

CLYDE F. E. ROPER
and WALTER L. BRUNDAGE, JR.

*Cirrate Octopods
with Associated
Deep-Sea Organisms:
New Biological
Data Based on Deep
Benthic Photographs
(Cephalopoda)*

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ABSTRACT

Roper, Clyde F. E., and Walter L. Brundage, Jr. Cirrate Octopods with Associated Deep-Sea Organisms: New Biological Data Based on Deep Benthic Photographs (Cephalopoda). *Smithsonian Contributions to Zoology*, number 121, 46 pages, 53 figures. 1972.—Twenty-seven photographs from seven deep-sea localities in the North Atlantic reveal cirrate octopods in their natural habitat. The photographs demonstrate that these octopods are benthopelagic, living just above the bottom at depths of 2,500 to greater than 5,000 m. Typical cephalopodan locomotion is exhibited as well as a drifting or hunting phase, and possibly a pulsating phase. Animals range in size from approximately 10 to 128 cm in total length, and up to 170 cm across the outstretched arms and webs. Scale size was determined mainly by a new technique termed shadow geometry, introduced here. Observations on shading (“coloration”) indicate the possibility of “reverse coloration” on some specimens. Cirrates are more abundant in the Virgin Islands Basin than in other areas sampled. Additional photographs of plant debris, animals and lebensspuren (evidence of organisms in the sediment) suggest that the abundance level of benthic and benthopelagic organisms is related to the presence of plant material of shallow-water origin.

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Cirrate Octopods with Associated Deep-Sea Organisms: New Biological Data Based on Deep Benthic Photographs (Cephalopoda)

Introduction

BACKGROUND OF STUDY

Cirrate or finned octopods are among the rarest and least known of all cephalopods. Not only are these deep-sea animals relatively rare in collections, but photographs of living specimens in their natural habitat have been nearly nonexistent. In November 1969, during a 9-day search mission aboard the USNS *Mizar* (T-AGOR-11), a total of at least twelve cirrate octopods was noted in a series of 20,000 exposures made by the Naval Research Laboratory (NRL) personnel. The purpose of the Navy mission was to conduct a photographic survey north of the island of St. Croix in the Virgin Islands Basin, Caribbean Sea, at depths of 1,900 to 2,200 fm (3,480 to 4,020 m) (Figures 1 and 2).

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¹Sea-floor photography has been practised by NRL for purposes of search and inspection since the loss of the submarine *Thresher* in 1963. Approximately 10⁶ photographs have been taken during missions in the North Atlantic Ocean and the Mediterranean and Caribbean Seas.

The cameras and other instruments which make up a precision deep-sea search vehicle¹ were towed from the *Mizar* at speeds of between 1 and 2 knots and at a nominal altitude above the bottom of about 5 m. The value of large numbers of bottom photographs from relatively small areas for assessing the environment and its inhabitants has been noted by Brundage et al. (1967).

A search through photographic files at NRL and several recent photographic cruises have produced additional photographs of specimens from the North Atlantic that now can be confirmed as cirrate octopods. Two of these photos, taken during the search for the *Thresher* and at the time unidentified, were published in Brundage et al. (1967, Figures, 6–19, 6–20). Two other finned octopods were photographed in the *Thresher* search area and other photos came from southwest of Bermuda, the Blake Basin and the Canaries Basin. The photographs were taken in depths that ranged from about 2,500 to 5,100 m. No octopods have been noted in NRL collections of photographs from shallower areas. Several additional underwater photographs of cirrate octopods have been brought to our attention by colleagues, some of whom supplied copies for use in this report (e.g., Figures 8, 28, and 30–33). Figures 30–33 were taken from the submersible *Alvin* at a depth of 1,300 m.

A lack of well-preserved specimens has led to a

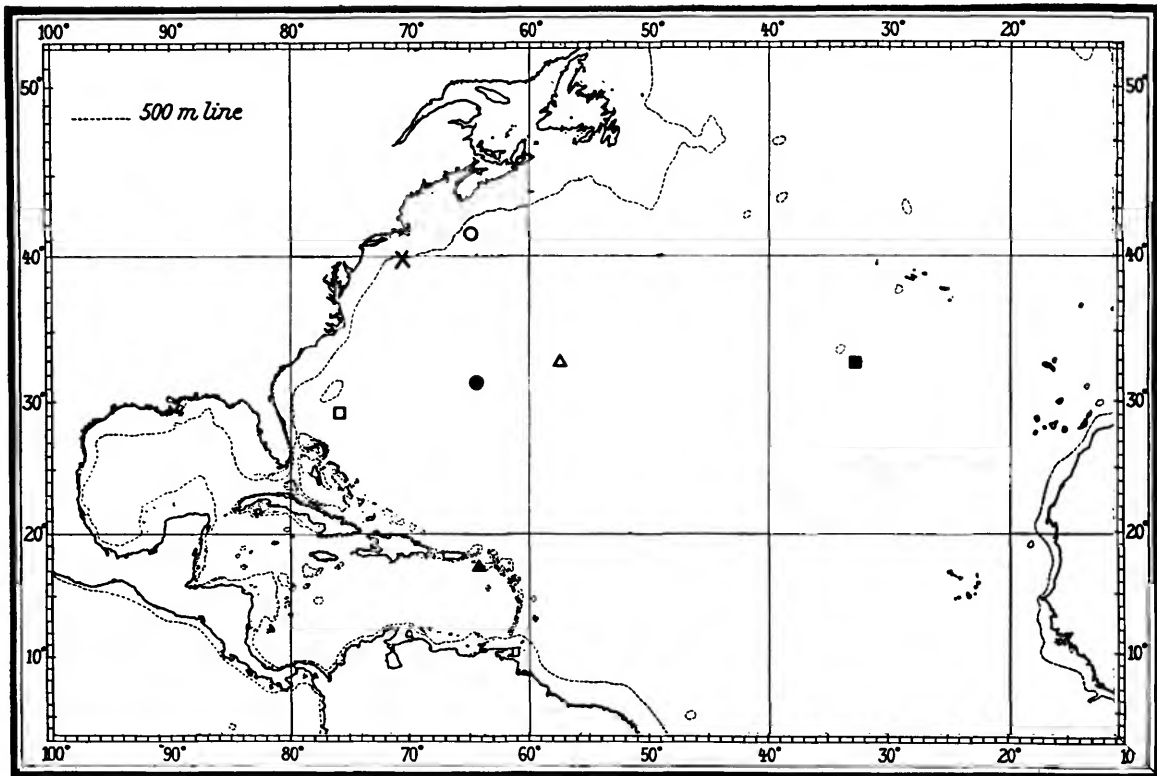


FIGURE 1.—Locations in the Atlantic Ocean of bottom photographs containing cirrate octopods (Figures 7 through 33).

- ▲—Virgin Islands Basin (VIB)
- Bermuda (BDA)
- Northeast Channel (NEC)
- Canaries Basin (CAB)
- Blake Basin (BLB)
- △—Sohm Abyssal Plain (SAP)
- X—Martha's Vineyard Slope (MVS)

present confusion in the literature concerning both the systematics and the biology of cirrate octopods. The unusual set of photographs presented here provides new information on the following aspects of the biology of these animals: habitat, depth distribution, locomotion, "coloration," size, and relative abundance.

In addition, a technique is discussed for calculating size and distance off the bottom of objects in deep-sea photographs.

LOCATION OF PHOTOGRAPHS

Virgin Islands Basin.—The majority of our photo-

graphs were taken in a small area at the bottom of the Virgin Islands Basin (VIB) in the vicinity of 17°52'N, 64°48'W (Figure 1).

The tracks of the towed camera vehicle ("fish") are indicated by fine lines in Figure 2. The hachures indicate areas of concentrated track coverage. Locations of the photographs of cirrate octopods are shown by numbers which correspond to figure numbers 7, 9, 14–20, 22, 23, 25–27. The numbers 34 and 35 locate two photographs of fish with corresponding figure numbers. A count was made of selected animals along a track located within the southwestern hachured area (see page 39). Figures 36 through 50, 52 and 53 were taken in that same area.

