

Abyssal community analysis from replicate box cores in the central North Pacific

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Abstract—A 0.25 m² United States Naval Electronics Laboratory box corer was used to take replicate samples from an oligotrophic bottom under the North Pacific Central Water Mass (~28°N, 155°W). The bottom is a red clay with manganese nodules at a depth of 5500–5800 m.

Macrofaunal density ranges from 84 to 160 individuals per m² and is therefore much the same as in Northwest Atlantic Gyre waters. Of the macrofaunal taxa, polychaetes dominate (55%), followed by tanaids (18%), bivalves (7%), and isopods (6%). Meiofaunal taxa were only partially retained by the 297 µm screen used in washing. Even then, they are 1.5–3.9 times as abundant as the macrofaunal taxa, with nematodes being numerically dominant by far. Foraminifera seem to comprise an important portion of the community, but could not be assessed accurately because of the inability to discriminate living and dead tests. Remains of what are probably xenophyophoridans are also very important, but offer the same problem.

Faunal diversity is extremely high, with deposit feeders comprising the overwhelming majority. Most species are rare, being encountered only once. The distributions of only three species show any significant deviation from randomness. The polychaete fauna from box cores collected from 90 miles to the north was not significantly different from that of the principal study locality. Concordance appeared at several taxonomic levels, from species through macrofaunal/meiofaunal relationships. As a result, the variation in total animal abundance shows aggregation among cores.

We discuss Sokolova's concept of a deep-sea oligotrophic zone dominated by suspension feeders, and reconcile it with our present findings. The high diversity of the fauna combined with the low food level contradict theories that relate diversity directly with productivity.

INTRODUCTION

THE LAST quarter-century has seen an exponential increase in research on the deep-sea benthos, involving workers from many countries. As a result, our understanding of this biotope is rapidly expanding. Not surprisingly, nearly all of this work is limited to the broad marginal zone of the deep sea, where even at abyssal depths the bottom is affected by higher surface productivity and continental factors. The latter may take a biological form, such as food from the shelf and terrestrial outwash, or a physical form, such as boundary currents and turbidity flows.

Few programs have extended into the open-ocean gyres far from land, where the great depth of water, the low surface productivity, and the modest degree of horizontal advective input result in an extremely low rate of food supply to the bottom. These gyres form regions of great physical stability, where there is only extremely slow pelagic sedimentation, and where water movement is limited to weak tidal currents.

The most extensive effort in such areas is that of the Soviet Union's Institute of Oceanology (summarized in ZENKEVICH, 1969), which has resulted in considerable data on standing crop, faunal distributions, and trophic structure. Unfortunately, it is very difficult to relate these results to those of others because of differences in technique and

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methods of reporting data. Another group which has worked in oceanic gyres is that of the Woods Hole Oceanographic Institution (SANDERS and HESSLER, 1969). Their Gay Head-Bermuda transect includes stations in the oligotrophic Sargasso Sea. A weakness in the published results of both of these programs is the lack of replicates, rendering it impossible to place confidence limits on the reported values. Replication is particularly important in central gyre communities, where one sample contains few individuals.

In 1969, the senior author initiated a deep benthic study of an oligotrophic, open-ocean community, to obtain as clear a picture as possible of its structure. Efforts were made to concentrate on a single site (the CLIMAX II locality, named for the cruise on which this work was initiated), which would be sampled repeatedly. The area is the deep abyssal zone 770 km north of Hawaii, beneath the unproductive North Pacific Gyre waters and within the boundaries of the 'oligotrophic zone' as mapped by Sokolova (in ZENKEVICH, 1969). The appropriateness of this site is enhanced by the active, integrated research on euphotic and midwater communities by a large group of S.I.O. ecologists.

Our initial effort relied on a single tool, the United States Naval Electronics Laboratory (USNEL) box corer, a device originally developed by sedimentary geologists, but one proven to be an accurate and versatile quantitative tool for benthic biological research. Subsequent work has included camera studies at the CLIMAX II locality and comparative sampling at other open-ocean sites.

METHODS

The box corer

Background. Quantitative investigation of the deep-sea benthos began in 1949, when the Soviet Union started its systematic surveys of the deep benthos (summarized in ZENKEVICH, 1969). Shortly thereafter the Danish Galathea Expedition used a Petersen grab at hadal depths (SPÄRCK, 1951). Since those pioneer efforts, many others (CAREY, 1965; Filatova, in ZENKEVICH, 1969; FRANKENBERG and MENZIES, 1968; HARTMAN and BARNARD, 1960; MENZIES and ROWE, 1968; RANKIN, CLARK and BIERNBAUM, 1969; ROWE, 1971; SANDERS and HESSLER, 1969; THIEL, 1971; WIGLEY and MCINTYRE, 1964) have produced standing crop estimates of the deep benthos. For these measurements, only the Okean and Campbell grabs, Sanders and Carey anchor dredges and Reineck box corer have been used extensively.

We decided to use a box corer for our work, although at that time it had not been used extensively in marine biology. Of all the available techniques, it offered hope for the fewest biases (SMITH and HOWARD, 1972). It is designed to sample a precise area for the full depth of bite, in contrast to grab techniques, which at best only take the surface layer precisely (MCINTYRE, 1971). Similarly, the anchor dredge, which should operate at a constant depth to be accurate, must be towed at least a small distance before it reaches full biting depth, and may not maintain that level precisely during the tow (SANDERS, HESSLER and HAMPSON, 1965).

The box corer yields relatively undisturbed samples. Those of grabs are at best usually folded, and the anchor dredge mixes the sediment completely, often scraping off the surface layer (HESSLER and SANDERS, 1967). The bow-wave effect (MCINTYRE, 1971), a difficult problem with any quantitative sampler, promised from the box corer design to be reasonably low, and the large size of our core would tend to minimize boundary effects. Because of its great weight and adjustable depth of bite, the box corer would

work in soft bottoms equally well, regardless of bottom type. This is not the case with grab or anchor dredge techniques.

Description. The basic design for nearly all box corers is that of REINECK (1958, 1963) for his 'Kastengreifer'. This design was modified by BOUMA and MARSHALL (1964), and again by ROSFELDER and MARSHALL (1967) with the support of the U.S. Naval Electronics Laboratory, to yield the USNEL Spade Corer. It bites a surface of 600 cm² (20 × 30 cm). To accommodate the low numerical densities one normally encounters in the deep sea, we enlarged the core to take an area of 0.25 m² (50 × 50 cm) (Fig. 1).

The following description supplements those in ROSFELDER and MARSHALL (1967) and BOUMA (1969). Upon contact, a rectangular gravity core sinks into the bottom. Its path is guided at its upper end by a column that sinks through a sleeve which is part of a frame that rests on the bottom. A friction release frees the spade arm when the weight of the corer is relieved from the wire. When wire is reeled in to return the device to the ship, the initial action is to lever the spade down into the substrate until it closes off the bottom of the core. Subsequent take-up on the wire pulls the apparatus out of the bottom.

To insure the successful operation of this basic design, many small elegances have

USNEL SPADE CORER

Modified for 0.25m²

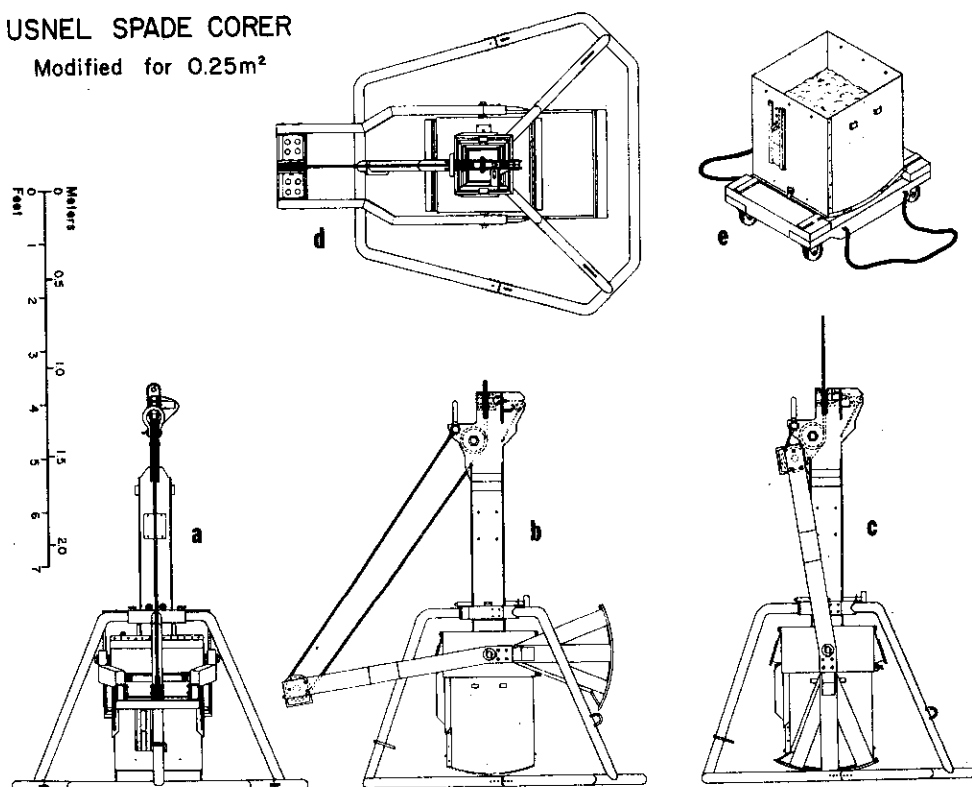


Fig. 1. The USNEL box corer, modified to take a 0.25 m² core. a: View from spade lever-arm end, with spade in open position. b: View from side, with spade in open position. c: View from side, with spade in closed position. d: View from top, with spade in open position. e: Disengaged core box on cart for processing of sample. These pictures are best studied in conjunction with those in BOUMA (1969) and ROSFELDER and MARSHALL (1967).

been incorporated into the device. The column and the sleeve have a square cross-section to keep the orientation of corer and frame constant. The guide-sleeve is gimbaled so that even if the frame is tilted as a result of landing on a sloping bottom, gravity will cause the apparatus to enter the bottom vertically. At the top of the core box are screened vents with flapper valves to allow free passage to water entering at the mouth. This reduces the bow-wave effect and of course allows the corer to sink into the bottom. The fulcral axis of the spade is keyed so that as the spade passes under the core box, there is ample clearance between the two components. Then, when the spade is completely under the box, the two are pulled together to complete the seal.

