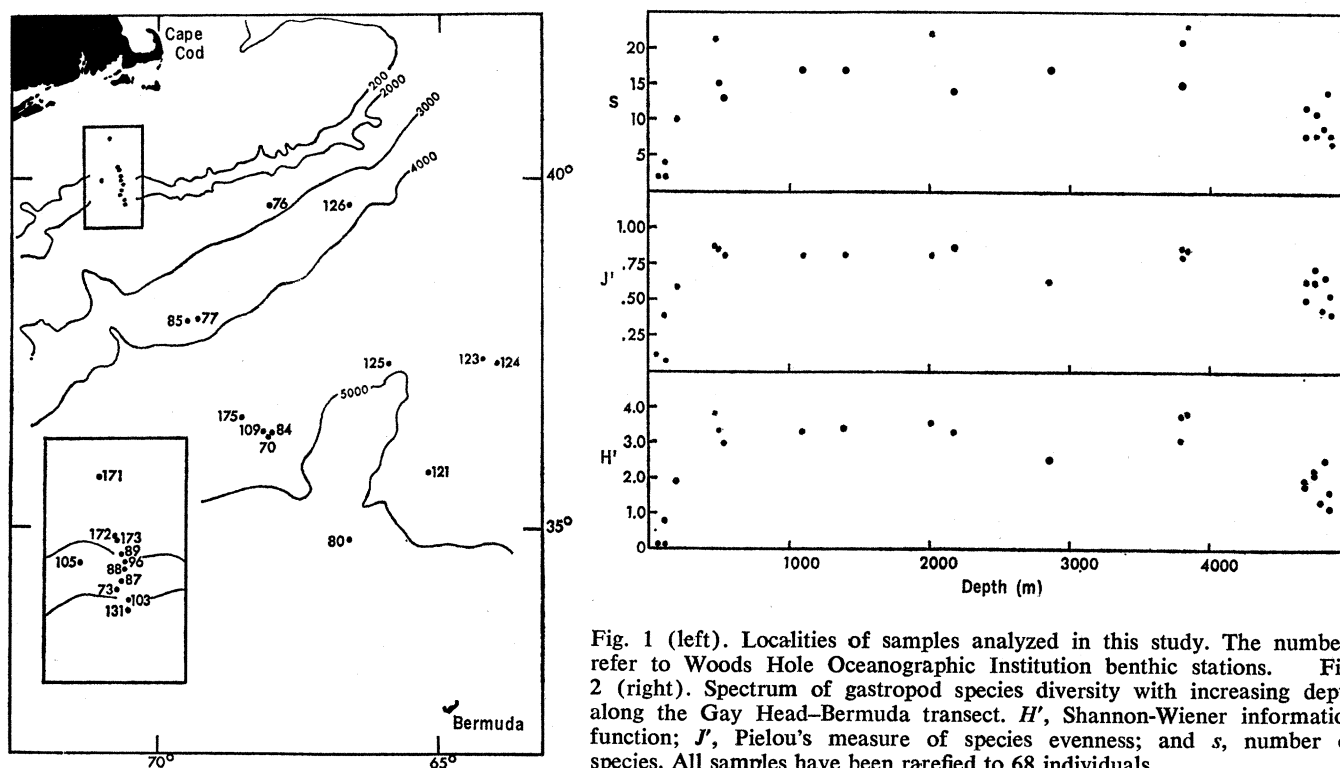


Fig. 1 (left). Localities of samples analyzed in this study. The numbers refer to Woods Hole Oceanographic Institution benthic stations. Fig. 2 (right). Spectrum of gastropod species diversity with increasing depth along the Gay Head–Bermuda transect.  $H'$ , Shannon-Wiener information function;  $J'$ , Pielou's measure of species evenness; and  $s$ , number of species. All samples have been rarefied to 68 individuals.