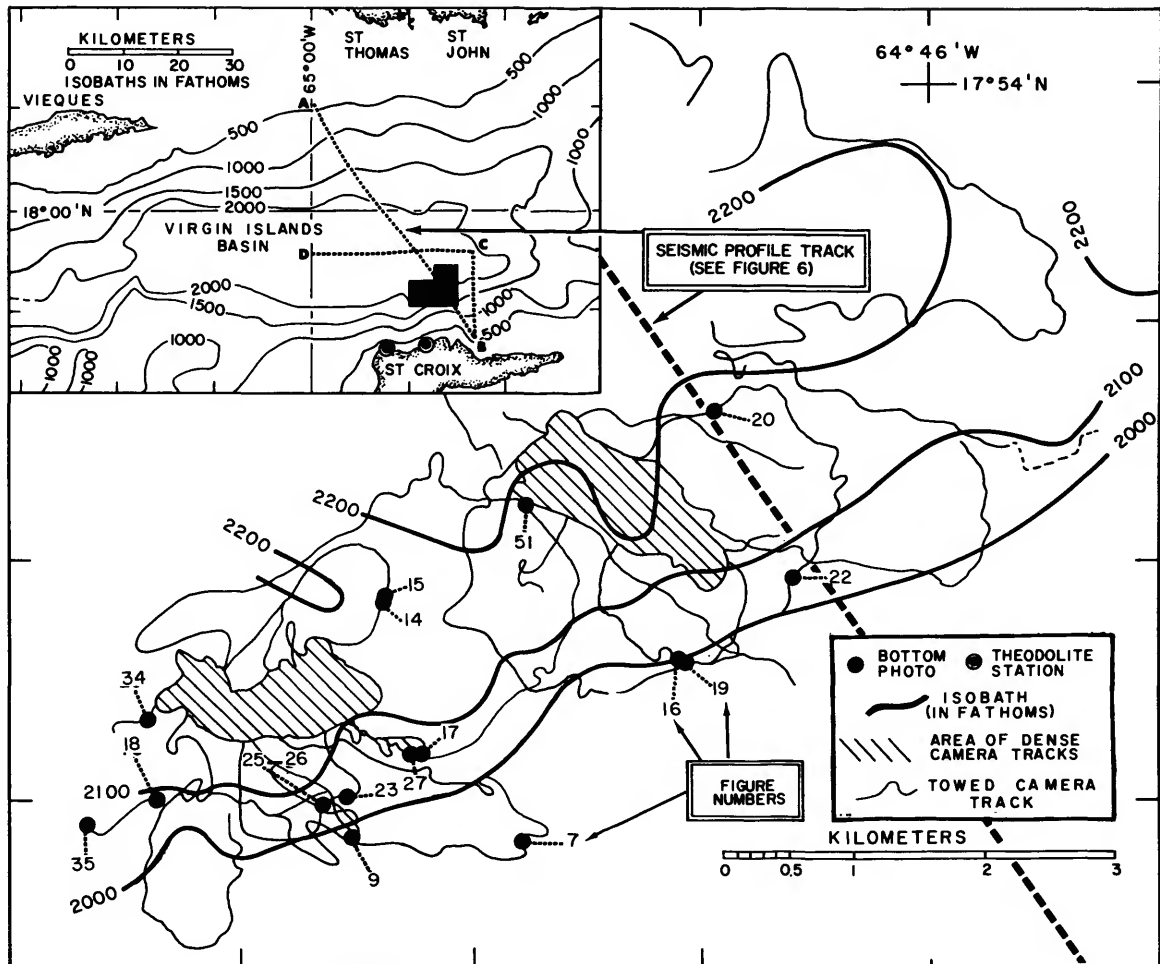


FIGURE 2.—Locations of bottom photographs in the Virgin Islands Basin. Thin lines indicate tracks of towed instrument vehicle which yielded almost continuous photographic coverage. Hachured areas represent dense concentration of tracks. Numbered symbols (except numbers 34 and 35) locate octopod photographs figured in this paper. Figures 36 through 50, 52 and 53 are confined to southwestern hachured area. Isobaths in fathoms (thick lines) developed from acoustic tracking data (see text). Thick dashed lines locate sections of seismic profile (see Figure 6). Inset chart adapted from Frassetto and Northrup (1957:139).

Mizar's surface navigation was obtained through a radio voice linked between the ship and two theodolite stations on St. Croix (see Figure 2, insert map). The location of the cameras relative to *Mizar* was obtained by an underwater acoustic tracking system (Andrews, 1965). The overall accuracy of location of the photographs is estimated to be ± 80 m. The isobaths were developed from the same data using a

harmonic mean sound speed of 4,950 ft/sec (1,509 m/sec).

A triangular array of three hydrophones mounted on *Mizar's* hull and a responder installed on the fish were the essential acoustic components of the tracking system used on this cruise (Figure 3). The computer-controlled system began a cycle when an electrical signal was transmitted down the coaxial towing

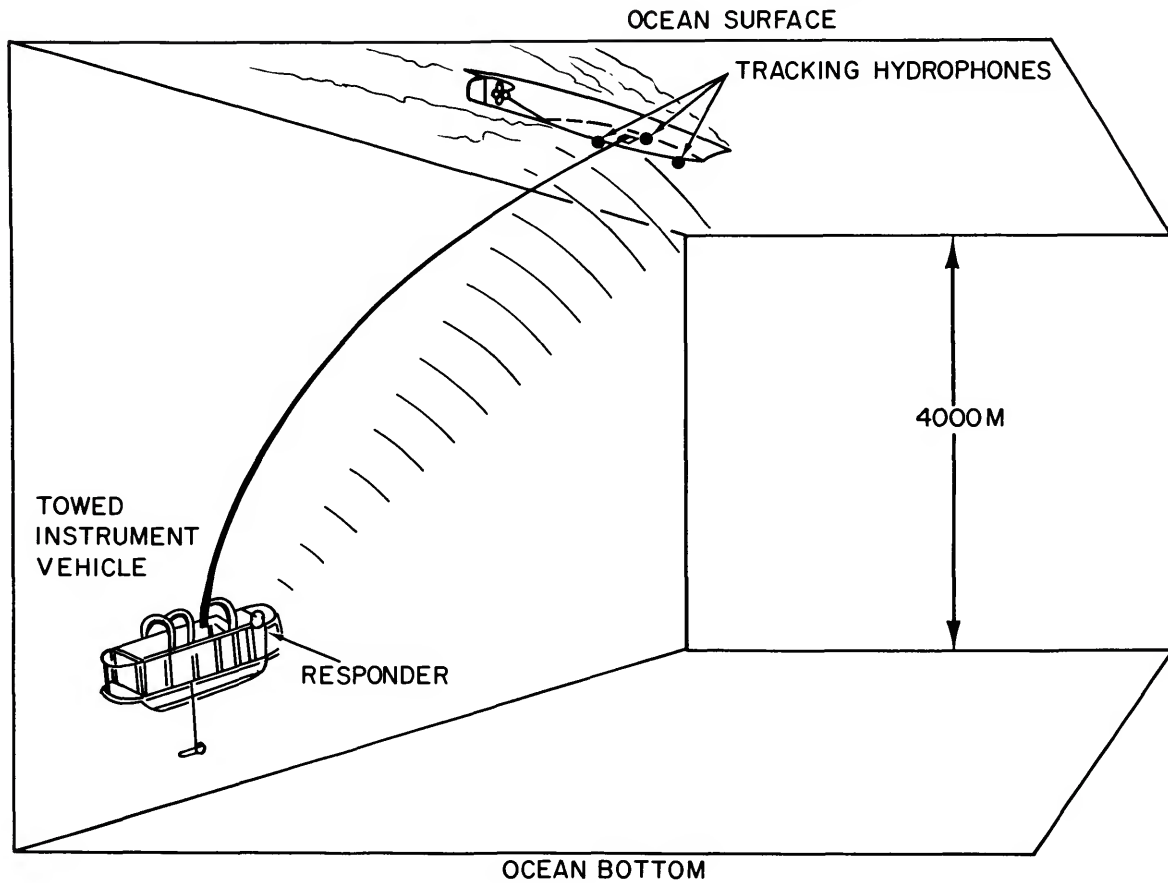


FIGURE 3.—Diagram of acoustic navigation system used to measure depth and to locate photograph with respect to ship which navigated precisely from theodolite stations on St. Croix (see Figure 2, inset). Electrical signal sent down coaxial towing cable initiates acoustic reply (upward expanding arcs) from responder on camera-equipped vehicle. Time of the interrogation (outgoing) signal and arrival times of reply at tracking hydrophones are processed by computer along with roll, pitch, and heading data to give location of towed vehicle in three dimensions.

