# Role of biological disturbance in maintaining diversity in the deep sea

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Abstract—This paper presents the hypothesis that the maintenance of high species diversity in the deep sea is more a result of continued biological disturbance than of highly specialized competitive niche diversification. Detrital food is the primary resource for most of the deep-sea species, but we suggest that in deposit feeding, most animals would consume available living particles as well as dead. We call this dominant life-style 'cropping'. Predictable cropping pressure on smaller animals reduces the probability of their competitive exclusion and allows a high overlap in the utilization of food resources. Since cropping pressure is in part proportional to the abundance of the prey, proliferations of individual species are unlikely.

Through time many species have accumulated in the deep sea because of speciation and immigration. Extinction rate is low because the biological and physical predictability of the environment has suppressed the possibility of population oscillations. Predictability in food supply for smaller deposit feeders is enhanced by the larger, mobile scavengers which consume and disperse large particles of food which fall to the ocean floor.

## INTRODUCTION

THE DEEP sea has long been regarded as one of the most rigorous environments on the planet. The combination of low temperatures, high pressure, absence of light, and low rate of food supply influenced the conclusion that this is not a likely place to find a rich fauna. Until recently most benthic samples from the deep sea supported this view. Though supposedly representing large areas of the bottom, these samples characteristically were low in numbers of both individuals and species. With the development of an improved sampling device, the epibenthic sled, a continuing series of samples has been obtained which demonstrates that, contrary to classical belief, deep-sea benthic communities have an extraordinarily high species diversity (HESSLER and SANDERS, 1967).

This discovery led SANDERS (1968) to review current ideas on the factors that control within-habitat diversity and to propose a general model which he called the Stability-Time Hypothesis. Stated briefly, this model says that physical instability in an environment prevents the establishment of diverse communities. However, if physically stable conditions persist for a long period of time, speciation and immigration will cause species diversity to increase gradually as the member species become biologically accommodated to each other. Thus, high diversity in the deep sea is a result of the great long-term stability of that environment. Basic to his view is the idea that each species must occupy an increasingly narrow, specialized niche.

Because of the high physical homogeneity, both temporally and spatially, of the

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deep-sea environment, there is little chance for the kind of niche diversification that results from environmental heterogeneity. It is generally agreed that by far the most important potentially limiting resource in the deep sea is food. It follows that if there is a high degree of specialization, it must relate to the food resource, and that empirical evidence of life habits of deep-sea organisms should indicate a trend toward higher specialization with regard to this resource than is found in less diverse shallow-water communities.

Deposit feeding is the dominant trophic type in the deep-sea, soft bottom communities. SOKOLOVA (1965) has argued that suspension feeders dominate in the deep, central, oligotrophic portions of the oceans, but no other workers have reported similar findings. Hessler (in preparation) finds a typical high diversity of deposit feeders in one oligotrophic area of the North Pacific. This suggests that even if suspension feeders are important in such areas, deposit feeders are at least as diverse as elsewhere in the deep sea.

There is no disagreement on the dominance of deposit feeders in deep eutrophic areas (as defined by SOKOLOVA, 1965). SANDERS and HESSLER (1969) claim that deposit feeders constitute well over half of the fauna, while SOKOLOVA (1965) calculates that they constitute over 70 %. The deposit-feeding habit is virtually universal in some taxa, such as isopods (MENZIES, 1962), that show high within-habitat diversity. Finally, increased within-taxon emphasis on deposit-feeding with increasing depth has been found to hold true even in groups thought of as not normally utilizing this mode of nutrition (ascidians for example: MONNIOT and MONNIOT, 1968; MILLAR, 1970). Thus, in a single sample from the epibenthic sled there may be hundreds of species of deposit feeders. As it has been stated to date (SANDERS, 1968, 1969; SLOBODKIN and SANDERS, 1969), the Stability–Time Hypothesis explains this high diversity in one trophic type by suggesting that each species has evolved a sufficiently high food specialization that there is no competitive overlap with other members of the community.

This degree of specialization seems highly unlikely, because it implies that deposited food can be categorized into a number of types equivalent to the large number of co-occuring deposit feeding species. To date, there has accumulated no direct evidence that the feeding habits of deep-sea species are any more specialized than those of species from shallow water. In the absence of such data, the idea that animals are evolving increased food specialization simultaneously with an emphasis on the deposit-feeding habit is difficult to accept.

While direct evidence on the specific types of detritus that deep-sea species consume is lacking for the present, SANDERS and HESSLER (1969) discuss two aspects of deep-sea communities that indirectly suggest that deposit feeders are flexible in their habits.

First, deep-sea species show strong depth zonation with the only major zonal break in community composition (defined as a peak in a depth-correlated graph of rate of species replacement) occurring at the continental shelf-slope transition band. Otherwise there is a continuous turnover in the species composition of the community as depth increases. This means that within its individual depth range, each species is associated with a continuously changing assemblage of species. This varying association with other species suggests that unless the competitively differentiated food niche changes over a depth gradient, the various detritus-feeding individuals are probably harvesting a spectrum of detrital material.