A pressure-powered safety (Model 1790A, Benthos Inc., North Falmouth, Massachusetts) acts to prevent accidental triggering of the spade arm on deck, as well as in the upper portions of the water column. It consists of a piston partially inserted into an air-filled chamber and restrained in this position by shear pins. The protruding end of the piston prevents the friction release from firing. When hydrostatic pressure exceeds the shear strength of the pins, they break, and the piston is pressed into the air chamber. The friction-release trigger is then free to fire. The depth of shearing is determined by the diameter and composition of the pins.

The whole core box with its included sample can be removed from the rest of the device so that the entire upper surface is exposed for inspection and manipulation, including subsampling (Fig. 1e). Water trapped in the box on top of the sediment surface will slosh around and put the surface layer of mud into suspension if the device is subjected to much disturbance after retrieval. For this reason, and to facilitate work at the sediment surface, a vertical line of runoff holes was added to the side of the box. These can be opened sequentially from top to bottom, to remove the water.

Operation at sea. Our current employment of the box corer is as follows. The pressure-powered safety is rigged to fire at about 1000 m off the bottom. A Benthos pinger (Model 2214) is placed on the wire 25 m above the corer, which is lowered at 50 m min^{-1} , its distance off the bottom being monitored via the pinger (Fig. 2).

Because of the bulk of the box corer and its proximity to the pinger, a detectable pulse is reflected from it. Thus, one can read four sonic pulses on the graphic recorder on board ship. One is generated by the ship's transducer and gives the bottom depth. The other three come from the pinger. They are the direct pulse back to the ship and the reflected pulses from the corer and from the bottom.

The acoustic reflection off the corer can be used to detect prefiring in the water column, and to confirm firing on the bottom. Because the closing of the spade is caused by pulling on a draw wire, the total distance between pinger and corer is increased by the length of the draw wire after closure. This increase is detectable on the graphic recorder.

When the sampler is about 100 m off the bottom, wire speed is slowed to $15\text{--}25 \text{ m min}^{-1}$. The slower the box makes its contact with the bottom, the smaller will be the bow-wave effect. On the other hand, contact cannot be made too slowly because, if the ship is drifting, the corer will be dragged over on its side before it has a chance to penetrate. Also, as a result of ship's surge, it might touch bottom, lift off again, and recontact in a slightly different position, thus having disturbed the surface of its own sample. We have seen a sample with the impression of a previous contact cutting across its surface.

Approach to the bottom, contact, and pullout are monitored in two ways. Bottom

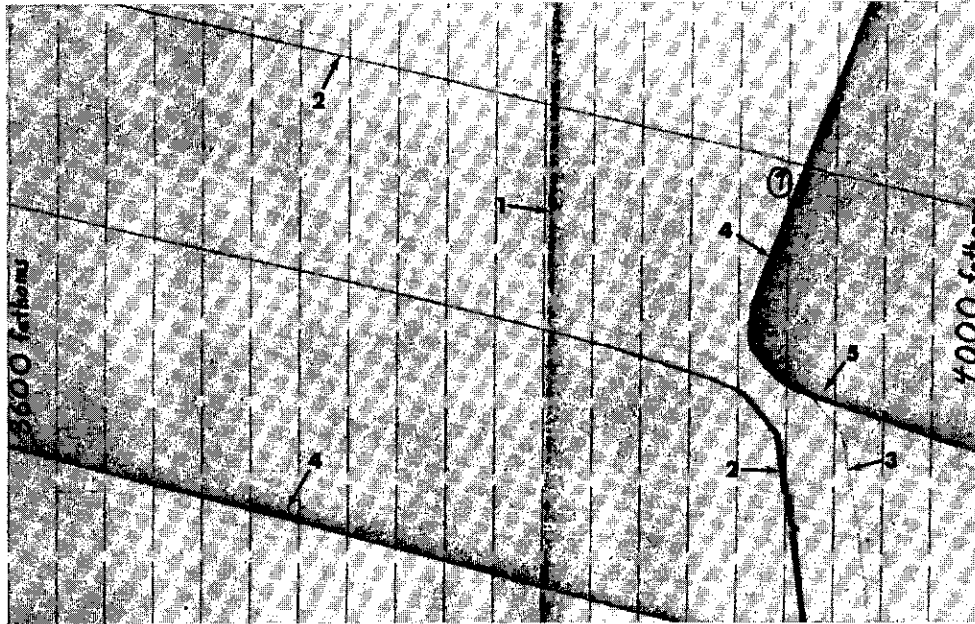


Fig. 2. Graphic depth record of a portion of Sta. H-40, in the Aleutian Trench. Vertical dashed lines are 20 fathoms apart; each dash equals 5 min. Time progresses from bottom to top. 1: Reflection from bottom, using ship's transducer, recording a depth of 3822 fathoms, uncorrected. 2: Direct return from pinger on wire. 3: Pinger reflection off box corer, 50 m below it. 4: Pinger reflection off bottom. 5: Contact between box corer and bottom; the record below this point is of the corer being lowered, while above it, the corer is being brought back up.

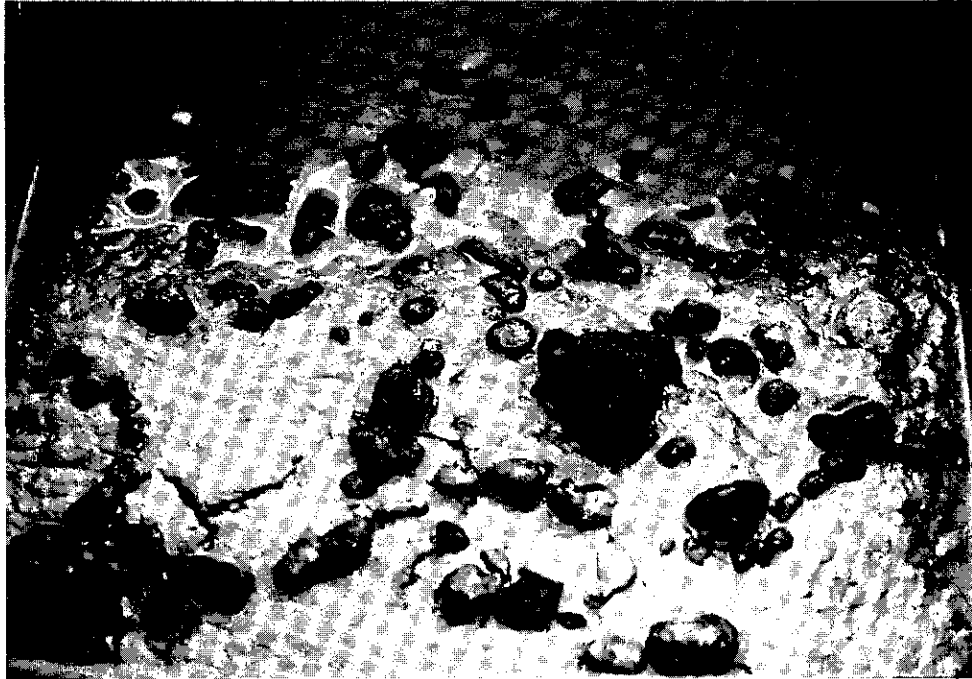


Fig. 3. Surface of a 0.25 m² USNEL box core just after most of the overlying water has been drained off. The fissures in the mud are caused by deck manipulations. Station H-5 from the CLIMAX II locality.

contact is seen on the graphic recorder as the convergence of the pinger reflections off the bottom and off the corer. A few seconds prior to this convergence, there is a distinct drop in tension on the trawl wire, as seen on the tensiometer. This indication that the heavy gear is on the bottom precedes the pinger's signal because the reduction in weight on the wire is transmitted to the ship instantaneously, whereas the pinger impulses move at the speed of sound.

On noting contact, one waits for a moment to allow a little extra wire out, then stops the winch. A few seconds thereafter, one starts bringing in wire at a slow rate, about 10 m min^{-1} or less. It is during this period that the spade is levered into the mud and the apparatus is pulled out. If the sample has been taken successfully, pullout is usually accompanied by a steady increase in wire tension to extremely high values, due to the generation of from 2000–5000 lb of suction, followed by a sudden drop to more normal values when the corer breaks free from the bottom. At this time wire speed may be increased to 50 m min^{-1} .

As soon as the sampler is again on the deck, the surface water is drained off the top of the core into a screen. If the water is clear, it indicates the sediment surface was not disturbed during ascent. The box is then disengaged for processing of the sediment.

Evaluation of the technique. In theory, and we think in actuality as well, the box corer yields the least biased quantitative samples of the total fauna available to biologists today. The device works equally well on any kind of unconsolidated bottom likely to be found in the open ocean. Up until the moment of capture, the surface of the bottom is left relatively undisturbed, as testified by the crystal clear, cold water one is usually able to draw off the surface of the core. The exposed surface of the sediment often displays animal tracks and burrows, sessile forms in living position, and undisturbed manganese nodules (Fig. 3). Such samples can be processed *in toto*, or subsampled either horizontally or vertically. Animal burrows and tubes are often found intact.