cable to the responder on the camera vehicle. The automatic acoustic reply from the responder was received by the three hydrophones. Interrogation time and the times of receipt of the replies were processed by the computer, taking into account roll, pitch, and heading of the ship. This resulted in a print-out of the camera's N/S, E/W and vertical coordinates relative to the ship.

Other localities.—Other photographs come from scattered areas in the North Atlantic. A number of cirrates were photographed in the Blake Basin (BLB)

at about $29^{\circ}20'N$, $76^{\circ}W$. A single photograph was taken southeast of Bermuda (BDA) at $31^{\circ}43'N$, $64^{\circ}48'W$. Four photographs of cirrates were taken in the vicinity of Northeast Channel (NEC) at the base of the continental slope off New England at $41^{\circ}45'N$, $65^{\circ}W$, one was taken in the Canaries Basin (CAB) at about $33^{\circ}N$, $33^{\circ}W$, another was photographed on the Sohm Abyssal Plain (SAP) at $32^{\circ}42'N$, $57^{\circ}11'W$ and four exposures (one specimen) were obtained from the submersible *Alvin* on the continental slope south of Martha's Vineyard

(MVS) at 39°46'N, 70°32'W. These locations and the Virgin Islands Basin locality are shown by different symbols on the chart of the North Atlantic (Figure 1).

ACKNOWLEDGMENTS

We express our gratitude to a number of people who have helped measurably during the preparation of this report: C. L. Buchanan, NRL, for the opportunity to study and publish the majority of the photographs; V. J. Linnenbom, NRL, for two of the Blake Basin photographs (Figures 12 and 13); J. Lamar Worzel, Lamont-Doherty Geological Observatory, for the Figure 8 photograph; R. Bridge, J. J. Gennari, D. Clamons, F. Heemstra and H. Barnes, NRL, for aiding in the preparation of the navigation, bathymetric and scale data; G. L. Voss, Institute of Marine Sciences, Miami, for providing records of *Cirrothau-ma murrayi* and for attempting to trawl specimens in the Virgin Islands Basin; E. S. McSweeney, IMS, for supplying data and checking specimens; R. E. Young, Department of Oceanography, University of Hawaii for valuable suggestions concerning cirrate systematics and biology; D. Cohen, Systematics Biology Laboratory, Bureau of Commercial Fisheries, for discussions about the benthopelagic habitat and fauna and for identifying some fishes; N. B. Marshall, British Museum (Natural History); R. H. Gibbs, Jr., Smithsonian Institution; J. Nielson, Zoological Museum, Copenhagen, and E. Bertelsen, Denmark Fisheries, for identifying fishes and for discussions about deep-sea organisms; D. Stanley, Smithsonian Institution, and H. Ladd, United States Geological Survey, for information concerning the sediments; T. Bowman, Smithsonian Institution, for data concerning the habitats of certain deep-sea crustaceans; H. J. Humm, University of South Florida, for confirming the identity of the sea grasses and for the suggestion concerning *Laurencia*; G. Mead, Los Angeles County Museum of Natural History, for identifying the bathysaurid fish; J. Allen, Dove Marine Laboratory for comments on mollusk identities; H. L. Sanders, Woods Hole Oceanographic Institution, for information about the deep-living sea urchin *Echinus* in the Western Atlantic; and J. R. Brown, Naval Air Development Center, for the unpublished data on the movements of deeply moored buoy systems in the Virgin Islands Basin.

Additional photographs taken from the submersible *Alvin*, along with observations on the specimen, were kindly supplied by R. R. Hessler, Scripps Institution of Oceanography. We acknowledge B. C. Heezen, Lamont-Doherty Geological Observatory, C. D. Hollister, Woods Hole Oceanographic Institution, and Oxford Press for permission to publish a photograph from their book (our Figure 28).

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R. Gattton and M. Sweeney, Smithsonian Institution, prepared Figure 1 and provided technical assistance. R. Sibley and G. Baker of the Naval Reconnaissance and Technical Support Center assisted with the preparation of some photographs.

All or parts of the manuscript were read by C. L. Buchanan, R. H. Gibbs, Jr., J. B. Hersey, C. C. Lu, R. J. Menzies, J. Nielsen, W. Percy, R. Swim, G. L. Voss and R. E. Young. Their comments and criticisms were especially appreciated. The manuscript was edited and typed by Mrs. V. Macintyre to whom we express our thanks.

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Techniques

PHOTOGRAPHY

Cameras.—All of the NRL photographs in our study were taken with EG&G (Edgerton, Germeshausen and Grier) 35-mm cameras using the Hopkins water-corrected f 4.5 lens (Hopkins and Edgerton, 1961) or modified to accept a Kinoptic® wide-angle (WA) lens behind a hemispherical view port (Patterson, 1967)². The normal angle (NA) Hopkins lens covers an underwater field of approximately 34° by 48° compared with the WA lens which has an effective coverage of about 106° in a circular image. Lens apertures generally were set at f 4.5 on the NA and f 4 on the WA cameras. With the exception of Figures 10, 11, 13 and 18, which are oblique photographs, all exposures were made with vertically oriented cameras. Other obliques supplied by col-

² Use of trade names does not imply product endorsement.

leagues were Figures 8 and 28 taken with the Thorndike camera (Thorndike, 1959), and Figures 30–33 taken with standard EG&G cameras mounted on the submersible *Alvin*.

The WA camera does not have the resolving power of the NA camera but serves well in its capacity as a search tool. Fortunately, most of our photographs of Virgin Islands Basin cirrates were taken with NA cameras. Data frames are photographed simultaneously with each bottom image; one type of EG&G camera (model 207A) projects the data image of clock, frame count and written information directly through a portion of the photograph, resulting in occasional interference (e.g., Figure 7).

Lights and control.—Light for the photographs was supplied by two EG&G 250 watt-second electronic flash lamps located side by side at the trailing end of the “fish.” Remotely operated, deep-sea cameras normally function with open shutters, permitting the short duration (approx. 1 millisecond) flash to take the picture.

During the Virgin Islands Basin cruise the interval between photographs usually was 10 seconds for the NA camera and 30 seconds for the WA camera, a procedure which required a shutter on the WA camera. Separate control for the cameras was provided by signals telemetered (Buchanan and Isaacson, 1968) down the insulated core and coaxial shield of the towing cable.

Height (altitude) of the camera off the bottom was monitored with a 12 kHz acoustic pinger. The sonar signals were received at a hull hydrophone and displayed alongside remote winch controls on a precision depth recorder (PDR). Electrical analogs of the same signals were telemetered directly up the cable and displayed on a nearby oscilloscope. Undesirable altitude changes, therefore, could be rectified immediately. Extra long “pings” were registered on the PDR at the time each exposure was taken. Timing of all signals was controlled by a digital clock aboard *Mizar*.