Table 1. Correlations between species diversity indices:  $H'$  is the Shannon-Wiener information function;  $J'$ , Pielou's evenness;  $S$ , Simpson's diversity index;  $MD$ , McIntosh's diversity index;  $ME$ , McIntosh's evenness;  $B$ , Brillouin's diversity index;  $F$ , Fager's scaled number of moves diversity index. All indices were calculated from raw sample data.

| Index | $J'$ | $S$   | $MD$  | $ME$  | $B$   | $F$   |
|-------|------|-------|-------|-------|-------|-------|
| $H'$  | .921 | -.970 | .977  | .947  | .994  | -.813 |
| $J'$  |      | -.956 | .970  | .976  | .864  | -.925 |
| $S$   |      |       | -.991 | -.987 | -.966 | .863  |
| $MD$  |      |       |       | .991  | .967  | -.886 |
| $ME$  |      |       |       |       | .940  | -.921 |
| $B$   |      |       |       |       |       | -.804 |

$H'$  for the total sample at  $r = .99$ ,  $P < .001$ .

Simpson's (7) diversity index, Brillouin's (8) diversity index, McIntosh's (9) diversity index and evenness, and Fager's (10) scaled number of moves diversity index were applied to the raw sample data. All yielded the same basic pattern shown in Fig. 2 and all were intercorrelated at  $r \geq .80$ ,  $P < .001$  (Table 1). Hurlbert's (11) expected number of species also gives this pattern and correlates with Sanders' (5) rarefied species number for sample sizes of 50 and 100 at  $r = .99$ ,  $P < .001$ .

As shown in Fig. 2, diversity on the continental shelf is low and is associated with both low evenness and low species number. A fairly uniform and high diversity is evident from the upper continental slope to a depth of 3834 m (station 85). On the whole, diversity values ( $H'$ ) at these depths are contributed to about equally by  $J'$  and  $S$ . Since the continental shelf is a more physically unstable environment than the continental slope and abyssal rise (2), these results are what would be expected from Sanders' (5) hypothesis concerning the effect of stability on the development of species diversity in time. No samples were collected between 3834 and 4667 m because of the great difficulty in dredging through the Gulf Stream, which overlies this depth range.

The surprising result was that the information function, evenness, and other indices all indicated decreased diversity below 4667 m. Samples collected at greater depths are characterized by both fewer species and increased dominance of the most abundant species. On the abyssal plain the most common gastropod was either *Cithna tenella* Jeffreys or, in one case (station 125), *Adeorbis umbilicatus* Jeffreys, both of which are deposit feeders. These two species accounted for an average of 65 percent of the individuals in abyssal samples, whereas on the abyssal rise the most abundant

gastropod species represented only 32 percent of the gastropod fauna. Low evenness confirms that low diversity on the abyss is not merely a sampling problem associated with low density. Since high faunal similarity among abyssal stations strongly suggests that the fauna is uniformly distributed (1, 12), it is doubtful that the low evenness results from patchy distributional patterns. The reduction in diversity on the abyss occurs despite the apparent stability of the physical environment at these depths (2). Decreased species diversity also occurs in bivalves (13) and cumaceans (14) at abyssal depths along the Gay Head-Bermuda transect. Relative diversity in other groups at these depths has not yet been investigated.

Diversity, measured as  $H'$ , in samples from the continental slope and abyssal rise was uncorrelated with either depth ( $r = .085$ ,  $P > .10$ ) or distance to the edge of the continental shelf, taken as the 200-m contour in Fig. 1 ( $r = .134$ ,  $P > .10$ ). In abyssal samples,  $H'$  correlated significantly with distance to the shelf ( $r = -.801$ ,  $P < .01$ ), but not with depth ( $r = -.576$ ,  $P > .10$ ), which varies only slightly (203 m) among abyssal stations.

Low gastropod diversity at abyssal depths may be related to the extremely low productivity afforded by abyssal sediments. The great distances from land runoff and the high primary productivity of the continental shelf result in abyssal sediments that are nutritionally depleted. Abyssal organic sediment from this region oxidizes less readily than sediments from shallower depths (15). The density of the macrobenthos decreases along the transect and reaches very low levels on the abyssal plain, presumably because of the low nutrient value of abyssal sediments (2). Some species in lower trophic levels may find resources on the abyss so low that they cannot maintain the critical densities needed to sustain viable populations. In turn, low density and diversity among consumers may permit fewer

predatory species (16). Productivity has previously been proposed as a cause of species diversity (17), but it has proved difficult to separate its effect from that of climatic stability and other factors (18). Deep-sea communities provide an opportunity to observe the influence of productivity on diversity with environmental stability held constant.