Nevertheless, this technique is not free from bias. In its descent, the device is undoubtedly preceded by a bow wave of unknown magnitude, which must be having some unassessable effect. Large, mobile epifauna may be warned and thus escape, although in productive inshore waters we collect large, mobile midwater organisms with surprising frequency, so that the rarity of mobile megafauna from our benthic samples may reflect their true scarcity. Small macrofauna of all sorts is abundant in the samples, suggesting that any bow-wave effect on that portion of the fauna is limited. MCINTYRE (1971) notes from experiments with open tubes that the greater the diameter of the core, the more reduced is this effect, giving rise to the possibility that our large cores minimize the problem.

In addition to the bow-wave, core boundary effects include frictional drag as the box penetrates the bottom. This explains the presence of small numbers of surface-dwelling creatures deeper in the sample. Again, these effects are minimized in a large core.

There are also practical difficulties. High ship's surge causes the device to reach terminal velocity during the descent through the water. The resulting loss of tension on the wire allows the trigger to prefire. The problem is not solved by the pressure-pin safety; with a vertical wire, the surge is felt at its end no matter how much wire is out. Terminal velocity is probably higher for corers having a smaller sampling area, thus offering a solution where large sample size is not essential.

The great size and weight of the box corer and its samples make it both cumbersome and complicated to maneuver. Launch and recovery are always challenging and

potentially dangerous. Removal of the core with its sample is complicated, although it presents no difficulty to one acquainted with the proper technique.

Finally, box corers are very expensive, although they are rarely lost and seldom damaged.

Post-sampling procedure

The top of the core sample, usually over 40 cm long, was washed in two layers, each approximately 10 cm thick. We used the elutriation technique of SANDERS, HESSLER and HAMPSON (1965) with a 297 μm screen (except sample H-29).

The samples were fixed in buffered formalin for 2 days and preserved in 70% ethanol. In the laboratory, they were stained with rose bengal and inspected under a dissecting microscope. All benthic organisms were picked out, sorted to major taxon, and then to species wherever possible. The nematodes were the only abundant taxon not sorted to species.

Terminology: macrofaunal and meiofaunal taxa

At Sta. H-29 an attempt was made to process the 0.25 m² core with a 62 μm (4.0 Phi units; KRUMBEIN and PETTJOHN, 1938) screen, in order to retain all the meiofauna. Most of the sample was washed in this way, but we finally shifted back to a 297 μm (1.75 Phi units) screen because of the extreme amount of time needed for washing with so fine a mesh. The fauna from that station, when compared to that from the CLIMAX II stations, demonstrates the effect of screen size on faunal composition (Table 3). The standing crops of all but three of the taxa are much like the average standing crops for the ten CLIMAX II samples. However, with the nematodes, harpacticoid copepods, and ostracods, they are significantly higher. Thus, most individuals of the latter three taxa are so small that they pass through a 297 μm screen, whereas individuals of the other taxa are large enough to be retained.

The 297 μm screen retained nearly all individuals of those taxa generally regarded as members of the macrofauna (see list on Table 3). Nematodes, harpacticoids, and ostracods are considered components of the meiofauna (permanent meiofauna of MCINTYRE, 1969). We utilize this distinction herein. Because most deep-sea studies will continue to rely on the coarser screens (297–500 μm ; 1.75–1.00 Phi units), it is important to distinguish between those taxa where the full fauna for a specified taxon is obtained in the sample, as opposed to those that are only fractionally retained. In the latter case, the extent to which this occurs may be correlated with the vigor with which the sample was washed, a bias that can easily mask environmental factors.

Contamination

Where benthic standing crop is very low, as it is in the area of this study, any introduction of individuals from other environments can introduce serious biases. Contamination from surface plankton, and from the fouling community on the hull of the ship has been a serious problem in the present investigation. To wash the samples on board ship, we use large volumes of sea water which enters the ship's plumbing via an intake that is flush with the hull, about 10 ft below the surface.

While most of these organisms (calanoid copepods, chaetognaths, euphausiids, macroalgae, etc.) can be readily identified as foreign contributions, there are many taxa

not so easily categorized by someone not a specialist with those groups, and often they are badly fragmented. Included are larval gastropods and bivalves, ostracods, amphipods, eucarids, bryozoans, and coelenterates.

Contaminants have been eliminated from the present study by several means. Specialists were consulted wherever possible. Plankton samples taken in the same area by Dr. John A. McGowan were searched for suspected taxa. This proved especially useful with bivalves and ostracods. Hull scrapings and wash water samples should have been taken for the same purpose, but this was not thought of at that time.

Common sense about natural history was frequently used in detecting exotic species. Pigmented forms and those with eyes were regarded with suspicion; some caprellid amphipods were rejected for both these reasons. One of the caprellids, as well as a balanomorph cirriped (unknown from abyssal depths) was fouled with a colonial hydroid. The hydroid was discarded for this as well as the following reason:

Use was made of the fact that the sample was processed in two layers. While boundary effects might drag occasional epibenthic forms down into the lower layer, one would not expect them to be found as abundantly there as near the surface. On the other hand, animals introduced through the sea-water system would be equally abundant in both layers, since about the same amount of water was used to wash both. This clue was useful in many decisions, particularly involving coelenterates.

SAMPLE SITES AND ENVIRONMENTAL SETTING

All sample sites were located by satellite navigation combined with computerized dead reckoning. For a reliable understanding of the community, during the cruise CLIMAX II we obtained as many replicate samples as possible. Ten 0.25 m² box core samples were acquired from two spots which were about 11 miles* apart (Table 1; Fig. 4). Samples H-14 to H-18 are closely clustered, and Samples H-3 to H-8 form a crude transect running northeast-southwest, with gradually decreasing depth. From all appearances, the samples are equally well collected.

The surface water at the CLIMAX II locality is the North Pacific Central Water Mass, a central gyre of North Pacific circulation (SVERDRUP, JOHNSON and FLEMING, 1942). Because of relative vertical stability, the existence of overall downwelling, and

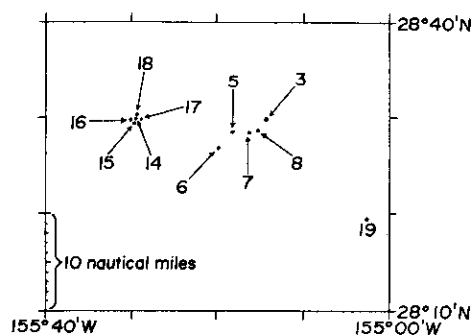


Fig. 4. Map of stations made on CLIMAX II cruise in the central North Pacific.

*1 nautical mile = 1.853 km.

Table 1. Station list. BC = 0.25 m² box core; Cam = tethered camera survey; ES = epibenthic sled (HESSLER and SANDERS, 1967); AD = anchor dredge (SANDERS, HESSLER, and HAMPSON, 1965). The 'H' in the station number indicates that the stations are part of the sampling program of Hessler.

| Station | Gear | Date | Latitude | Longitude | Depth (m) |
|---|------|------------|-----------|------------|-----------|
| Expedition CLIMAX II (SIO cruise 117-6), R.V. <i>Argo</i> | | | | | |
| H-3 | BC | VIII/21/69 | 28°29.9'N | 155°14.3'W | 5497 |
| H-5 | BC | VIII/22/69 | 28°28.6'N | 155°18.3'W | 5696 |
| H-6 | BC | VIII/22/69 | 28°26.7'N | 155°20.0'W | 5825 |
| H-7 | BC | VIII/22/69 | 28°28.6'N | 155°16.4'W | 5637 |
| H-8 | BC | VIII/23/69 | 28°28.7'N | 155°15.4'W | 5526 |
| H-14 | BC | IX/6/69 | 28°29.9'N | 155°29.5'W | 5615 |
| H-15 | BC | IX/7/69 | 28°29.6'N | 155°29.7'W | 5660 |
| H-16 | BC | IX/7/69 | 28°29.8'N | 155°30.0'W | 5631 |
| H-17 | BC | IX/7/69 | 28°29.9'N | 155°28.8'W | 5623 |
| H-18 | BC | IX/8/69 | 28°30.2'N | 155°29.3'W | 5654 |
| H-19 | Cam | IX/10/69 | 28°19.5'N | 155°02.3'W | 5678-5694 |
| Expedition SEVENTOW (SIO cruise 123), R.V. <i>T. Washington</i> | | | | | |
| H-29 | BC | VII/8/70 | 30°05.1'N | 156°08.5'W | 5899 |
| H-30 | ES | VII/8/70 | 30°05.0'N | 156°11.8'W | 6065-6079 |
| H-31 | AD | VII/8/70 | 30°03.5'N | 156°12.7'W | 6044-6056 |
| H-32 | BC | VII/9/70 | 30°04.1'N | 156°11.0'W | 6036 |
| H-33 | BC | VII/10/70 | 30°02.5'N | 156°13.1'W | 6040 |
| H-34 | ES | VII/10/70 | 30°00.6'N | 156°12.4'W | 6017-6029 |

the paucity of horizontal advective input, this water is low in nutrient chemicals. As a result, it possesses, along with other bodies of central gyre water in the world's oceans, minimal primary productivity, about 40 gC m⁻² yr⁻¹ (KOBLENTS-MISHKE, 1965).

The bottom is just south of the western end of the Murray Fracture Zone, in a region of abyssal hills with a relief of up to approximately 200 m, although it is often much less (Table 1). While steeper slopes may occur, slopes of about 2° seem typical. As a result, bottom photographs reveal little relief (Fig. 5). Sediment cover seems uniform, uninterrupted by outcrops.

The sediment of this area is a red clay (Fig. 5) studded with manganese nodules (Fig. 6). Only 0.1% of the non-nodular portion of the sediment is of sand size (<4 Phi), and consists of manganese nodule fragments, sponge spicules, radiolarians, foraminiferans, and detrital quartz fragments. Fifteen per cent of the red clay is silt, whereas the bulk (85%) is clay size.

Manganese nodules were found on the surface of every core (Fig. 3), but below the surface in only two cores, possibly as a sampling artifact. Maximum and minimum values for abundance of coarse clastics, primarily nodules, differed by a factor of 16 (Table 2). Although large-scale differences cannot be ruled out, much of this variation can be explained as small-scale patchiness (Fig. 6).