Film and processing.—All cameras were loaded with black and white 35 mm Kodak Linagraph shellburst film which has a “qualified” ASA rating of 400. Development was carried out aboard *Mizar* using a two-bath developer (Diafine®) that tends to enhance image details near the edges of photographs where illumination is normally reduced (see Brundage and Patterson, 1966, Fig. 13).

PHOTOGRAMMETRY

Accurate scale is easily determined with a matched pair of (stereo) cameras aligned to form an overlapping field of view (Boyce, 1964; Pollio, 1969). Priorities established for the NRL-*Mizar* search camera system have rarely permitted the use of stereo; therefore other methods of measuring scale had to be worked out. The photograph in Figure 21 is one of a stereo pair, the only one presented in this study. The methods used to determine the 30-cm scale mark shown in the other photographs (Figures 7–53, except 28 and 30–33) are discussed below. The mark is shown at the midwater level of the octopods in photographs preceding Figure 30 and as a bottom scale in Figures 36–53. Because of a lack of information, scale could not be calculated for Figures 9, 14, 15, 18, and 31–35.

Known altitude.—Estimates of bottom scale in single photographs are usually based upon knowledge of the angle of view of the camera and altitude above the sea floor. Angle of view for a lens behind a flat port can be calculated from the simple relationship:

$$\tan x = 0.5b f^{-1} n^{-1}$$

where x is one-half the view angle, b is the image size on the film plane, f is the calibrated focal length of the lens in air and n is the index of refraction of the water.³ Altitude is more difficult to establish and usually entails correlation with simultaneously recorded acoustic data. Record matching is eased if the “blank ping” method of Hersey (1967:61) or some other system (see above) is used to mark the time of exposure directly on the acoustic record. Difficulties in reading the record often result in scale measurement errors of up to plus or minus 20% at the altitudes usually “flown.” This method was applied for Figure 51.

Known reference.—An accurate but usually fortuitous method of measuring scale makes use of an object of known size in the field of view. For example when a 34-cm-long EG&G model 260 compass is suspended from the camera vehicle it frequently strikes the bottom at the moment an exposure is made, thereby allowing establishment of scale. Such a compass appears in many photographs presented

³The typical index for sea water of 1.34 is accurate enough for these methods.

here and it was used to measure the scale in Figure 24. In Figure 12 the swimming octopod was scaled from the known sizes of the compass and magnetometer to either side of its position. White sea urchins⁴, so common in the *Thresher* search area, were measured on or near objects of known size and provided a secondary comparative scale (see Brundage et al., 1967: 77–78) because the population had a very narrow size distribution. This method was applied in Figures 8 and 11.

Non-stereo overlap.—Simultaneous photographs taken by non-stereo cameras can be used to accurately measure scale when the optic axes of the cameras are parallel. Displacement of the same object measured from the centers of each photograph is plotted as the known separation between the cameras. The method works best if the plane of reference is normal to the optic axes. This technique was applied in Figures 13, 25, 26 and 29.

Shadow geometry.—Relatively accurate scale in a single photograph can be determined from the position of a shadow cast by an object suspended in the field of view. Care must be taken to measure the light-to-camera distance and to place the suspended object so that its image will appear near the side of the photograph toward the light. In the typical arrangement shown in Figure 4, a 34-cm-long EG&G model 260 compass is suspended about 3 m beneath the vehicle.⁵ Light from a pair of flash lamps casts a double shadow (image) easy to distinguish at high altitudes. The distance between images of shadows and compass (H on Figure 4) becomes a measure of altitude and hence of bottom scale. Figure 5 illustrates a determination of scale by shadow geometry in which the size of an octopod in midwater is determined using an extension of the method. Details of the method are beyond the scope of this work and are reported elsewhere (Brundage, in press). Scale in Figures 7, 16, 17, 19, 20, 22, 23, 27, and 36 through 53 was determined by shadow geometry. The scale in Figure 10, an oblique photograph, was determined by a complex combination of the above and other methods.

Errors.—No systematic treatment of errors can

⁴ These all appear to be members of a single species of *Echinus* (Howard L. Sanders, pers. comm.).

⁵ Distance below the vehicle should be about one-half the expected altitude.

be made for the above photogrammetric methods short of duplicating the measurements over a known bottom grid. The following estimate of errors is based on experience gained while applying and comparing the methods and by taking the occasional opportunity to measure an object of known size (e.g., the vaned compass) on the bottom:

- ± 10% known reference
- ± 15% known secondary reference (e.g. "urchin scale")
- ± 3% non-stereo overlap
- ± 5% shadow geometry

These should be regarded as maximum estimates of error.

Oceanographic Setting—Virgin Islands Basin

BATHYMETRY

All camera runs were made near the base of a steep escarpment that was contoured by Frassetto and Northrup (1957). These isobaths are in good agreement with those constructed from the NRL data (Figure 2 and inset) but the photographs indicate that the area is more complex than is shown by either study. Many small erosion channels, ledges and rock outcrops were photographed especially in the central and eastern sections. This study area borders on the flat floor that begins with the 2,300-fm (4,210-m) contour. The basin is completely encompassed by sills that rise more than 1,200 fm (2,200 m) above the floor.

A recent seismic reflection study (Perry and Masingill, 1971) revealed a small ridgelike feature which parallels our contours and behind which the seismic reflection surfaces look somewhat disturbed (Figure 6). The location of the crest of the ridge coincides approximately with our longest continuous 2,200-fm (4,020-m) isobath. The companion troughlike feature has a relatively flat floor and is located between the ridge and the 2,100-fm (3,840-m) contour (see Figure 2).

WATER MASS AND CURRENTS

Below sill depth the basin water has nearly uniform physical parameters characterized by temperatures between 3.7° and 3.9°C and a salinity between 34.96 and 34.98‰ (Wüst, 1964). Westerly currents domi-