The data suggest that if productivity is relevant, then it must be extremely limited to have any appreciable influence on species diversity. The density of organisms along the transect drops from 6,000 to 23,000 per square meter on the upper continental slope, to 1,500 to 3,000 per square meter on the lower continental slope, to 500 to 1,200 per square meter on the abyssal rise, and to 31 to 270 per square meter on the abyssal plain (2). Yet this marked decrease in density with depth is unaccompanied by any change in species diversity until the abyssal plain is reached. The diversity then drops with increasing distance out onto the abyssal plain. Environmental stability still appears to be the most important determinant, or at least the most consistent positive correlate, of macrofaunal species diversity. The stable, but nutritionally poor and faunally sparse abyssal plain supports more species than does the unstable, but nutritionally rich and faunally dense continental shelf.

One adaptation to low productivity in the deep sea is small body size (2). While the macrofauna suffers a decrease in diversity at abyssal depths, foraminiferans, which are usually smaller and less complex, reach their highest diversity there (19). Coupled with a stable environment, even the exceedingly low productivity of the abyss is evidently sufficient to support a highly diverse meiofauna. This suggests that productivity affects macrofaunal diversity in some major taxa only when the lower limits of adaptation in size are approached.

MICHAEL A. REX

Department of Biology, University of Massachusetts, Boston 02116

#### References and Notes

1. H. L. Sanders and R. R. Hessler, *Science* **163**, 1419 (1969).
2. ———, G. R. Hampson, *Deep Sea Res.* **12**, 845 (1965).
3. R. R. Hessler and H. L. Sanders, *ibid.* **14**, 65 (1967).
4. R. H. MacArthur, *Biol. Rev.* **40**, 510 (1965).
5. H. L. Sanders, *Amer. Natur.* **102**, 243 (1968).
6. E. C. Pielou, *An Introduction to Mathematical Ecology* (Wiley, New York, 1969).
7. E. H. Simpson, *Nature* **163**, 688 (1949).
8. L. Brillouin, *Science and Information Theory* (Academic Press, New York, 1962).

9. R. P. McIntosh, *Ecology* **48**, 392 (1967).
10. E. W. Fager, *Amer. Natur.* **106**, 293 (1972).
11. S. H. Hurlbert, *Ecology* **52**, 577 (1971).
12. M. A. Rex, thesis, Harvard University (1972).
13. H. L. Sanders, personal communication.
14. N. S. Jones and H. L. Sanders, *Deep Sea Res.* **19**, 737 (1972).
15. S. A. Waksman, *Soil Sci.* **36**, 125 (1933).
16. G. E. Hutchinson, *Amer. Natur.* **93**, 145 (1959).
17. J. H. Connell and E. Orias, *ibid.* **98**, 399 (1964).
18. R. H. MacArthur, *Geographical Ecology* (Harper & Row, New York, 1972).
19. M. A. Buzas and T. G. Gibson, *Science* **163**, 72 (1969).
20. I thank H. L. Sanders, F. Grassle, and R. D. Turner for reading the manuscript. The material reported on was collected under NSF grants 6027, 810, and 31105. Contribution No. 3178 from the Woods Hole Oceanographic Institution.

10 May 1973

## Two Visual Systems in the Frog

**Abstract.** *After unilateral removal of the optic tectum in frogs, the cut optic tract regenerates to the remaining ipsilateral tectum. Although the orienting movements elicited by moving objects (food or threats) are now directed mirror-symmetrically to normal responses, these frogs correctly localize stationary objects as barriers. Apparently, thalamic and tectal visual mechanisms can operate independently.*