Most of the manganese nodules were flattened and oval in outline. Not uncommonly, such pebbles were fused. Larger nodules were proportionately thicker and more irregular in shape. Far less common were rounded, gravel-sized pumice particles, small irregular ash particles, shark teeth, and squid beaks, all with incipient manganese overgrowth.

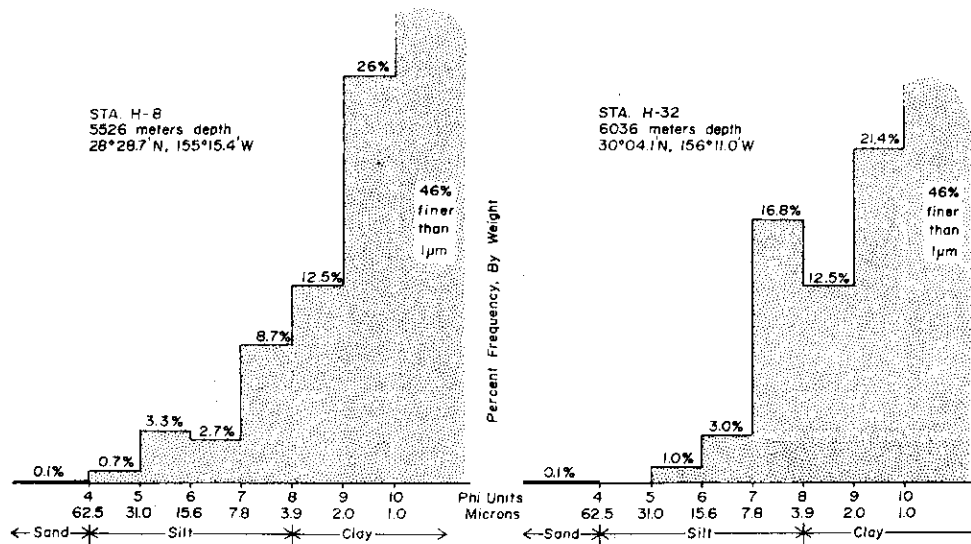


Fig. 5. Grain-size analysis of sediment from the top of a box core. Manganese nodules are excluded from this analysis. Silt-clay fraction analyzed by pipette method. Sand fraction segregated by wet sieving.

Table 2. Analysis of coarse clastics and of per cent organic carbon of the dry weight of fine clastics. All samples from CLIMAX II box cores.

| | Station | | | | | | | | | | |
|---------------------------|---------|------|------|------|------|------|------|------|------|------|-----------|
| | 3 | 5 | 6 | 7 | 8 | 14 | 15 | 16 | 17 | 18 | \bar{X} |
| Manganese nodules | | | | | | | | | | | |
| Wet weight (g) | 286 | 1268 | 648 | 1644 | 166 | 232 | 228 | 105 | 356 | 102 | 503.5 |
| Number | 138 | 127 | 56 | 171 | 29 | 28 | 11 | 11 | 23 | 15 | 60.9 |
| Volume (cm ³) | 136 | 568 | 315 | 797 | 82 | 117 | 118 | 51 | 187 | 50 | 242.1 |
| Weight/number | 2.1 | 10.0 | 11.6 | 9.6 | 5.7 | 8.3 | 20.7 | 9.6 | 15.5 | 6.8 | 10.0 |
| Shark teeth (number) | — | 1 | 2 | — | 1 | — | 1 | 2 | 2 | 1 | 1 |
| Organic carbon (%) | 0.22 | 0.31 | 0.29 | 0.23 | 0.25 | 0.22 | — | 0.22 | 0.27 | 0.27 | 0.25 |

The amount of organic carbon in the red clay was quite uniform (0.22–0.31 %).

Sedimentation rate in this portion of the Pacific is in the order of 1 mm (1000 yr)⁻¹ (MENARD, 1964).

No information is available for deep water characteristics at the precise CLIMAX II locality, but a deep hydro-cast was made 165 km to the north, to a depth of 5900 m, with the bottom only 120 m below that. The values obtained would seem to be a reasonable approximation for the whole area, considering the temporal and spatial uniformity of deep, open-ocean water masses. The values were as follows:

Temperature — 1.63°C

Salinity — 34.71‰

Oxygen — 3.71 ml l⁻¹

Phosphate — 2.37 µM.

This measurement for oxygen and phosphate should be treated with caution. As shown by KOCZY (1950) and in BRUUN (1957), there may be a considerable gradient in water properties just above the bottom.

In summary, the physical conditions in this environment are those of a typical deep-sea, oligotrophic environment as defined by SOKOLOVA (1965, 1972). Sedimentation rate is very low, as is the amount of organic carbon in the sediment ($\sim 0.25\%$). The sediment is well-oxidized red clay with manganese nodules and smaller concentrations of shark teeth and squid beaks. All these features result from the minimal surface productivity and horizontal advective input of organics, as well as the great depth of water, far below calcium carbonate compensation depth.

The depth of water, remoteness from land, and position in central oceanic gyre water all confer a high degree of temporal stability and spatial homogeneity on hydrographic physical factors, and probably on rate of nutritive input as well. These same considerations, in restricting the contribution of sediment almost completely to processes of pelagic sedimentation, result in a basically homogeneous sediment type. This homogeneity is reduced by the original ground plan of abyssal hills and proximity to the Murray Fracture Zone. In addition, the autochthonous formation of manganese nodules adds a degree of microenvironmental complexity as well as the possibility of large-scale differences in distribution of nodules. Clastics of volcanic origin do not seem important.

Subsequent to the CLIMAX II cruise, we revisited the central North Pacific Gyre on cruise SEVENTOW. At this time we made a transect of stations running from Hawaii to the Aleutians. Only one of the sites was in central gyre waters. The water was a little deeper than at the CLIMAX II locality, over 6000 m, but the bottom was a similar red clay with manganese nodules.

RESULTS AND DISCUSSION

Standing crop and general faunal composition

Table 3 lists the number of individuals of various higher taxa in each box core. The macrofaunal taxa of the ten cores are summed, and the resulting faunal composition listed as percentage of the total in Table 4. Polychaetes are by far the most abundant component, followed by tanaidacean crustaceans, bivalves and isopods. All the other taxa, in total less than 15%, each contain only 2% of the fauna or less. Excluding meiofaunal taxa, the ten samples yielded 21–40 individuals per 0.25 m^2 core (standard deviation = 6.38), which converts to 84–160 individuals per m^2 (average 115). Most of the major taxa are so sparsely distributed that they are either missing from most of the cores, or are represented by only one or two individuals. Only the polychaetes, tanaiids, and bivalves are present in all cores. In addition to these groups, only the isopods and scaphopods are present in more than half of the cores.

Some major taxa usually obtained in benthic samples are completely missing. Among the most noticeable absences are those of the amphipods, cumaceans, and echinoids. It is likely that these groups are present in this environment, but are sufficiently rare that they did not happen to be captured. Gastropoda and Holothuroidea, major taxa each represented by only one individual, and Ophiuroidea, represented by only two individuals, are so rare they might easily also have been missed in the sampling program. Thus, they illustrate the danger of attaching undue significance to the absence of taxa in these samples.

The macrofaunal numerical densities are in line with those of seven quantitative samples from the Sargasso Sea (Stas. JJ No. 1 to OO No. 2; SANDERS, HESSLER and

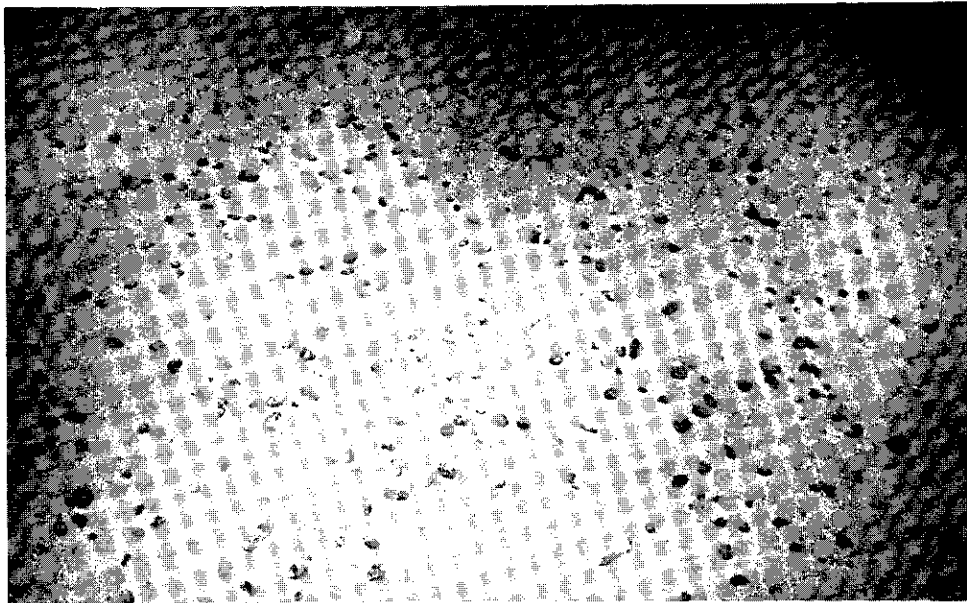


Fig. 6. The bottom at the CLIMAX II locality as seen in tethered camera lowering H-19, about 15 miles southeast of the box core station. All photographs taken during this lowering, as the ship drifted, showed the same type of bottom. The optical axis of the camera is approximately 45° from the horizontal. See Fig. 3 for an impression of the scale of this figure; the core box in that figure is 0.5 m on a side.