Second, although diversity for the community is high, density is so low that the average, small, non-vagile individual will be in direct interaction with far fewer species (SANDERS and HESSLER, 1969). Unless these communities are highly structured mosaics (which we have no reason to believe), different individuals of a species will be interacting with different suites of species. Again, under these conditions, food specialization is hard to accept, and it seems more likely that each species is indeed harvesting a variety of available food particles. Both of these points suggest that species must possess a certain flexibility in order to survive.

In considering the question of food specialization, we purposely ignore the fact that deposit feeders are constructed differently and behave differently, thus handling their food in diverse ways. In the present context, when a resource is limiting, it does not matter what method an organism uses to obtain it as long as it is no longer available to other members of the community. This means that degree of taxonomic affinity *per se* may have no bearing on whether two species are competing for the same resource. In the deep sea, all deposit feeders are potentially competing provided that they are utilizing the same kind of detritus from the same level in the bottom. We believe that the number of such food-space categories is low, far lower than the number of species they maintain.

If greater niche specialization is concomitant with higher diversity, an obvious place for this to occur would be in prey preference of predaceous forms. SOKOLOVA (1959) inspected decapods, asteroids, and ophiuroids from the Northwestern Pacific and adjacent areas, and SCHOENER (1969) studied two species of ophiuroids from the North Atlantic. Both studies show the same thing: rarely are the animals in the stomachs of these predators confined even to one phylum. Even when one phylum predominates, several species are represented. Sokolova finds that within a predaceous species, prey may vary with locality, suggesting that to some extent faunal composition of the food simply reflects composition of the community. Thus, contrary to the predictions of the Stability–Time Hypothesis, deep-water predators are apparently as generalized as those in shallow water, in spite of the fact that this is one area where a clear-cut opportunity for specialization exists.

In summary, we can find no evidence suggesting increased food-niche specialization in the deep sea, and in fact what little information there is on feeding habits suggests the opposite. These considerations lead us to believe that the Stability–Time Hypothesis in its present form is not adequate to explain the diversity in deep-sea communities.

*General factors limiting the growth of populations*

There are two classically understood ecological mechanisms by which the growth and distributions of populations are regulated. Populations may be limited when some requisite resource is in short supply, or they may be limited by some disturbance operating somewhat independently of the resources which otherwise potentially limit the populations. In the former situation, the population is said to be limited by either intra- or interspecific competition. In the latter situation the outside disturbance limits the growth of the population before any resource becomes limiting.

Probably all populations share some potentially limiting resources with other populations. As such resources become predictably more limiting, those populations

potentially limited by these resources are exposed to increased competition. So long as a few scarce resources are limiting the growth of the competing populations, the intensity of competition will increase the probability of competitive extinction (HARDIN, 1960). If, on the other hand, there are sufficient independent resources, competition can cause adaptive changes in the competing species. Such character displacement can result in the coexistence of species. The degree of similarity allowable which still permits coexistence between such species in a competition based system has been carefully considered and built into a strong theoretical model which predicts that there can be no more species than there are independent resources within a given level of environmental stability (MACARTHUR and LEVINS, 1964; 1967). This is part of the theoretical framework which gives support to the Stability–Time Hypothesis.

Disturbance is an equally effective mechanism by which the sizes of populations can be regulated. An immediate effect of disturbance is that the resources become less limiting, and the probability of competitive exclusion is reduced. The importance of disturbance in the form of predation and fire is well known (DARWIN, 1859; HUTCHINSON, 1961; LOUCKS, 1970), and the general ecological significance of predation in this role has recently been experimentally demonstrated (SLOBODKIN, 1964; CONNELL, 1970; PAINE, 1966; DAYTON, 1971). There is ample evidence that under predictably disturbed conditions, the probability of competitive exclusion is reduced, more overlap in the utilization of the resources is tolerated, and potential competitors for these resources will have greater opportunity for coexistence. Under such conditions it would be possible for a community to support more species than there are independent resources.

### Reduction of competitive exclusion by croppers

Physical factors are relatively constant in the deep sea and therefore are unimportant as disturbance agents, but the role of biogenic disturbance is probably significant. Since the general importance of predators as disturbers is well recognized in other communities, their effect must be considered in the deep sea as well. Here their role essentially merges with that of the deposit feeders, which will probably readily accept living animals as well as dead organic and inorganic material as they forage (SANDERS, GOUDSMIT, MILLS and HAMPSON, 1962). Therefore, any distinction between predators and deposit feeders in the deep-sea is probably somewhat arbitrary, and none will be made here. To describe this broad but unified life style, we will use the term ' cropper ' as applying to any animal that ingests living particles, whether exclusively or in combination with dead or inorganic materials.

We suggest the hypothesis that by preying on the populations of other, smaller deposit feeders, croppers such as holothurians, echinoids, ophiuroids, asteroids, cephalopods, and some polychaetes, decapods, and fish are largely responsible for the maintenance of the high species diversity of small deposit feeders observed by HESSLER and SANDERS (1967) by reducing the probablity of competitive exclusion. To a certain extent, our hypothesis merges and applies earlier hypotheses of WILLIAMSON (1957), PAINE (1966), and LEVIN (1970).