One of the primary tasks for the neurobehaviorist is to dissociate components of behavior that are generated by distinct elements of the nervous system. Although the sensory systems of vertebrates have considerable anatomical and functional independence, attempts to disentangle behavioral functions within a particular system have produced few definitive conclusions at any level of vertebrate phylogeny. Schneider (1) has provided new support for the belief that the mammalian visual cortex and superior colliculus (or optic tectum) have distinct behavioral functions. In the golden hamster, lesions of the striate cortex produced pattern discrimination deficits, while tectal ablations abolished visually elicited turning of the head toward interesting objects, such as food. Because the striate cortex and optic tectum receive information

from independent retinofugal pathways, Schneider labeled the geniculostriate and tectal pathways as two visual systems. In the study reported here, I have sought to dissociate certain behavioral functions of the frog's visual thalamus from those of the optic tectum by using natural orienting behaviors—rather than discrimination training methods. It appears from these results that tectum and thalamus can mediate spatial localizing responses which are morphologically identical but are elicited by different classes of visual stimuli.

The first set of observations that seemed to dissociate two types of visual function were made on four specimens of *Rana pipiens*, in each of which one tectal hemisphere had been totally removed by use of a microknife, hook, and aspiration. As histological checks later showed, each frog had lost all of

the tectum plus some of the immediately subjacent tegmental region. These subjects were typical of more than 20 unietal frogs in that they vigorously pursued mealworms or dummy prey objects viewed by the eye contralateral to the intact tectum, but totally ignored prey moving within the monocular field contralateral to the damaged side. As Bechterew (2) reported in the 19th century, such blindness also included failure to jump away or duck the head in response to a looming dark object. Unietal frogs reacted to a motor-driven, black "looming" disk (~ 10 cm wide) moved briskly through 30 cm to within 3 cm of the normal eye in 49 of 60 trials, but never reacted when the stimulus was confined to the field of the "bad eye." Yet the same subjects readily jumped away from a light touch of the limbs on the "blind" side. With respect to food pursuit and avoidance behavior, tectal ablation in the frog produces a "blindness" very similar to that reported for the hamster (1) or the tree shrew (3) after total removal of the optic tectum.

Although these unietal frogs did appear blind by such criteria, they could nevertheless discriminate the presence of stationary visual objects, just as the hamster and tree shrew could after ablation of the optic tectum. Five frogs deprived of the right tectum consistently avoided stationary grid barriers after the "good eye" had been sewn tightly shut. By contrast, when both eyes were sewn shut and a frog was motivated to escape a light touch or pinch of the left heel by a long pair of tweezers, all jumps were made

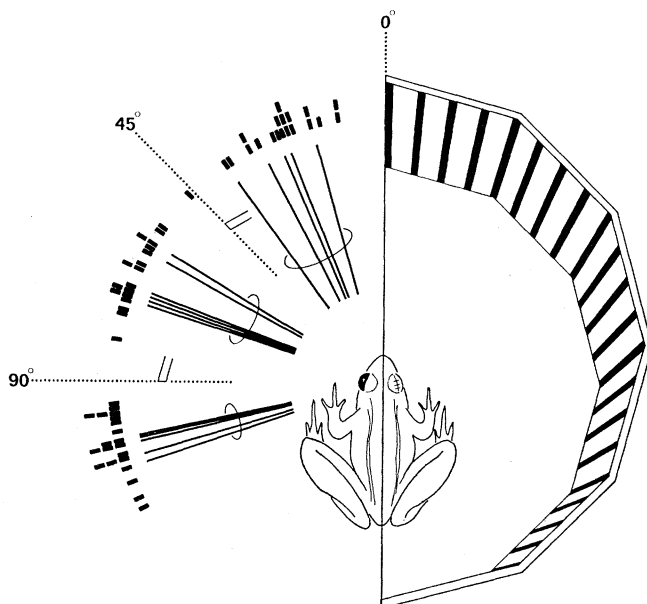


Fig. 1. Results of the barrier avoidance tests for five unietal frogs using the eye projecting to the injured half of the brain. The visible edge of the 15-cm-high barrier was set at either 0°, 45°, or 90°, and the avoidance jump directions were measured from stopped cine projections. The angle by which the frog cleared the barrier is represented here for each trial by a vertical black rectangle to the left of the barrier edge. Group data are presented as radial histograms, and the responses of one individual are shown by three sets of radial lines, corresponding to the three barrier locations.