[facing p. 194]

Table 3. Faunal composition of ten 0.25 m² LIMAX II area, collected on SEVENTOW. Asterisk (*): minimum sum from statode sample was lost (see text).

| Macrofaunal taxa | 3 | | 5 | | | Total | | 29 | | 32 | |
|---------------------------|------|------|------|------|------|-------|------|---------|------|------|------|
| | ind. | spp. | ind. | spp. | spp. | ind. | spp. | ind. | spp. | ind. | spp. |
| Porifera | 1 | — | — | — | — | 3 | ≥2 | 1-2 | — | — | — |
| Cnidaria | 1 | 1 | 1 | — | — | 4 | ? | 1 | — | — | — |
| Polychaeta | 12 | 6 | 5 | 5 | 12 | 156 | 46 | 19 | 11 | 14 | 10 |
| Oligochaeta | — | — | 1 | 1 | 1 | 6 | 4 | — | — | — | — |
| Sipunculida | — | — | 1 | 1 | — | 1 | 1 | — | — | — | — |
| Echiurida | — | — | — | — | — | 1 | 1 | — | — | — | — |
| Tanaidacea | 6 | 5 | 5 | 5 | 3 | 52 | ≥17 | 8 | — | 10 | — |
| Isopoda | 1 | 1 | 2 | 2 | 2 | 17 | 16 | 2 | — | — | — |
| Aplacophora | — | — | — | — | — | 1 | 1 | — | — | — | — |
| Bivalvia | 4 | 2 | 3 | 2 | 1 | 20 | 7 | 2 | — | 1 | — |
| Gastropoda | — | — | — | — | — | 1 | 1 | 1-2 | — | — | — |
| Scaphopoda | — | — | 1 | 1 | 1 | 7 | 2 | — | — | — | — |
| Ophiuroidea | — | — | — | — | — | 2 | ≥1 | — | — | — | — |
| Holothuroidea | — | — | — | — | — | 1 | 1 | — | — | 1 | — |
| Bryozoa | 1 | 1 | 2 | 2 | — | 6 | 4 | — | — | 1? | — |
| Brachiopoda | 1 | 1 | — | — | — | 2 | 1 | — | — | — | — |
| Ascidiacea | — | — | — | — | — | 3 | 1 | — | — | — | — |
| Indeterminate | — | — | — | — | ≥1 | 4 | ≥2 | 6 | — | 1 | — |
| Total number | 27 | 18 | 21 | 20 | ≥22 | 287 | ≥108 | 40* | — | 28 | — |
| Number/m ² | 108 | — | 84 | — | — | — | — | 160* | — | 112 | — |
| <i>Meiofaunal taxa</i> | | | | | | | | | | | |
| Nematoda | 50 | — | 30 | — | — | 497 | — | > 482** | — | 43 | — |
| Copepoda | 13 | 9 | 3 | 3 | 15 | 120 | 57 | 82 | — | 8 | — |
| Ostracoda | 3 | 3 | 4 | 3 | 2 | 31 | — | 9 | — | 6 | — |
| Total number | 66 | — | 37 | — | — | 648 | — | > 573 | — | 57 | — |
| Number/m ² | 264 | — | 148 | — | — | — | — | > 2292 | — | 228 | — |
| <i>Meiofauna, number</i> | 2.4 | — | 1.8 | — | — | 2.3 | — | 14.3 | — | 2.0 | — |
| <i>Macrofauna, number</i> | — | — | — | — | — | — | — | — | — | — | — |



Table 4. Faunal composition (in per cent of total macrofauna) of the central North Pacific (CLIMAX II) compared to that of the Northwest Atlantic (SANDERS, HESSLER and HAMPSON, 1965). Percentages whose differences are not significant at the 95% confidence level are underlined in common.

| | | Northwest Atlantic | | Central North Pacific |
|------------------|-------------|--------------------|----------|-----------------------|
| | | < 4000 m | > 4000 m | ~ 5600 m |
| | Porifera | < 0.1 | 0.2 | 1.1 |
| | Cnidaria | 0.5 | 0.5 | 1.4 |
| | Polychaeta | 70.4 | 55.0 | 55.1 |
| | Oligochaeta | 0.7 | — | 2.1 |
| | Sipunculida | 5.8 | 4.5 | 0.4 |
| Priapulioidea | Echiurida | ≤ 0.1 | — | 0.4 |
| Nemertina | → | 0.9 | 0.6 | — |
| Pogonophora | Tanaidacea | 1.6 | 19.2 | 18.4 |
| | Isopoda | 1.0 | 12.1 | 6.0 |
| | Amphipoda | 4.1 | 1.5 | — |
| Cumacea | → | 0.1 | 0.2 | — |
| Misc. Arthropoda | Aplacophora | 0.6 | 0.3 | 0.4 |
| | Bivalvia | 13.0 | 4.2 | 7.1 |
| | Gastropoda | 0.3 | 0.6 | 0.4 |
| | Scaphopoda | 0.5 | 0.2 | 2.5 |
| | Ophiuroidea | 0.3 | 0.8 | 0.7 |
| Asteroidea | Echinoidea | 0.1 | 0.2 | — |
| Crinoidea | → | 0.3 | — | 0.4 |
| Holothuroidea | Bryozoa | > 0.4 | — | 2.0 |
| | Brachiopoda | — | — | 0.7 |
| | Asciacea | ≤ 0.1 | — | 1.1 |

HAMPSON, 1965). The latter are somewhat shallower (4540–5001 m), but are from similarly unproductive gyre waters, and are from silt-clays of similarly low organic carbon content (0.24–0.34%). The standing crops of the abyssal Sargasso Sea samples are 33–264 individuals per m² (average 109.4). ROWE (1971) compares standing crop with depth from a variety of localities: Sargasso Sea, off equatorial Brazil, Gulf of Mexico, and off Peru. All of the samples from deeper than 4000 m have standing crops within the range already mentioned, except for one from 5750 m off Peru. This had only 5 individuals per m², perhaps due to the fact that it was collected with a grab and washed with a 550 μm screen whereas all the rest were collected with an anchor dredge and washed with a 420 μm screen.

Even though the 297 μm screen used for washing was much too coarse to yield a complete sample of meiofaunal taxa, these components are present in reasonable abundance, with nematodes, copepods and ostracods always being present (Table 3). The nematodes are by far the most abundant, followed by copepods. They comprise 53 and 13% of the total metazoan fauna, respectively, thus being the first and third in numerical abundance, in spite of their incomplete representation. Summing the ten cores, the combined meiofaunal taxa average 2.2 (range: 1.5–3.9) times more numerically abundant than the macrofauna, although their relative biomasses might show very different ratios (WIGLEY and MCINTYRE, 1964).

Meiofaunal animals which seem to be as abundant as the nematodes are the testaceous, rhizopod Protozoa, including the Foraminifera and probably the Xenophyophorida (LOEBLICH and TAPPAN, 1964; TENDAL, 1972; HESSLER, in press). Unfortunately, it is still not possible to enumerate the abundance of these taxa because of the problem of discriminating living from dead tests, and because those species whose chambers or branches are delicately connected to each other are often broken and therefore hard to count. In the case of the abundant, small clusters of branching and sometimes anastomosing tubules which we are tentatively calling xenophyophoridans, we are still not able to determine whether any were alive upon capture. For these reasons, the protozoans we collected are excluded from the consideration of standing crop.

Nevertheless, the tests of living and dead foraminiferans combined are extremely abundant, involving 135–1808 individuals or chamber-fragments (average 759.8) per core. Agglutinating species overwhelmingly dominate the fauna. Of the total list of up to 54 tentative species (average 40.1) in these cores, 40 were almost exclusively limited to the top 10 cm. The other 14 species, which dominated the foraminiferan fauna of the 10–20 cm layer of the cores, were extremely robust and therefore likely to be preserved.

In spite of uncertainty about the amount of the total foraminiferan fauna that was alive upon capture, there is some evidence to support the idea that living foraminiferans are abundant. One species whose living protoplasm can be seen through the test is never found as dead remains, the matrix of the test apparently being quite susceptible to decay. This species is present in abundances of up to 40 individuals per 0.25 m² (average 15). This quantity far exceeds the abundance of any metazoan species.

Trophic composition

The polychaetes were chosen for an analysis of feeding types because of their numerical dominance. Gut contents were cursorily classified by clearing whole specimens in glycerol at the time they were being sorted to species. These data were combined with published information on feeding mechanisms and with observations on morphology to give an assessment of feeding types and their relative abundances (Fig. 7). The analysis is admittedly subjective, but does bear out a few salient points.

The distribution of individuals among species is roughly logarithmic. Four species make up over half the total polychaete individuals in the twelve CLIMAX II and SEVENTOW cores. The most (*Chaetozone* sp., 18.5%) and the least (*Tharyx* sp., 6.0%) abundant of these four are cirratulid polychaetes whose guts are invariably full of mud. Second in abundance is a capitellid (15.8%), another deposit feeder which always contains mud. Third is a fauveliopsid (*Flabelligella* sp., 11.4%) which sometimes has an empty gut, though usually has a few pieces of pelletized mud in the hindgut.