Since we do not here distinguish between predators and deposit feeders, the entire community (except perhaps suspension feeders and bacteria) can be regarded as consisting of croppers. Viewed simplistically each of these croppers should be able to eat

everything that is sufficiently smaller than itself unless that food item employs avoidance. Even the smallest meiofaunal animal is cropping bacteria. There would be croppers available to harvest the complete resource spectrum, from sporadic, high-yield food to relatively constant, low-yield foods; fish and holothurians, respectively, exemplify these extremes among the croppers.

The larger croppers probably exhibit size selectivity in that their prey must be large enough to be worth interrupting their search processes (MACARTHUR and PIANKA, 1966). The more motile croppers should have become efficient at locating and cropping patches of prey. It is important to note that this efficiency need not imply food specialization. Indeed, with the supposed low densities of prey patches and surface-derived carrion, search time for these large, motile croppers is probably high, and they would be expected to be food generalists (MACARTHUR and PIANKA, 1966).

These feeding patterns suggest that the smaller animals have more species of predators than do the larger animals. Because the probability of being resource limited is inversely related to the intensity of the cropping pressure, the logical result of this situation in which the cropping pressure becomes increasingly severe on populations of decreasing-size animals is that the smaller animals will be less resource limited. The obvious corollary is that the larger the animal, the greater the probability of resource limitation and therefore the lower the diversity of populations of increasingly large animals. While data on the larger, more motile deep-sea croppers are scanty, this prediction may be supported, as there does seem to be an inverse relationship between size and diversity.

The predicted motile efficient searcher and food generalist fits the observed pattern. Lack of trophic specialization among larger invertebrates has already been discussed. The efficiency with which the larger croppers find and consume patches of food is dramatically demonstrated by the Monster Camera photographs taken by John Isaacs and colleagues in the Marine Life Research Group (Scripps Institution of Oceanography). Cans of bait (usually fish) are dropped on to the deep-sea bottom with a camera arranged to photograph the bait and surrounding area at regular intervals. Figures 1 to 4 show that even in extremely sterile areas motile animals representing many species of a number of phyla (fish, natantian decapods, octopods, amphipods, ophiuroids, holothurians, polychaetes, brachyurans) were quick to locate and consume the bait (ISAACS, 1969). The alignment of these croppers frequently suggests that they have utilized current-borne clues to find the bait (Fig. 3) This quick response to the bait by apparently widely scattered individuals reinforces the supposition of searching efficiency. Furthermore, the fact that several species of large croppers quickly consume the bait denies obligate feeding specialization and supports our predicted food generalization.

In summary, given the generalized diets and foraging efficiencies of croppers, it seems logical to suggest that the prey populations are maintained at a sufficiently low level that their food resources are rarely limiting. Since competition would then be relatively reduced, the diets of these prey species would be expected to overlap extensively because the best strategy in a habitat with a relatively low productivity would be to eat any food item that they encountered and could handle.

The present hypothesis does not deny the presence of some niche specialization in the deep sea. It is clear that in being adapted to swimming, ambulation, or burrowing, etc., different species are adapted to operating in levels or zones within or

above the sea bottom. Animals of different sizes or morphologies will prefer particles of different sizes. In contrast to nonselective deposit feeders such as holothurians, some croppers may show some qualitative selectivity. However, there is no evidence that the tastes of deep-sea animals are any more refined than those of shallow water; indeed the high search time suggests an advantage to being less specialized (MACARTHUR and PIANKA, 1966).

*Role of predictability*

Besides being ultimately responsible for relatively more flexible strategies with the corresponding loss of efficiency (MACARTHUR and LEVINS, 1964), unpredictable oscillations in the physical environment usually result in corresponding oscillations in the size of the populations. This can occur either by affecting mortality directly or by setting up oscillations in a critical resource or level of predation. The indirect result of the latter is that resources will aperiodically become limiting, with the utilizers of the resources being thrown into direct competition. In addition, with predators over-exploiting their prey, further oscillations will result. Thus, extinctions can occur, lowering species diversity.
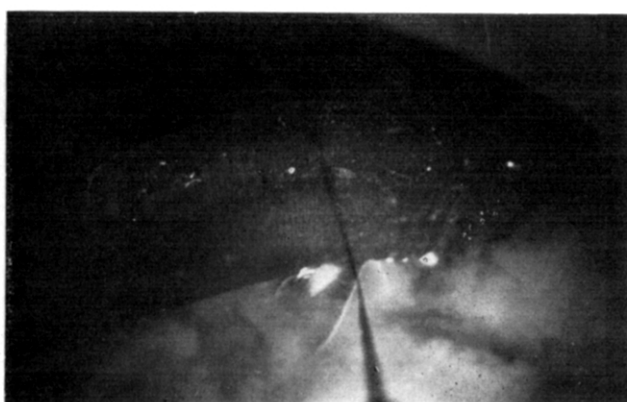
In the deep sea, the primary stimulus for biological oscillation is for the most part missing; that is, the physical conditions are highly stable, and the food supply possibly more predictable than in other environments (see below). Therefore, the oscillations considered above will rarely be initiated. The most important consequence of this is that the amount of available food and the amount of predation pressure are relatively predictable for each species. Instead of arguing, as does the Stability–Time Hypothesis, that this biological accommodation results in competitive niche differentiation, we suggest that the species remain generalists. Indeed, Sanders' idea of the highly buffered structure of biologically accommodated communities requires generalized feeding, because only in that way can buffering cross-linkages exist. High trophic specialization results in straight chain linkages. If food is a limiting resource, such chains would actually be unstable configurations.