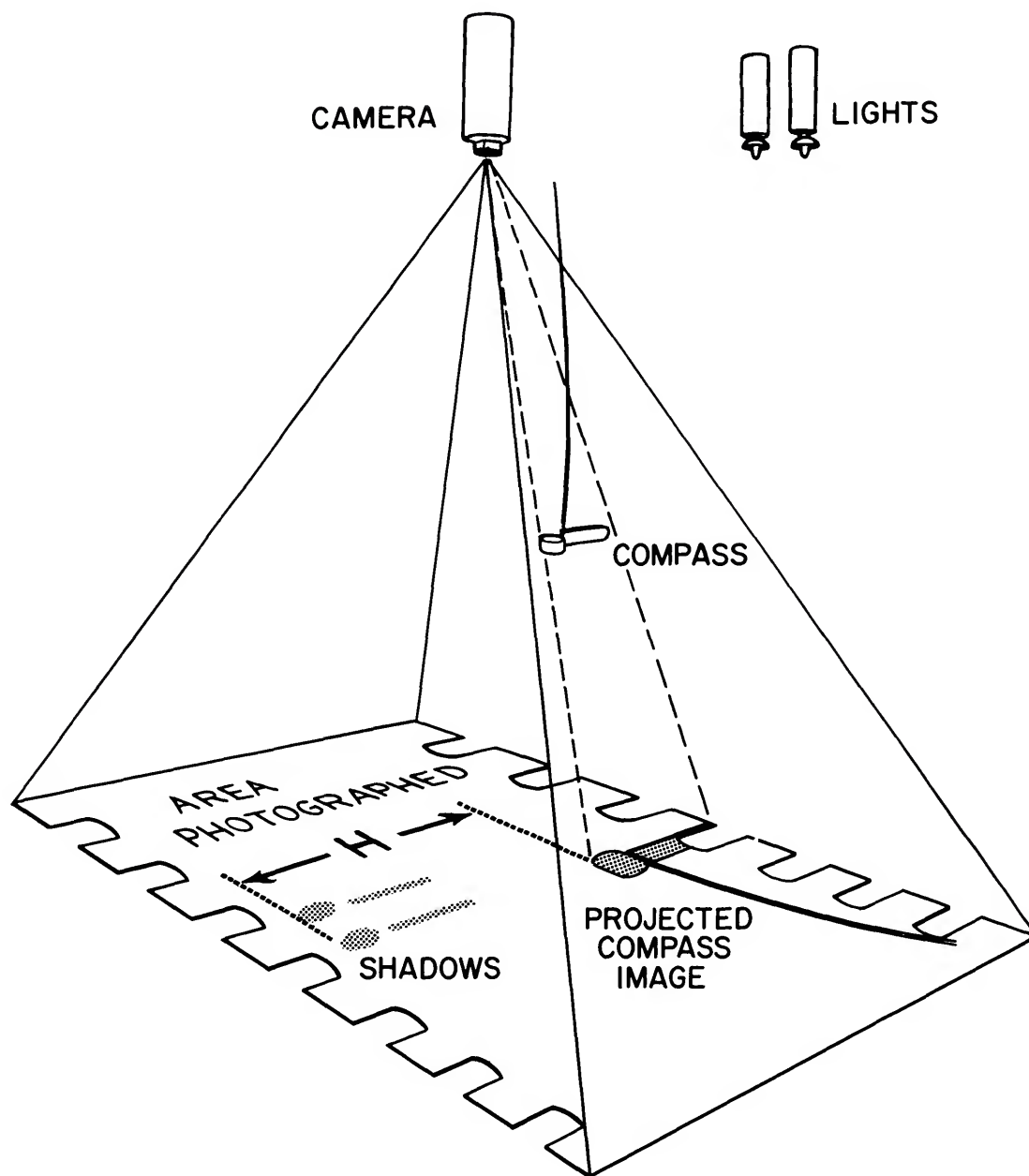


FIGURE 4.—Spatial relationship of camera system components essential for measurement of bottom scale using “shadow geometry.” Electronic flash lamps located at trailing edge of vehicle cast double shadow of suspended compass. “Area photographed” represents the hypothetical maximum coverage in a single photograph of a flat bottom when camera is vertical. Distance between image of compass head and its shadow (H), measured on a line parallel to the camera-lights axis, changes linearly with altitude of camera above sea floor. Details in Figure 5 and text.

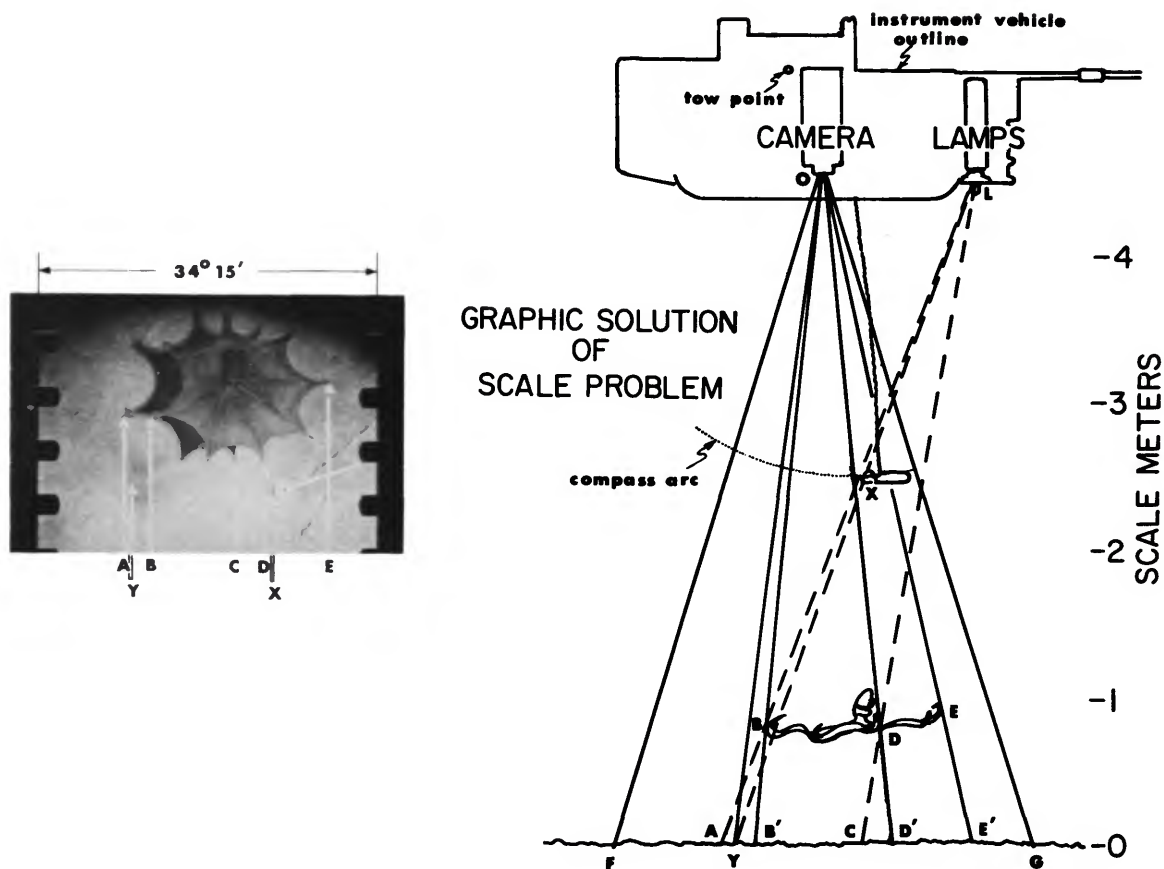


FIGURE 5.—Scale determination by “shadow geometry.” The octopod photograph (left) is marked with reference points X and Y for measurement of camera altitude and with points A, B, C, D and E for determination of the midwater location and scale of the animal. The simplified graphic solution to the problem (right) shows the most important relationships. Angle FOG is camera angle of view in the camera-light plane. Location of compass on camera arc permits a rough correction for vehicle pitch. For a detailed explanation of the method see Brundage, in press.

nate the surface waters but a section of potential temperature (Wüst, 1964, Plate L) through the Virgin Islands Basin exhibits isotherms bending upwards toward the perimeter indicating a possible rotary circulation pattern below sill level. While it can be argued that such non-synoptic data are often misleading, the data from three other stations (Worthington, 1966:737–738) taken over a period of about two days disclosed a similar upward bending of potential temperature isotherms. Direct measurements of deep currents are lacking in this region.

However, Naval Air Development Center personnel experienced what appeared to be a northeasterly current at depth in the southeast corner of the basin for several days following the November 1968 deployment of deep-moored experimental buoy systems (J. R. Brown, per. comm.), some of which were sunk and later photographed during the NRL survey. A northeasterly current in that corner of the basin fits a pattern of cyclonic circulation.⁶

⁶Two sets of observations are pertinent regarding the buoy systems which failed to anchor themselves (see Hal-