Cirratulids burrow sluggishly just beneath the sediment surface (DAY, 1967), and capitellids also burrow (DALES, 1963). Because Fauveliopsidae seem to be limited to deep water, very little is known of the habits of *Flabelligella*. Next in abundance come paraonids and spionids. These groups are shallow-burrowing detritus feeders (DAY, 1967), and our representatives are always found with abundant mud in the gut. In fact, every detritus feeder found in the 12 cores appears to fall into the category of a creeping or actively burrowing deposit feeder. Potential exceptions to this generalization are two species of Sabellidae, but both of these belong to the subfamily Fabricinae, some of whose members retain the primitive, well-developed palps and creep actively about the

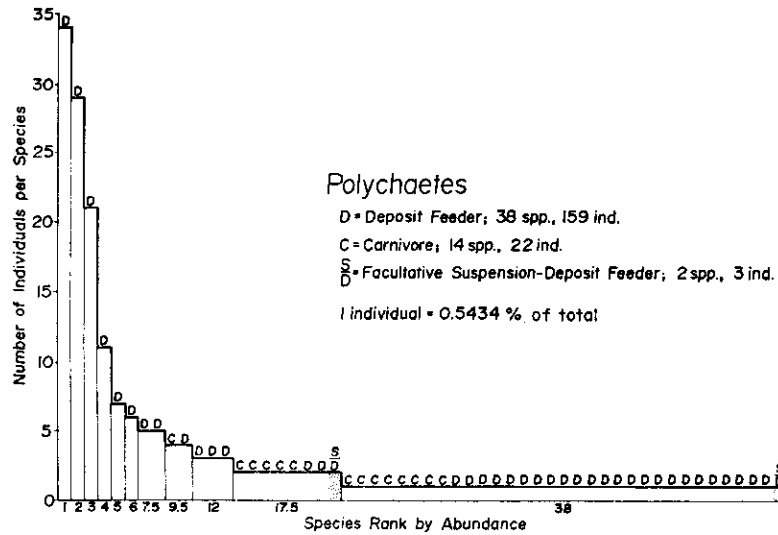


Fig. 7. Histogram of trophic composition of the polychaete fraction of the fauna for the total of 12 cores from the CLIMAX II and SEVENTOW cruises. Species placed in decreasing rank order of abundance.

sediment surface (DAY, 1967). Thus, these apparent exceptions may be facultative deposit and suspension feeders.

No obligate suspension feeders were found in the cores. Therefore, their maximum abundance cannot be more than 3 per 3 m² (at the 95% confidence limits assuming a Poisson distribution). Similarly, no sedentary deposit feeders (Ampharetidae, Terebellidae, or Trichobranchidae) were recovered from the cores. However, the epibenthic sled samples do reveal the presence of serpulids, ampharetids, terebellids and trichobranchids. The first of these families contains sessile, tube-building suspension feeders, and the other three contain sedentary, tube-building surface deposit feeders (DALES, 1963).

Thus within the Polychaeta of the central gyre benthos, more or less actively burrowing or creeping deposit feeders overwhelmingly predominate. Carnivores are numerically the next most important feeding type. Finally, sessile, tube-dwelling suspension feeders and sedentary, tube-dwelling deposit feeders together must comprise ($p > 0.95$, ROHLF and SOKAL, 1969, p. 212) less than 3% of the number of polychaete individuals.

The rest of the fauna also shows dominance of deposit feeders. With these we do not attempt to discriminate between detritus feeders, scavengers, or carnivores, but simply tabulate the number of animals that are definitely or possibly suspension feeders. Only six of the other major taxa from our central gyre cores contain species which are potential suspension feeders. These are the Porifera, Cnidaria, Echiurida, Bryozoa, Brachiopoda and Ascidiacea. Adding to these the two sabellid polychaete species mentioned above, the total count of potential suspension feeders is 24–26 individuals, or about 7% of the total fauna. The remaining 93% are deposit feeders (Table 4). While biomass was not measured, we estimate it would yield comparable ratios.

At first glance these findings appear incompatible with those of SOKOLOVA (review

in 1972) who has divided the deep benthos (3000–6000 m) into two regions, the eutrophic and oligotrophic zones, based on an extensive study of faunal distributions, particularly in the Pacific Ocean. Her maps of the distributions of many different kinds of benthic invertebrates show that certain types are rarely taken in the central waters of major oceans (North Pacific, South Pacific, Indian, etc.), even though they are characteristic members of samples from waters closer to the continents (several families of Asteroidea, Ophiuroidea, Echinoidea, Holothuroidea, Bivalvia, and Decapoda—all basically deposit feeders or carnivores). Other taxa, all suspension feeders, are found no matter where the sample is taken (Porifera, serpulid Polychaeta, Brachiopoda, and perhaps scalpellid Cirripedia).

The apparent disappearance of carnivores and detritivores accompanies a general decrease in benthic biomass, one which is reflected in a decrease of suspension feeders as well. On bottoms around the perimeter of the oceans and in equatorial waters, where standing crop is relatively high, deposit feeders overwhelmingly dominate the community, and carnivores comprise a significant fraction. It is on the deeper bottoms of central gyre water masses, where standing crop is very low, that suspension feeders are in the majority.

Total standing crop is thought to be dependent primarily on the rate of food supply (e.g. SANDERS and HESSLER, 1969). In the broad ocean margins and in equatorial waters, primary productivity is highest, and in the former, the contribution of food from terrestrial runoff is at its maximum. On the other hand, in the central gyres, primary productivity is much lower, and contribution of food through horizontal advection is minimal. In addition, the great depth of water further reduces the chances that a nutritious particle will reach the bottom. Because of these differences in rate of food supply, Sokolova uses the words eutrophic and oligotrophic to label the detritivore- and sestonivore-dominated communities.

Eutrophic and oligotrophic regions can be recognized on physical grounds as well. Sedimentation rate is much higher on the former because of higher surface productivity or continental outwash, and thus biogenic oozes or terrigenous sediments predominate. In central oceanic waters of the oligotrophic zone, sedimentation rate is very low, and sediments tend to be red clays with manganese nodules, although there may be calcareous oozes (SOKOLOVA, 1972).

Oligotrophic bottoms contain a low percentage of organic carbon, a low biological oxygen demand, and are deeply oxidized. These facts lead Sokolova to believe that because of the low sedimentation rate, only refractory organics are buried in the sediments. Thus in her view the sediment is not sufficiently nutritious to support any but the most selective deposit feeders, ones which can limit ingestion to the thin surface layer. Presumably organic particles still in suspension are more nutritious, and suspension feeders persist.

On eutrophic bottoms, organics which are still nutritionally labile are supposedly buried as a result of the higher sedimentation rate, thus creating conditions conducive to the maintenance of a broad spectrum of deposit feeders. This explanation seems inadequate. Except under conditions of slumping or turbidity flows, sedimentation rates in the eutrophic zone are fractions of a millimeter per year. It is difficult to believe that a labile organic particle would escape surface feeders under such conditions or would remain immune to bacterial action for so long, even given the slow decay rates suggested by JANNASCH and WIRSEN (1973). It seems more likely that it is the unwitting

activity of organisms that carries labile organics below the surface to make them available to subsurface feeders.

Furthermore, it seems unlikely that many of the detritivores Sokolova mentions are truly subsurface feeders. Rather, they feed on the surface layer and somewhat below it. Their problem becomes one of accuracy in that their mode of feeding is not precise enough to allow them to limit ingestion to just the rich surface layer. Thus, under oligotrophic conditions, the energy required to acquire and process their food is more than they could derive from it.

A variation in this explanation would suffice to account for Sokolova's reported reduction of carnivores in the oligotrophic region. In regions of such low standing crop, the expense of the search is too high compared to the nutritive value of the sparsely distributed prey. Under these circumstances, one would expect carnivores to be generalists, in order to reduce search time to a minimum (MACARTHUR, 1972). This, indeed, seems to be the case. SOKOLOVA (1957a, 1957b) and LITVINOVA and SOKOLOVA (1971) have enumerated the gut contents of a variety of decapods, asteroids and ophiuroids. While one may wonder whether it would not be more appropriate to regard these animals as facultative scavengers than as carnivores, it does not negate the fact that these animals are feeding on benthic macrofauna, and that the gut contents typically contain a broad spectrum of taxa, even at the level of phylum.

This concept of an oligotrophic region in which suspension feeders dominate is perplexing. Samples from the Gay Head-Bermuda transect yielded the same preponderance of deposit feeders in the seemingly oligotrophic Sargasso Sea as in samples from the more coastal deep sea. The data provided no substantiation for Sokolova's point of view. Sokolova (in ZENKEVICH, 1969) clarified the issue by pointing out that her conclusions only apply to the 'large benthic animals' one would catch in a trawl. Such animals are too sparsely distributed to be caught by grab samplers, or by inference, the anchor dredge or epibenthic sled, both of which process relatively small areas of the bottom. The latter devices are best for collecting what Sokolova calls the 'meiofauna'—animals passing through a 5.0 mm screen, but catching on a 0.5 mm mesh. This size class is, of course, more usually regarded as the macrofauna and roughly coincides with the faunal segment being considered at Woods Hole and herein. Animals in this size category are primarily deposit feeders, even in the oligotrophic zone, the explanation being that their smaller size makes them more efficient at concentrating on the richer surface layer. Sokolova's inclusion of serpulid polychaetes and brachiopods in the trawl analyses in spite of their usually small size is presumably related to their habit of encrusting larger objects, such as nodules.

The relative proportions of subtaxa within the Crustacea and Bivalvia change along the Gay Head-Bermuda transect (SANDERS, HESSLER and HAMPSON, 1965). In the crustaceans, amphipods comprise a rapidly diminishing percentage of the total numbers, going into the abyss. On the other hand, isopods increase in importance. The biggest proportional increase is in the tanaids, which do not appear in the shelf samples, but dominate among the crustaceans in the Sargasso Sea samples. Bivalves show a similar pattern, with eulamellibranchs dominating in the shallow continental samples, but decreasing in importance in the Sargasso Sea, accompanied by a corresponding increase in protobranchs.

Similar changes in the relative ratios of some macrofaunal components at a higher taxonomic level can also be demonstrated. Table 4 splits the Gay Head-Bermuda

transect samples of SANDERS, HESSLER and HAMPSON (1965) into those from shallower or deeper than 4000 m. The dividing point coincides with the position of the Gulf Stream and thus offers the best division between the oligotrophic Sargasso Sea and the eutrophic coastal waters. Station II No. 2 is excluded from this analysis because the large number of opaque pogonophoran tubes renders a calculation of the total macrofauna impossible. The four Bermuda Slope samples are also eliminated from consideration because of the possible confusion that would result from their being in oligotrophic waters, yet from shallow depths. In the oligotrophic waters, polychaetes are distinctly proportionately less important, as are the bivalves and amphipods. The increasing importance of tanaids and isopods is responsible for this shift.