*Predictability of food*

One of the basic tenets of most deep-sea theories is that the habitat lacks the various stimuli causing biological oscillation and that the extreme environmental predictability is one of the most important components of the deep-sea community (SLOBODKIN and SANDERS, 1969). However, the possibility of unpredictability in food supply has been ignored, and thus deserves special attention. It is not known how food actually arrives at the deep-sea floor, but there cannot be much dispute that in the open ocean it comes from above. Every condition of this food, from organic aggregates and copepod ecdyses to dead fish and whales, has been postulated (MENZIES, 1962; SANDERS and HESSLER, 1969).Given the variable and extremely slow sinking rates, the smaller particles should arrive at the bottom in a homogeneous pattern from which unpredictable pulses of primary productivity at the surface have been damped out, except perhaps in coastal waters. In the deep sea, assimilation by the various animals and bacteria in the water column render it unlikely that these smaller particles have directly utilizable food value when they arrive. If this is so, the most significant
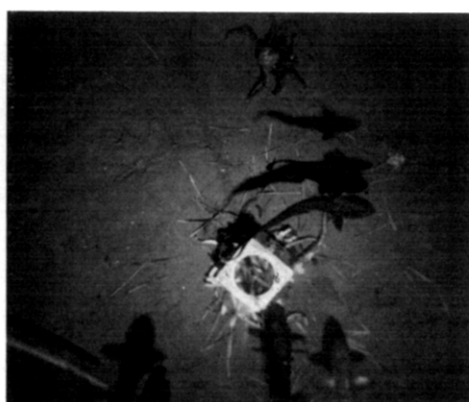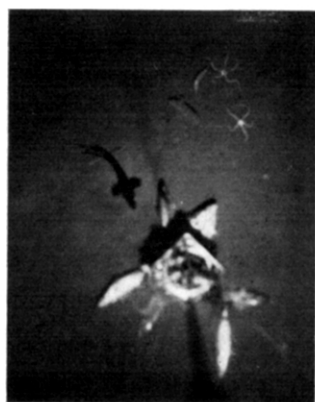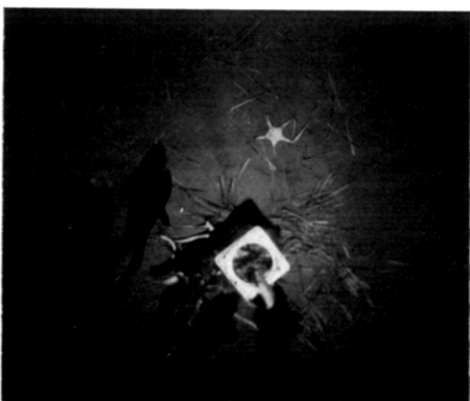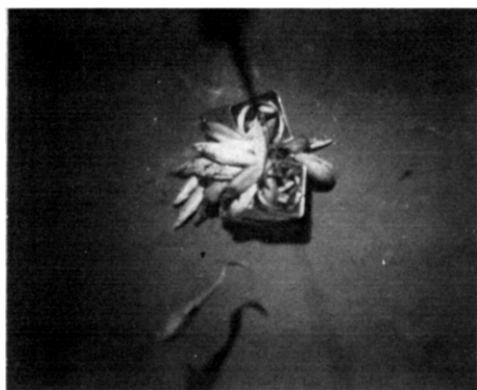
0.25 hours      3.25 hours