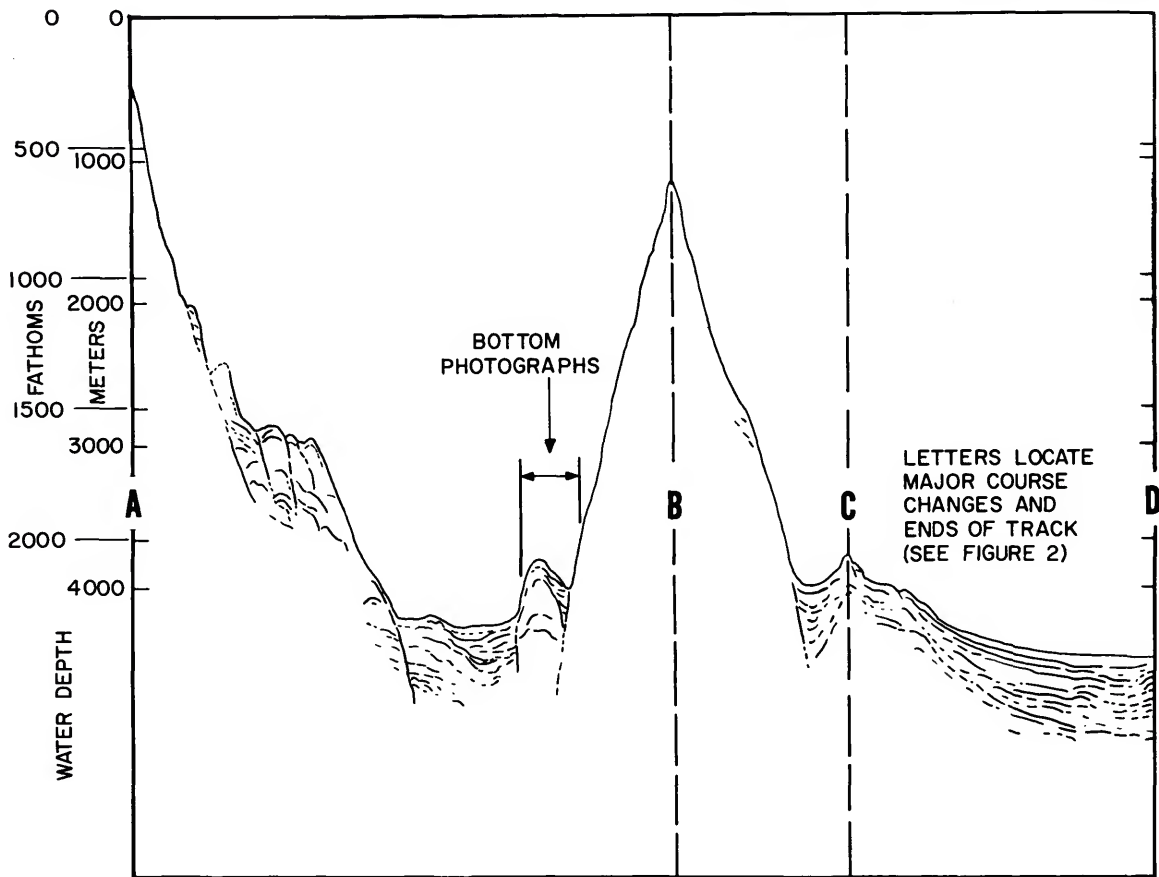


FIGURE 6.—Reconstruction of seismic profile (after Perry and Massingill, 1971). Area of interest is around sharp ridge and gentle depression. Ridge apparently acts as a dam, impounding large quantities of organic debris. A 2,150-fm (3,931-m) isobath (not plotted on our figure) between 2,100 fm (3,840 m) and 2,200 fm (4,023 m) outlines several closed depressions. Depths corrected for sounding speed of 4,950 ft/sec (1,509 m/sec).

Although we seem to have given undue attention to probable deep currents we show later that a reversal of flow at depth could play a role in the concentration of organic detritus in the area where the octopods were photographed.

Near-bottom current evidence in the form of ripple marks was lacking in thousands of bottom photographs studied even though there was an abundance of particles in the medium to coarse sand-size range (0.25 to 1.0 mm), the size most easily transported

berg and Meyers, 1966, for description of similar buoy system): (a) surface floats with mooring cables which parted at lengths shorter than 2,000 m moved immediately westward at close to the half-knot speed of the surface current and, (b) surface floats with cables which broke near the bottom (ca. 4,000 m) appeared at first to be firmly anchored. However, after several days of careful position checks they were observed to have been moving

towards the north-northeast at a rate of approximately 1.1 km/day.

Atlantic water cascading periodically into the eastern end of the basin through the Anegada Passage might supply the impelling force for a gyral much as the cold water flowing over the sill between Iceland and Greenland imparts cyclonic angular momentum to the bottom water of the basins to the south (Bjerkness, 1960).

(Inman, 1963:126). The filling of numerous animal trails and depressions in the bottom by light-colored surface sediment indicates however that either sporadic bottom currents of variable direction do occur or that the movement is caused by the stirring action of the relatively numerous bottom and near-bottom animals.

SEDIMENT

A grab sample was recovered from the western edge of the study area at 17°51.2'N, 64°49.5'W in 2,130 fm (3,895 m) of water. The primarily calcareous sediment consists of material of shallow-water origin (from the reef front platform and possibly from the margin) and of pelagic origin (D. Stanley, pers. comm.). The results of a size analysis on this sample are presented in Table 1 along with a commentary on the composition of the particles within each size fraction. Shallow-water influence is evidenced especially by constituents of the coarser sand and fine gravel sizes which include a whole polyp of a solitary scleractinian coral. Photographs of whole shallow-water gastropod shells, a brain coral head, mangrove leaves and sea grass fragments are additional evidence of shallow-water materials.

Although the grab sample contained very little material finer than sand (< .062 mm) other evidence indicates that clay and silt-sized sediment occurs in the area. One sample of opportunity was packed into the cup-shaped hollow fitting on the end

of one of the cylindrical arms which jut out from the grab sampler. The innermost unwashed portion of this sediment was composed of a light-tan-colored, sticky calcareous clay. Photographs show that the clay was picked up when the sampler plunged sideways into the bank of an erosion channel about 20 cm below the rim. Evidence of other fine sediment on the bottom comes from many photographs of clouds of silt stirred up by the vaned compass which was suspended beneath the camera vehicle.

Systematics

Knowledge about the systematics of the finned octopods (suborder Cirrata) is fragmentary, and an understanding of the relationships of the numerous nominal entities, even at the familial level, is lacking. This is a result of several related factors. (1) Relatively few specimens exist in research collections. (2) The animals are semigelatinous and fragile; therefore few complete, undamaged specimens exist. Material generally comes out of collecting nets damaged, undergoes shrinkage and distortion during fixation and preservation, and continues to deteriorate during storage. (3) Few reliable taxonomic characters have been delineated in this group. (4) No modern systematic treatment of the cirrates has been undertaken.

The most comprehensive information on the cirrate octopods is found in Robson's monograph (1932). Robson compiled all known records and

TABLE I.—Sediment Size Analysis and Description

Size (mm)	Percent by Volume	Composition
>2	11	Coral, pelecypod, gastropod, sea urchin and bryozoan fragments from shallow water and chips of dark volcanic rock with pelagic pteropod and heteropod shells. (Fine calcareous granules.)
1 to 2	12	Pteropods and foraminifera shells with fragments of pelecypod and gastropod shells plus 3% volcanic and other terrigenous lithic fragments.
0.5 to 1	29	Coarse foraminiferal sand mainly of planktonic origin with lithic constituents which include black shale-slate.
0.25 to 0.5	24	Medium pelagic foraminiferal sand (75–80% globigerina), shells and fragments of forams and pteropods—terrigenous fragments present but rare.
0.125 to 0.25	10	Fine fragmented foraminiferal sand and shells with fragments of sponge spicules—rock fragments increase to about 10%.
0.062 to 0.125	5	Very fine fragmented foraminiferal sand (3–5% whole tests)—terrigenous fragments present but rare.
<0.062	9	Not examined.

species and attempted to characterize species and delineate the systematics of the group. In spite of this effort, with few exceptions, e.g. *Cirrothauma murrayi* and *Opisthoteuthis* species, identification of finned octopods remains a difficult if not impossible task. At the present time the suborder Cirrata is comprised of about 8 nominal genera and nearly 30 nominal species distributed in the families Cirroteuthidae, Stauroteuthidae and Opisthoteuthidae.

DESCRIPTION OF PHOTOGRAPHED OCTOPODS

The description is based on an analysis of most of the photographs through Figure 29. A figure reference is given for each described character. We recognize

the possibility that more than one species may be represented in the series of photographs.