Interestingly, the relative proportions of the major taxa under the central North Pacific gyre are similar to those of the Sargasso Sea (Table 4). Such changes may be a general trend of differences between deep eutrophic and oligotrophic zones. The general importance of tanaids or isopods in SOKOLOVA's (1970) transitional and oligotrophic macrofaunal (= her 'meiofaunal') samples is suggestive of this as well. While not enough is known of the biology of these organisms to explain these changes, it seems reasonable that they are in response to trophic conditions. Most of the taxa involved in this shift are mainly deposit feeders in both eutrophic and oligotrophic zones, so the cause of the shift must be at a more subtle level.

The question remains whether megafaunal deposit feeders, animals of the size collected in trawls, are indeed essentially absent in the oligotrophic zone. At least one segment of this trophic class, the scavengers, has not disappeared. Benthic trawling is notoriously ineffective at catching active swimmers. Therefore, the usual absence of such animals from abyssal samples such as Sokolova's should not be regarded as an accurate reflection of the real situation.

The baited, time-lapse Monster Camera (ISAACS, 1969; DAYTON and HESSLER, 1972; HESSLER, ISAACS and MILLS, 1972) sheds light on the contribution of mobile scavengers. In the coastal eutrophic waters of Southern California, a variety of organisms are attracted to the bait: brachyurans, polychaetes, octopods, asteroids, amphipods, natantian decapods, and a variety of demersal fishes. These scavengers quickly consume the bait. Oligotrophic gyre waters reveal a similar pattern. After a few hours, the density of scavengers is remarkably high, even though their numerical density under unbaited conditions must be quite low, as documented by the rarity of such creatures in photographic surveys.

In oligotrophic waters, it is only swimming forms that appear at the bait: fish, natantian decapods, and amphipods. Absent are the ambulatory taxa seen in eutrophic coastal waters. These are precisely the taxa whose disappearance in the oligotrophic is noted by Sokolova. We suggest that the absence of large facultative scavengers in oligotrophic waters is a result of their ambulatory mode of life. The low rate of food supply in oligotrophic waters dictates sparse population densities. Hence, the likelihood of a large nutritious particle becoming available within short walking distance is very low. More distant particles, even if they were detected by an ambulatory scavenger, would remain unavailable; by the time it reached the site, the food would be gone—consumed by the more mobile scavengers.

Thus, ambulatory megafaunal deposit feeders are at a double disadvantage in the oligotrophic zone. The general sediment is too low in organic content to allow them to prosper, and large nutritious particles are too sparse to be reached in time. Natatory

megafauna would be at the same disadvantage regarding general deposit feeding, but they are ideally suited for utilization of the rare, large organic particles. We suspect their strategy is to remain relatively dormant during the long intermediate periods when no food is available, thereby conserving energy. When the stimulus of food is borne to them by the ubiquitous tidal currents, they become active. In this way, a low food supply would suffice to support them.

Spatial distribution

The most obvious feature of the distributional patterns of the encountered species is rarity. Of the 108 macrofaunal species in the ten CLIMAX II cores, 67 were encountered only once. In all probability, then, the typical species in this environment has an abundance of less than one individual per 2.5 m². In considering this statistic, one should remember that a typical individual is less than 0.5 cm in length and has an ambulatory mode of life. Little else can be said about distributional patterns when only a single individual is found.

Forty-one species in the macrofaunal taxa, 22 species in Copepoda, and six species in Ostracoda were encountered at least twice in the ten cores. However, only one polychaete species (six individuals, $p < 0.001$) and two tanaid species (four and three individuals, $p < 0.001$, $p < 0.01$, respectively) fall outside the 95% confidence limits for the index of dispersion (s^2/\bar{x}) from a Poisson distribution of individuals among samples. All three of these species deviate from expectation by having a high variance, that is, by being aggregated.

Apparent aggregation can be produced either by 'patches of individuals dispersed over otherwise empty ground' or by gaps in an otherwise random distribution of individuals (PIELOU, 1969, p. 105). The high variance for each of the three species is due to examples of the former case, specifically to a single core with a higher-than-expected number of individuals. Potential causes of these patterns include reproduction without a completed dispersion, movement into an area with higher food abundance, intraspecific social interaction, or some combination of these and other factors (HUTCHINSON, 1953). The existence of only one 'patch' per species makes the conclusions from any closer analysis tenuous. The three aggregated species are not numerically important (14 individuals total). One hundred and seventy-three of the 176 analyzed species fit the Poisson model.

However, species distributions are not independent of each other. Only four species have a sufficiently high frequency of occurrence (> 0.5) for meaningful correlation analysis—three polychaete species (*Chaetozone* sp., a capitellid species, and *Flabelligella* sp.) and one harpacticoid copepod species. None of these species considered alone departs significantly from the Poisson model of distribution among cores. The Kendall concordance procedure (TATE and CLELLAND, 1957), however, shows that these four species are concordant ($W_c = 0.47$, $p \ll 0.01$); where one species is abundant, so are the others, and where one species is rare, so are the rest. Similarly, when species are grouped into higher taxa, these groups prove to be concordant; Polychaeta, Harpacticoida, and Nematoda all agree where to be abundant ($W_c = 0.66$, $p \ll 0.01$). The same pattern is evident for combined macrofaunal and combined meiofaunal taxa (Table 3). The abundances of the two groups are strongly positively correlated (rank-difference correlation, *op. cit.*; $r_a = 0.70$, $p < 0.05$). All these correlations are not due simply to the four most abundant species; the number of macrofaunal species per core is strongly

positively correlated ($r_d = 0.67$, $p < 0.05$) with the number of macrofaunal individuals per core. The result of this covariance is a strongly aggregated distribution of the total numbers of individuals per core.

An apparently aggregated distribution of individuals among samples can be produced by randomly locating samples along a simple gradient of abundance (GREIG-SMITH, 1964). Such a gradient might be expected with depth or with geographic distance from a given point. Distances between pairs of cores and differences in depth of water over cores fail, however, to correlate with the JACCARD (1912) coefficient of similarity or the per cent similarity of the polychaete fraction in pairs of the cores. Furthermore, the average similarity between pairs of samples within a geographic cluster (Fig. 4) is no different from that in pairs between the two clusters. Nor is there any statistically significant correlation between faunal numbers and abundances of nodules, although sessile forms such as brachiopods may be limited to nodule surfaces. Per cent organic carbon in the sediment also fails to correlate with numerical abundances of macrofauna or meiofauna.

We cannot rule out the possibility that the apparent patchiness of the fauna is due to variable sampling efficiency during the coring process. However, the three species which show aggregation are not aggregated in the same core. On the other hand, of all the major taxa, the molluscs show the least tendency toward aggregation. One might expect the shelled forms to be less susceptible to displacement by the corer's bow wave than are the other, generally lighter-bodied animals. If, however, the apparent aggregation in total numbers of individuals is due to sampling bias, the individual species distributions must in actuality be more evenly dispersed than we indicate, and it is difficult to conceive of an effective spacing mechanism in such small, sparsely distributed animals.

Consideration of species distributional patterns is important in the placement of confidence limits around population estimates and with the evaluation of spatial segregation of potential competitors as a mechanism for maintaining diversity (DIAMOND, 1973) in the deep sea. In the latter regard, our evidence is entirely negative; samples on this scale give no reason to suspect that spatial segregation is an important factor in maintaining the diversity observed.

Diversity

Diversity values are strongly dependent on sample size, particularly with low numbers of individuals (SANDERS, 1968; HURLBERT, 1971; DEBENEDICTIS, 1973). Clearly, in the present situation, where the standing crop is extremely low, and where the ratio of individuals to species in a single sample is between one and two, this factor is critical. To minimize this problem, we have combined the CLIMAX II box core results to yield one large, artificial sample. The justification for this manipulation of the data is that the samples are all in such close proximity that all their localities could conceivably be traversed by two epibenthic sled hauls, and that the data provide no indication of being other than random samples from a single community. The resulting ratio of individuals to species, a little over three, indicates a somewhat better representation of the total fauna, but still one that is far from the saturation point, where addition of individuals does not increase species number.

In considering diversity, we have concentrated on the polychaetes and copepods because only these groups are present in sufficient abundance to permit meaningful

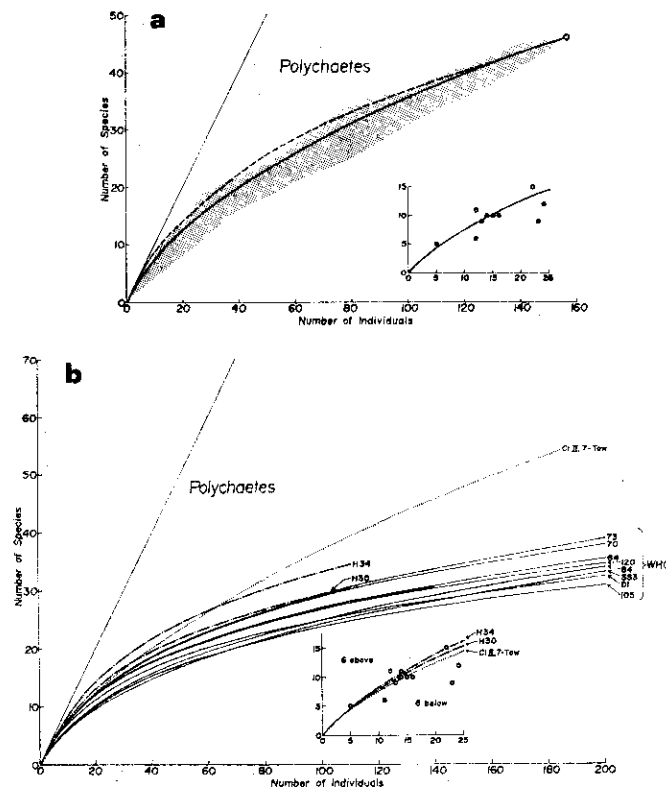


Fig. 8. a: Number of polychaete species versus number of polychaete individuals for the combined CLIMAX II box cores. Solid rarefaction curve produced by Hurlbert method; dashed curve by Sanders rarefaction; shaded area encompasses ten cumulative curves produced by combining the ten individual core contents in ten different random orders. The straight line plots the hypothetical condition of maximum diversity, where every individual belongs to a different species. The insert plots the observed numbers of individuals and species in each of the ten cores, in relation to the Hurlbert curve. b: Number of polychaete species versus number of polychaete individuals by the Hurlbert rarefaction method for the combined twelve CLIMAX II and SEVENTOW box cores, for two SEVENTOW epibenthic sled samples, and for eight Gay Head-Bermuda transect samples (HARTMAN, 1965; HARTMAN and FAUCHALD, 1971). Of the latter, SS3 and D1 were collected with an anchor dredge; the others involved an epibenthic sled. The insert plots the observed numbers of individuals and species in each of the twelve cores against the combined box core curve and to the two SEVENTOW epibenthic sled curves.

analysis. Figure 8a deals with polychaetes, using both SANDERS' rarefaction approximation (1968) and HURLBERT's (1971) more accurate formula for determining the number of species in a hypothetical smaller sample from the distribution of individuals among species in a larger sample. Hurlbert's method uses the maximum likelihood solution based on random selection from all the possible combinations to reveal the most likely number of species for a given sample size. Figure 9a shows analogous plots for the copepods.