5.00 hours      12.50 hours

18.00 hours      22.25 hours

Fig. 1.  Monster camera sequence from 2009 m depth in coastal waters off Baja California, 30° 53′N, 116° 45′W. The pictures show the variety of organisms that are attracted to bait (=large parcels of food): several species of fish, including *Antimora rostrata*, *Somniosus pacificus*, *Coryphaenoides acrolepis*, *Eptatretus stoutii*, *Lycodes* sp., and *Raja* sp.; asteroids, lithodid crabs, and the quill worm, *Hyalinoecia tubicola* (the rod-shaped objects). The camera's arrival on the bottom is the datum point for the time given under each picture.
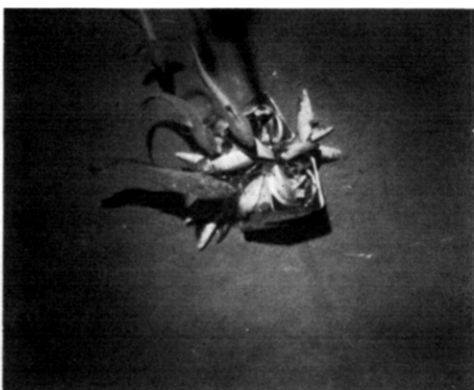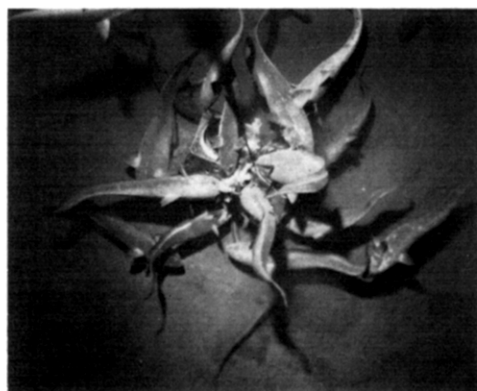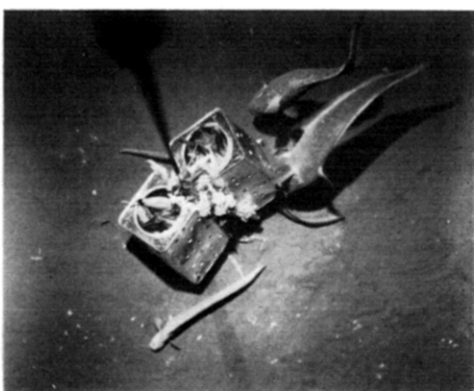
0.50 hours       2.25 hours

8.50 hours       20.25 hours

I day, 19.75 hours       2 days, 18.75 hours

Fig. 2. Monster camera sequence from 3435 m depth in coastal waters off Baja California, 29°59′N, 118° 23′W. The diversity of mobile scavengers is distinctly lower than in Fig. 1. Note that the fish shown at 0·50 hr are actually the dead bait; this bait on the outside of the cans has been mostly removed by the last shot of the sequence (2 days, 18·75 hr).

0.25 hours          2.00 hours

7.00 hours

22.25 hours          I day, 5.75 hours

Fig. 3.   Monster camera sequence from 5856 m depth in the northwestern Pacific, 34° 03′N, 163° 59′E. Except for the holothurian at 2 hr, all the scavengers are fish. In this area benthic standing crop is only moderately low (about 0·1 g wet wt. / m² according to Filatova, in ZENKEVICH, 1969), and the environment has been regarded as eutrophic by Sokolova (*ibid.*). Nevertheless, many more scavengers have been attracted than one would have expected in a manganese nodule environment from open-ocean waters so deep. The orientation of fish at 7 hr suggests an appreciable current may have done much to spread the odor of the bait.
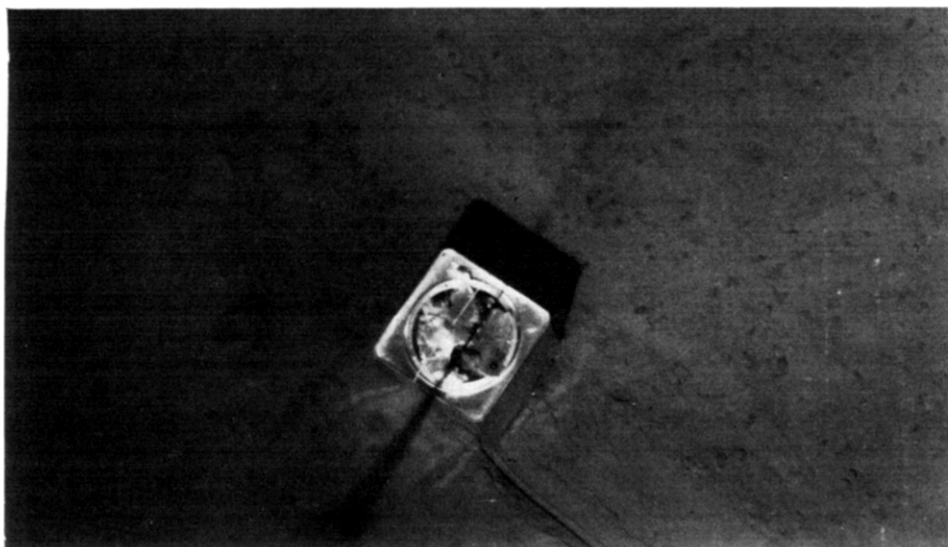
0.50 hours
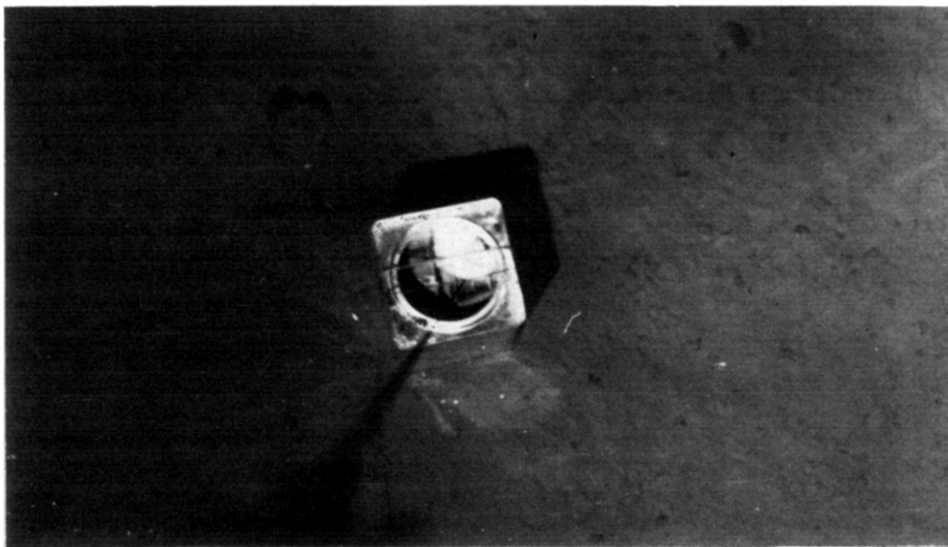