The *mantle*, or body, is a relatively long, bluntly rounded, cylindrical sac (e.g. Figures 7, 8, 9, 11, 13). The *head* is well defined and is the widest part of the body as a result of the large somewhat bulging eyes (Figures 7-9).

The *fins* are long and broad; each is as long (axis perpendicular to the body) as or longer than the width of the mantle (Figures 9, 11, 20, 22, 25). The posterior borders of the fins are attached at or slightly anterior to the midpoint of the mantle, so that the fins extend anteriorly nearly to the posterior border of the eye openings (Figures 7-9). The posterior borders arise perpendicular to the body axis and re-

TABLE II.—Data for Photographs of Cirrate Octopods

Specimen Figure No.	Area ^a	Location		Date	Bottom Depth (meters)	Altitude ^b (meters)
		North	West			
7	VIB	17°50.8'	64°47.8'	20.XI.69	3480 ^c	<1
8	NEC	41°45'	64°56'	15.VI.63	2500	<1
9	VIB	17°50.8'	64°48.5'	21.XI.69	3620	<1
10	BDA	31°43'	64°48'	19.IV.65	4250	1.1
11	NEC	41°44'	65°56'	10.IX.64	2500	<1
12	BLB	29°23'	75°58'	12.X.70	5030	~2
13	BLB	29°23'	75°58'	14.X.70	5030	1.1
14-15	VIB	17°51.8'	64°48.4'	25.XI.69	3990	-
16	VIB	17°51.6'	64°47.1'	19.XI.69	3660	1.7
17	VIB	17°51.2'	64°48.2'	27.XI.69	3770	0.5
18	VIB	17°51.0'	64°49.4'	21.XI.69	3790	<1
19	VIB	17°51.6'	64°47.1'	19.XI.69	3620	1.8
20	VIB	17°52.6'	64°46.9'	20.XI.69	3970	<1
21	BLB	29°22'	75°58'	19.VI.71	5110	0.5
22	VIB	17°51.9'	64°46.6'	20.XI.69	3770	0.8
23	VIB	17°51.0'	64°48.5'	26.XI.69	3710	0.5
24	CAB	33°	33°	28.VIII.68	3500	<1
25-26	VIB	17°51.0'	64°48.6'	26.XI.69	3730	~3-4
27	VIB	17°51.2'	64°48.3'	27.XI.69	3770	0.5
28	SAP	32°42'	57°11'	16.II.67	5202	<1
29	BLB	29°22'	75°58'	19.VI.71	5110	~4.5
30-33	MVS	39°46'	70°32'	26.IX.67	1300	<1

^a Areas are located on chart (Figure 1) by the following abbreviations:

- VIB — (Virgin Islands Basin)
- BDA — (Bermuda)
- NEC — (Northeast Channel)
- CAB — (Canaries Basin)
- BLB — (Blake Basin)
- SAP — (Sohm Abyssal Plain)
- MVS — (Martha's Vineyard Slope)

^b Altitude=average altitude of specimen above bottom.

^c VIB depths corrected to nearest 10m.

main straight or slightly convex nearly to the bluntly rounded anterior angle (Figures 9, 25). The anterior borders are lobed or convex so that a small notch is formed at the anterior basal attachment (Figure 25).

The *arms* are long and comprise about $\frac{2}{3}$ the total length of the animal (Figures 8, 9, 11, 14). Arm pairs I and II appear to be the longest (Figures 7–9). The arms are drawn out into fine, attenuate tips (Figures 8, 9, 20, 22). Long cirri are present along at least the distal $\frac{1}{3}$ to $\frac{1}{2}$ of the arms (Figure 20). All the arms are connected by a thin, membranous interbrachial web (Figures 20–22, 25, 27) that is attached to the dorsal (aboral) surface of each arm by an intermediate or secondary web (Figures 20–22). The interbrachial web reaches nearly to the tips of the arms when fully expanded (Figure 22).

DISCUSSION

Many of the characters that have been used in classifying the cirrates are internal features. The primary character for distinguishing genera (or families) is the configuration of the cartilaginous shell-vestige or fin support that is embedded in the posterodorsal part of the mantle (body) and serves as a base for the attachment of the fins. The support can be "saddle shaped," with or without limbs, U- or V-shaped. Other internal characters include the presence or absence of the median adductor muscle, the presence or absence of a crop, the size of the gills and the arrangement of gill filaments.

External characters that have been utilized in the past are, chiefly, the presence or absence of a secondary or intermediate web between the primary interbrachial web and the arms, the extent of the mantle opening, relative proportions (and shapes) of the body, fins, head and arms, and configuration of suckers and cirri.

In attempting to identify the specimens in the photographs presented here it is possible to eliminate some of the more distinctive cirrates solely on the basis of external characters. Members of the monotypic family Opisthoteuthidae are eliminated because of their flattened or belllike shape characterized by the absence of a well-developed body posterior to the head, as well as small, short fins. Comparison of our photos with the illustrations in Berry (1952, Figure 1) and especially with living specimens of *Opisthoteuthis californiana* shown in Pereyra (1965, Figure 3)

emphasizes these differences.

Grimpoteuthis (Stauroteuthidae) also has a short body (although it is not as flattened as in *Opisthoteuthis*), relatively short fins—shorter than the width of the head, and no intermediate web. Fin size may be too variable to be a dependable character in this genus, but the short body and the absence of an intermediate web in *Grimpoteuthis* appear to preclude a close relationship with the photographed specimens.

Although *Cirrothauma murrayi* (Cirroteuthidae) is known only from the original specimen, a second specimen noted by Voss (1967) and Mohr and Geiger (1968), and three additional specimens reported in this paper (courtesy of G. L. Voss, pers. comm.), it is readily distinguished from other known cirrates by its extremely reduced eyes that are embedded in and covered over by gelatinous tissue (Chun, 1914, Figures 7, 9; 1915, Pls. 92, 93). Three of our specimens show distinct eyes and large eye openings (Figures 7–9) which are sufficient to preclude their identity with *Cirrothauma*.

So little is known of most of the remaining genera, e.g. *Stauroteuthis* Verrill, 1879, *Frokenia* Hoyle, 1904, and *Chunioteuthis* Grimpe, 1916, that comparison is fruitless. In fact, future systematic studies may well show that considerable generic overnaming has occurred in the Cirrata.

Cirroteuthis muelleri Eschricht, 1838, was the first cirrate octopod to be described, and it has been reported from the North Atlantic on several occasions (see Robson, 1932). *Cirroteuthis* possesses an elongate body, a "prominent" head, a secondary or intermediate web, a moderately narrow mantle aperture, large, broad fins set closer to the eyes than to the apex of the body (or at least at the midpoint between eye and apex in some specimens), and arms about $\frac{2}{3}$ the total length of the animal.

Reinhardt and Prosch (1846) published an account of *Cirroteuthis muelleri* and included good illustrations. Some of the specimens in our photographs (e.g., Figures 9, 25) very closely resemble their illustrations.

On the basis of the current status of systematics in cirromorph octopods, it is impossible to definitely place the specimens in our photographs in one of these genera. However, the general features of these octopods are in many ways similar to those of *Cirroteuthis* and we tentatively assign our animals to this genus.

The following table lists the described characteristics of *Cirrotheuthis* that are also visible in our photographs:

Character	Figures
Elongate body	7-11, 13, 27
Prominent head	7-9
Intermediate web	16, 20, 22
Long fins	9-11, 20, 22, 25, 27
Anteriorly placed fins	7-10
Long arms	8-10, 13, 20, 22, 25, 27
Prominent eyes	7-9

Whether the photographed specimens are indeed *Cirrotheuthis* must await a systematic revision of the suborder as well as the capture of specimens so that internal as well as external characters can be studied.