In 1970, on Leg 7 of Cruise SEVENTOW, three box cores (H-29, H-32, H-33) and two epibenthic sled samples (H-30, H-34) were collected 90 nautical miles* north of the CLIMAX II locality (Table 1). Because H-33 was used for other purposes, it is not

*1 nautical mile = 1.853 km.

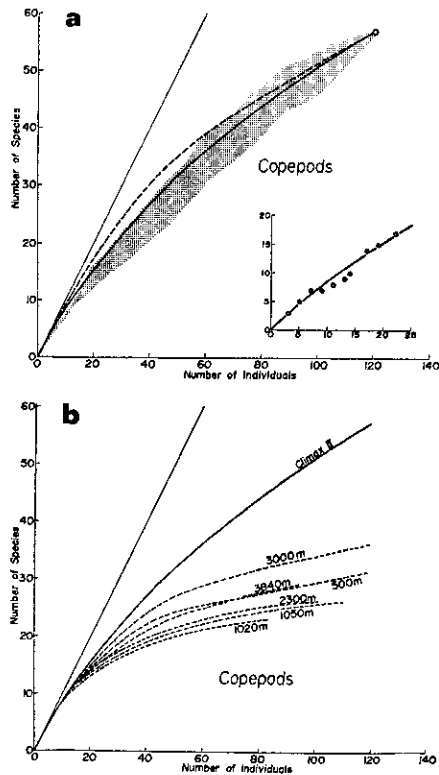


Fig. 9. a: Number of copepod species versus number of copepod individuals for the combined CLIMAX II box cores. Symbols as in Fig. 8a. b: Number of copepod species versus number of copepod individuals for the combined CLIMAX II box cores and for the Cape Hatteras transect data of COULL (1972, Fig. 1a). CLIMAX II curve (solid line) produced by Hurlbert method. Because Coull's paper did not include the data necessary to plot a Hurlbert rarefaction we use his Sanders rarefaction curves for the Cape Hatteras stations (dashed lines).

included in the present analysis. The depth of water, sediment type, and conditions of the water column are similar, as are the standing crops and proportional contributions of major taxa (Table 3). The polychaetes of these cores were compared to those of the CLIMAX II cores on the basis of the JACCARD (1912) and the per cent similarity indices. No significant difference was found, either in between-area or within-area comparisons. This result gives some justification for combining the data from both cruises.

We also compared the SEVENTOW sled samples to the summed CLIMAX II and SEVENTOW cores. The sled samples (Table 1) have a polychaete diversity generally lower than that of the cores (Fig. 8b). This difference may be explained through consideration of taxonomic composition. Only 1.6% of the 184 polychaetes in the summed cores were tube dwellers, as opposed to 30.9% of the 217 polychaetes in the sled samples. No reasonable explanation in terms of sampling bias of the box cores could account for a diminution of the number of tube dwellers. On the other hand, it is very likely that relative tube-dweller abundance is enhanced in the sled samples, where it is well known that winnowing selectively eliminates the delicate and unprotected forms (HESSLER and SANDERS, 1967). Conceivably, infaunal tube dwellers are also enhanced as

the sled mesh becomes partially clogged during sampling, as a result of a bow-wave effect. There is no way of distinguishing between the effects of these two potential biases in our samples. By whatever means, we conclude that the observed diversity of the sled samples is partially artifactual.

SANDERS (1968, 1969) has drawn many comparative rarefaction curves from a variety of deep- and shallow-water environments for the combined polychaete and bivalve subfaunas. The polychaete-bivalve diversity of the CLIMAX II area is higher than for Gay Head-Bermuda transect slope samples, and comparable to those from the shallow-water tropics (HESSLER, in press). Because of the artificiality of combining only certain taxa, in the present paper we restrict ourselves to comparison of individual taxa, specifically the polychaetes (Fig. 8) and copepods (Fig. 9). The polychaete data for the Gay Head-Bermuda transect are compiled from HARTMAN (1965) and HARTMAN and FAUCHALD (1971). The comparable copepod data come from the Atlantic Coast off North Carolina (COULL, 1972). In Figs. 8a and 9a, the envelope of curves generated by summing the box cores in ten different random permutations represents the actual way the species list increases with increasing sample size, but only with the assumption that the ten cores reflect the condition of ten contiguous samples. The Sanders rarefaction curve falls above the envelope for much of its length, because it overestimates the evenness component of diversity (HURLBERT, 1971). The Hurlbert curve lies within the envelope for most of its length, suggesting greater accuracy.

Graphical representation of the Hurlbert rarefaction modification is useful in several ways in addition to those suggested by Hurlbert. The slope of the curve (i.e. the rate of addition of new species with additional individuals) shows the evenness of the distribution of individuals among species. This slope equals one for the perfectly even case in which each additional individual represents an additional species; it equals zero for the case in which one species contains all the individuals.

If species are randomly distributed among samples, the Hurlbert curve derived from the sum of the samples should bisect the group of actual data points; the probability of the point defined by the number of individuals and species in a given core falling above the curve equals the probability of its falling below the curve. If a significant fraction (read from a table of binomial probabilities with $p \cong q \cong 0.5$) of the points falls above the line, species are evenly distributed among the samples, and if a significant fraction falls below the line, species are aggregated in their distribution among the cores. The latter case may imply that more than one habitat has been sampled. The inserts in Figs. 8a and 9a show that there is no reason to suspect other than a random distribution of species among the cores.

When the total numbers of polychaete individuals and species for the summed cores are used to generate a curve by Hurlbert's method, the diversity appears to far exceed that found on the Gay Head-Bermuda transect (Fig. 8b). However, as already shown, the higher diversity may largely result from biases in sled samples. A completely objective comparison between the Gay Head-Bermuda transect and the North Pacific gyre awaits the use of comparable quantitative sampling techniques in the two areas.

The copepod population from the CLIMAX II cores displays a much higher diversity than those of the Cape Lookout-Bermuda transect (COULL, 1972, Fig. 1a) (Fig. 9b). At 120 individuals (the total for the summed CLIMAX II cores), Coull's richest sample, from 3000 m, contained 36 species, whereas the summed CLIMAX II cores contained 57.

The difficulty with this comparison is that Coull washed his samples with a 62 μm screen as opposed to our 297 μm mesh. The coarser mesh passes young individuals of the species that are retained, thus artificially enhancing the diversity value. On the other hand, it also passes all the smaller species, thus depressing the measurement. Until further samples are collected, there is no way of knowing how these factors would balance out. Accepting for the moment our data at face value, we conclude that the samples display a very high diversity.

The high values seen in this study are, of course, completely compatible with hypotheses that stress environmental stability and predictability over long periods of time (SANDERS, 1969; DAYTON and HESSLER, 1972). However, while long-term environmental stability/predictability is a necessary prerequisite for high diversity, it is insufficient as a mechanism for its production or maintenance (BUZAS, 1972; GIBSON and BUZAS, 1973).

In considering high species richness along the Gay Head-Bermuda transect, HESSLER and SANDERS (1967) argue that the amount of food available to the community is not a determining factor or is at best easily masked by other aspects of the physical regime. For example, Samples WHOI 70 and 84, from the abyssal plain at the edge of the Sargasso Sea, have a species diversity as high as that of samples from the continental slope (WHOI D-1, S1-3, 105), as illustrated by the polychaetes (Fig. 8b), in spite of a much lower nutrient supply. The samples from the oligotrophic central North Pacific show even higher values.

Theoretically, the amount of available food should have some effect on community diversity (CONNELL and ORIAS, 1964). MACARTHUR (1972) points out that where food is more abundant, species can be more specialized, thus allowing more to coexist. Where total nutrient supply is low, certain categories of food are so rare that species which rely on those items could not persist. In effect, this is the explanation for the rarity of megafaunal, ambulatory scavengers in the oligotrophic zone.

Where food is absent, faunal diversity must be zero (MACARTHUR, 1972). Furthermore, where food is scarce to the degree that individuals of a population are so sparsely distributed that they cannot find each other for reproductive purposes, nutrient supply must have an effect on diversity. While these theoretical limits are sound, and may apply to specific taxa or life styles, it does not appear that total communities to which they apply have ever been studied, or perhaps even occur. The benthos of the deep-sea oligotrophic zone should be the most nutrient-poor, major community that exists (ephemeral and minor environments such as the face of a granitic outcrop are excluded from this consideration). Although the proportions of component taxa may be affected, its total faunal diversity shows no sign of food limitation.

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