14.17 hours

Fig. 4.   Monster camera photographs from 5307 m depth in the north central Pacific, 23° 54·5′N, 144° 05′W. The two shots, one at the beginning of the sequence, the other, 13·67 hr later, demonstrate the efficiency with which the bait was dispersed. In the second shot, the can appears to be empty except for one voracious amphipod.

source of nutritive energy to the deep sea could be the faster falling, larger parcels of food such as various-sized dead euphausids, fish, squids, whales, etc. In terms of seasonality, the rate of supply of large particles to the deep sea should be more constant than with smaller organisms because the longer life span of larger animals will damp out many of the seasonal oscillations. Nevertheless, from such a source, food supply to any given small area in the deep sea would probably be more unpredictable than anywhere on the planet, and this could be a potent source of biological oscillation.

However, the Monster Camera data demonstrate that the deep benthic community contains a surprisingly large number of efficient scavengers which are widely dispersed but quick to concentrate on any such large parcel of food (Figs. 1–4). After they have consumed the food parcel, these scavengers again disperse. The important point is that such large patches of food are promptly homogenized and dispersed over the bottom as feces (or some other organic product) from the scavengers before a local population build-up of small detritus feeders can take place. That is, the majority of species in the community are never given an opportunity to take advantage of a large piece of food. Thus, a potential source of biological unpredictability is very much reduced. It is still an open question, of course, whether the feces from the scavengers furnish a predictable source of food. We think that in relation to the presumably very low turnover rates of the community, the organic by-products of the scavengers would be a rather reliable source of energy. That is, in terms of the generation time of the deposit feeders, the supply rate of such organics to any given small area may be reliable.

Although we feel that the possible importance of larger food particles has been under-rated in recent years (see also ISAACS, 1969), the present discussion is not meant to discredit organic aggregates or the rain of dead plankton as possible sources of food for the deep sea. What is important here is that regardless of their energy content, small particles are not likely to result in patchiness, either spatially or temporally.

## DISCUSSION

It is becoming clear that some of the better known communities, such as forests (LOUCKS, 1970; JANZEN, 1970), lakes (BROOKS and DODSON, 1965; DODSON, 1970), and the intertidal (PAINE, 1966; CONNELL, 1970; DAYTON, 1971), are structured by patterns of natural disturbance that reduce the effects of competition. This is also seen to be the case with certain plant–insect associations (JANZEN, 1968; CANTLON, 1969). We envision that, in general, deep-sea communities are dominated by disturbance, as are these other communities. However, biological disturbance by cropping may play an even greater role here because of the environmental predictability and the fact that relatively few of the prey have refugia in size or space from their potential consumers.

Sanders' Stability–Time Hypothesis was developed to explain the high faunal diversity observed in the deep-sea. The essence of this hypothesis is that long term environmental predictability has allowed a highly refined competitive niche differentiation to result in a great many essentially non-overlapping niches. We agree that predictability is probably ultimately responsible for the high diversity; however, we do not agree that this increase in diversity need result from competitive niche differentiation. Rather, we propose the hypothesis that high diversity in this stable environment is allowed by predictable disturbance by the croppers, which in effect

reduces the importance of competitive exclusion and thus allows the continued coexistence of many species which share the same resources.

An important criterion of any scientific hypothesis is that it generates testable predictions. The predictions discussed by SANDERS (1969) are designed to allow a test of the effect of environmental stability, but do not permit an evaluation of the mechanisms by which the high diversity is maintained. It is difficult to identify and contrast the roles of competition and disturbance in the deep-sea community. The precise experiments in the intertidal (DAYTON, 1971) and lake (DODSON, 1970) communities in which predators are experimentally excluded are clearly impossible in the deep sea. Neither can we extract convincing evidence such as that proposed by LOUCKS (1970) in his argument that fire is an important component of forest diversity.

Predictions or consequences which could be used to test our basic hypothesis include the following: (1) the smaller organisms such as polychaetes and small arthropods should be complete food generalists able to consume any appropriately small organic food particle which becomes available to them; (2) the intermediate-sized croppers such as holothurians, ophiuroids, echinoids, larger polychaetes, etc., should also be food generalists which do consume living animals smaller than themselves as well as detritus; and (3) the larger, more motile croppers such as the largest crustaceans and fish should be extreme food generalists capable of locating and quickly consuming the large rapidly settling parcels of food. We have presented observations which support these predictions, but clearly the data are fragmentary, and much more needs to be done.

It might be objected that if we agree that this deep-sea community has an extremely low rate of food income, it is not possible to argue that most of the species are in fact not food limited considering that the community as a whole is clearly food limited. However, all communities are ultimately energy limited, and all communities, especially terrestrial communities, have many species which are limited by disturbance, especially predation and weather (SLOBODKIN, SMITH and HAIRSTON, 1967).

The deep-sea community differs only in that the trophic levels are almost completely merged, so that the roles of most predators are not distinguishable from those of the decomposers. The situation that we envisage is that the smaller the organism, the more potential predators it will have and the less probability of its being food limited. Conversely, the larger the organism, the more it will have to search for sufficient food and the more likely it is that it will be food limited. The populations of some of the largest croppers seen in Isaac's deep-sea photographs are almost certainly food limited most of the time. Thus the HAIRSTON, SMITH and SLOBODKIN (1960), concept of decomposers being food limited is ultimately true also in the deep sea in that potential energy is not accumulating. However, in the deep sea, many of the predators which are limiting the growth of the populations of smaller organisms are also cropping the decomposers within the detritus.

It has been theoretically demonstrated that unselective predation can allow two otherwise competing species to coexist (SLOBODKIN, 1962; MURPHY, 1968); therefore the situation which we envision should not be unstable. In fact, the almost total intermeshing of the food webs might offer the community an ability to resist perturbations (MACARTHUR, 1955). It is also germane to point out that predation is the active selection agent which differentially reduces the more abundant populations of prey species in the apostatic selection discussed by CLARKE (1962).

In this paper we have not been concerned with the possible sources of the species in the deep-sea community. Rather, we assume, with others (SLOBODKIN and SANDERS, 1969), that both speciation and immigration are occurring and act to enlarge the species list. Our only concern here has been to consider the question of what enables the species to coexist so that a high species diversity is maintained.

We are aware that we have taken a relatively extreme position in this paper, and we agree with LEVINS (1966) that the truth is usually the intersection of independent lies. However, we suggest that realistic deviations from our model such as less predictable food supply, the temporary formation of search images such as discussed by TINBERGEN (1960) and HOLLING (1965), various types of escape responses, nonpredator mortalities, etc., will all act to strengthen our main point: that it is unlikely that the patterns of coexistence in the deep sea depend entirely on competitive niche differentiation. In this context, future areas of deep-sea research should include a more sophisticated analysis of diet, determination of optimal predator foraging strategies, elucidation of the importance of formation and duration of search images (MURDOCH, 1969), evaluation of the cost and effectiveness of any existent defense mechanisms, both behavioral and chemical, and detailed analysis of microdistribution patterns of species within the community. With the improvement of deep-sea submersibles, experimental manipulation should be undertaken. This type of research will almost certainly demonstrate that community organization in the deep sea is much more complex than is currently envisioned in this paper and elsewhere.

## REFERENCES

BROOKS J. L. and S. I. DODSON (1965) Predation, body size, and composition of plankton. *Science*, **150**, 28–35.

CANTLON J. E. (1969) The stability of natural populations and their sensitivity to technology. *Brookhaven Symp. Biol.*, **22**, 197–203.

CLARKE B. (1962) Balanced polymorphism and the diversity of sympatric species. *Systematics Assoc. Publ.* No. 4., 47–70.

CONNELL J. H. (1970) A predator–prey system in the marine intertidal region. 1. *Balanus glandula* and several predatory species of *Thais*. *Ecol. Monogr.*, **40**, 49–78.

DARWIN C. (1859) *On the origin of species.* Murray, London.

DAYTON P. K. (in press) Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.*, **41**, (4), in press.

DODSON S. I. (1970) Complementary feeding niches sustained by size-selective predation. *Limnol. Oceanogr.*, **15**, 131–137.

HAIRSTON N. G., F. E. SMITH and L. B. SLOBODKIN (1960) Community structure, population control, and competition. *Am. Nat.*, **94**, 421–425.

HARDIN G. (1960) The competition exclusion principle. *Science*, **131**, 1292–1297.

HESSLER R. R. and H. L. SANDERS (1967) Faunal diversity in the deep-sea. *Deep-Sea Res.*, **14**, 65–78.

HOLLING C. S. (1965) The functional response of predators to prey density and its role in mimicry and population regulation. *Mem. Entomol. Soc. Can.*, **45**, 1–60.

HUTCHINSON G. E. (1961) The paradox of the plankton. *Am. Nat.*, **95**, 137–145.

ISAACS J. D. (1969) The nature of oceanic life. *Scient. Am.*, **221**, 146–162.

JANZEN D. H. (1968) Host plants as islands in evolutionary and contemporary time. *Am. Nat.*, **102**, 592–595.

Janzen D. H. (1970) Herbivores and the number of tree species in tropical forests. *Am. Nat.*, **104**, 501–528.

Levin S. A. (1970) Community equilibria and stability, and an extension of the competitive exclusion principle. *Am Nat.*, **104**, 413–423.

Levins R. (1966) Strategy of model building in population biology. *Am. Scient.*, **54**, 421–431.

Loucks O. L. (1970) Evolution of diversity, efficiency, and community stability. *Am. Zool.*, **10**, 17–25.

MacArthur R. H. (1955) Fluctuations of animal populations and a measure of community stability. *Ecol.*, **36**, 533–536.

MacArthur R. H. and R. Levins (1964) Competition, habitat selection and character displacement in a patchy environment. *Proc. natn., Acad. Sci., U.S.A.*, **51**, 1207–1210.

MacArthur R. H. and R. Levins (1967) The limiting similarity, convergence and divergence of coexisting species. *Am. Nat.*, **101**, 377–385.

MacArthur R. H. and E. Pianka (1966) On optimal use of a patchy environment. *Am. Nat.*, **100**, 603–609.

Menzies R. J. (1962) On the food and feeding habits of abyssal organisms as exemplified by the Isopoda. *Int. Revue ges. Hydrobiol.*, **47**, 339–358.

Millar R. H. (1970) Ascidians including specimens from the deep sea, collected by the R.V. *Vema* and now in the American Museum of Natural History. *Zool. J. Linn. Soc.*, **49**, 99–159.

Monniot C. and F. Monniot (1968) Les Ascidies de grandes profondeurs récoltées par le navire océanographique americain *Atlantis II. Bull. Inst. océanogr. Monaco*, **67**, 3–48.

Murdoch W. W. (1969) Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecol. Monogr.*, **39**, 335–354.

Murphy G. I. (1968) Pattern in life history and the environment. *Am. Nat.*, **102**, 391–403.

Paine R. T. (1966) Food web complexity and species diversity. *Am. Nat.*, **100**, 65–75.

Sanders H. L. (1968) Marine benthic diversity: a comparative study. *Am. Nat.*, **102**, 243–282.

Sanders H. L. (1969) Benthic marine diversity and the stability–time hypothesis. *Brookhaven Symp. Biol.*, **22**, 71–80.

Sanders H. L., E. M. Goudsmit, E. L. Mills and G. R. Hampson (1962) A study of the intertidal fauna of Barnstable Harbor, Massachusetts. *Limnol. Oceanogr.*, **7**, 63–79.

Sanders H. L. and R. R. Hessler (1969) Ecology of the deep-sea benthos. *Science*, **163**, 1419–1424.

Schoener A. (1969) Ecological studies on some Atlantic ophiuroids. Ph. D. dissertation, Harvard University, 115 pp.

Slobodkin L. B. (1962) *Growth and regulation of animal populations.* Holt, Rinehart, and Winston, 172 pp.

Slobodkin L. B. (1964) Experimental populations of Hydrida. *J. Anim. Ecol.*, **33**, (*suppl.*), 131–148.

Slobodkin L. B. and H. L. Sanders (1969) On the contribution of environmental predictability to species diversity. *Brookhaven Symp. Biol.*, **22**, 82–93.

Slobodkin L. B. and F. E. Smith and N. G. Hairston (1967) Regulation in terrestrial ecosystems, and the implied balance of nature. *Am. Nat.*, **101**, 109–124.

Sokolova M. N. (1959) The feeding of some carnivorous deep-sea benthic invertebrates of the far Eastern Seas and the Northwest Pacific Ocean. (In Russion). In: *Marine biology.* B. N. Nikitin, editor. *Trudy. Inst. Okeanol., Akad. Nauk. SSSR.*, **20**, 227–244. Transl. publ. by A.I.B.S.

Sokolova M. N. (1965) Uneven distribution of bottom feeders in the deep-sea benthos as a consequence of uneven sedimentation. (In Russian). *Okeanologiia*, **5**, 498–506. English transl.; 85–92.

Tinbergen L. (1960) The natural control of insects in pinewood—I. Factors influencing the intensity of predation by songbirds. *Arch. néerl. Zool.*, **13**, 265–343.

Williamson M. H. (1957) An elementary theory of interspecific competition. *Nature, Lond.*, **180**, 422–425.

Zenkevich L. A., editor (1969) *Deep-sea bottom fauna, pleuston.* (In Russian). *Biologiia Tikhogo Okeana Tikii Okeana*, V. G. Kort, Chief editor, Isdated Nauka. Moskva, **7**, (2), 3550 pp.