Biology of Cirrates

HABITAT

Considerable discussion appears in the literature concerning the habitat of cirrate octopods (see reviews in Robson, 1932; Voss, 1967). It is now fairly well established that *Opisthoteuthis* is a benthic form, first on the basis of morphological interpretation, and more recently through the more direct observations of Pereyra (1965). All except one of Pereyra's specimens of *O. californiana* were taken in bottom-fishing trawls; the exception was captured in a net set to fish 6 meters above the bottom. As Pereyra described the swimming capability of *O. californiana*, occasional

off-bottom excursions and captures may be expected.

Chun (1914:16, 21) described *Cirrothauma murrayi* from a single specimen taken at *Michael Sars* Station 82 with a pelagic trawl with 3,000 meters of wire out (Murray and Hjort, 1912:xix). The bottom depth in that locality (48°24'N, 36°53'W) generally exceeds 4,000 m, so clearly the net almost certainly was not on or near the bottom. A series of seamounts occurs about 2° eastward of the recorded locality along the 35° meridian between 38° and 40° N Latitude so that the possibility that the net fished over an uncharted seamount—therefore closer to the bottom—cannot be completely ruled out. Bruun (1943:15) suggested that fishing depths for pelagic trawls used on the *Dana* Expeditions could be estimated as one-half the amount of wire out for tows with greater than 1,000 m of wire out and one-third the amount for shallower tows. Most pelagic trawls do not achieve so low an angle, so that in the absence of wire angle or other data from the *Michael Sars*, we may take one-half as the maximum estimate. Chun's specimen, therefore, probably was captured in less than 1,500 m, and he stated (p. 21) that the species is pelagic. Robson (1932:84) mistakenly listed the depth of capture as 3,000 m (1,641 fms).

Additional specimens of *Cirrothauma* are in the collections of the Institute of Marine Sciences, Miami (Voss, 1967; and pers. comm.). The records of capture are tabulated here as a further indication of depth range, habitat and geographic distribution of the species:

Location	Sampling Depth (meters)	Bottom Depth (meters)	Gear	Vessel-Station
40°46'S 76°48'W	2893	3700	3m IKMT	<i>Eltanin</i> -175
57°39'S 52°02'W	3980-4136	4013-4136	10'Blake	<i>Eltanin</i> -1514
55°25'S 78°28'W	3440-3705	4337	3m IKMT	<i>Eltanin</i> -878
86°N 173°E	0	-	dipnet	<i>Arliss</i> II (Ice Island)

The *Eltanin* specimens come from off southern Chile, in the Drake Passage, and in the Scotia Sea; two were caught in midwater trawls at least 630 meters above the bottom. The third specimen was captured in a Blake trawl that was set to fish on the bottom at over 4,000 m. Whether the specimen was captured on the bottom or in midwater during the long period required for set and retrieval, which seems more likely, cannot be known. The specimen from the Arctic Ocean was dipped at the surface from a hole in the ice on drift station *Arliss II*. The

specimen was noted to be "alive" at the time of capture (Ronald McPeak, University of Southern California, collector). These records verify the pelagic habitat and broad geographic range of the genus. The surface capture of the Arctic specimen certainly contradicts the otherwise very deep records. This may, however, be an example of polar emergence.

Knowledge about the habitat of remaining cirrates, however, is contradictory. Robson (1932:19) believed that it was safe to infer a benthic habitat for a deep-water member of a group if its shallow-water

relatives were benthic dwellers. This type of inference, whether valid or not, is not applicable to the cirrates since no shallow-water representatives are known. (*Opisthoteuthis*, the shallowest living cirrate genus, has been recorded as shallow as 125 m [Pereyra, 1965:429] and as deep as 2,251 m [Verrill, 1885:446] with the great majority in excess of 400 m; it can hardly be considered shallow living.) Robson (1932), after considerable discussion, was inclined to assign a benthic or near-bottom habitat for the cirrates, while Voss (1967:522) considered them abyssopelagic organisms (except *Opisthoteuthis*). Dollo (1912) and Abel (1916) attempted to determine the habitat of some cirrates on the basis of structure. Dollo (p. 129) thought that *Cirrotheuthis muelleri* was nektonic because of its fins. Abel (pp. 18, 55, 72, 105) regarded *C. muelleri* and several other *Cirrotheuthis*-like species as nektonic or planktonic because of the fins (as balance structures) and webs. He considered other species benthic because they had depressed bodies and dorsal eyes, or because they resembled *Sepiolo*, a sepoid squid. The last reason, especially, is untenable. Abel (p. 55) also believed that *Cirrothauma murrayi* was a benthic form that burrows in the mud (hence, the atrophied eyes). In his attempt to derive function and habitat from morphological considerations alone, Abel led himself astray, since the only recorded specimen of this species was captured at a maximum estimated depth of 1,500 m in a water depth of over 4,000 m.

Chun (1914:16, 20) considered that *Grimpoteuthis umbellata* was a bottom dweller because it was captured only in bottom trawls.

Inference of habitat on the basis of type of gear which captured cirrates was inconclusive. Although most captures have been made in non-closing benthic trawls, this could not preclude the possibility of capture in midwater while the net was being retrieved. Personal observations (C. F. E. Roper and R. E. Young) as a result of occasional captures in the Antarctic Ocean in 1963–1964 of cirrates in deep-fishing midwater trawls that approached the bottom led to the conjecture that some cirrates must be benthopelagic organisms that spend their lives in association with, but not restricted to, the bottom.

Stomach contents from a *Grimpoteuthis* species from 2,425 fms (4,438 m) included remains of 9 species of benthic crustaceans (Scott, 1910:52) and Robson (1930:378) reported fragments of polychaetes from the stomach of *G. glacialis*; presumably

these food items were captured on or near the bottom. The isopods, amphipods, and one of the copepod species identified by Scott are known to be deep-living benthic forms. Single specimens of species of copepods, known to be shallower living pelagic species, may represent contamination (e.g. in the mantle cavity), secondary ingestion, or misidentification (since the specimens were minute and in poor condition) (T. Bowman, pers. comm.).

All of the photographs presented here, plus several others in our files, show the octopods above the bottom. All but three specimens are within two meters of the bottom; the remaining three are 3–4 meters above the bottom (see Table II). While it is possible that the approaching camera and lights aroused the specimens from the bottom, the attitude of the animals with outstretched arms in many photos, as well as the lack of a tell-tale puff of sediment (as is frequently noted in photographs of deep-sea benthic fish), suggests that this is not the case in these photos.

Two photographs (Figures 12 and 29) show specimens in close proximity to the compass and magnetometer; the specimen in Figure 12 is 2 meters above the bottom and that in Figure 29 is 3–4 m above the bottom. A stereo pair in our files (BBIII-1-123-427 and BBIII-1-13-432) shows a specimen just over 2 m above the bottom and within 1 m of the compass at the same level. Figures 25 and 26 depict a specimen 3–4 m above the bottom and only 150 cm from the camera. Only one specimen which is more than 2 m off the bottom does not appear to be in close proximity to the equipment. This seems to suggest that these specimens may have been attracted further off the bottom by the camera vehicle. While this observation could merely be a sampling bias due to a reduced areal coverage close to the camera, it is noted that specimens closest to the equipment (Figures 12, 25, 26, 29) exhibit attitudes that no other specimens show.

On the basis of current photographs and previous experience with trawls, it seems reasonable to conclude that at least some cirrate octopods (exclusive perhaps of *Opisthoteuthidae*) are indeed benthopelagic. Furthermore, the gelatinous consistency of these cirrates suggests that they are neutrally buoyant, which would allow them to "float" above the bottom; and their fragile structure is more similar to that of a bathypelagic cephalopod than to that of a benthic form. Finally, we have no evidence to even suggest that these animals do live on the bottom.

The term benthopelagic was introduced by Marshall and Bourne (1964:226, 237, 240) to apply to species of deep-sea fishes with swimbladders that are able to attain neutral buoyancy and to hover and swim over the deep-sea floor. Marshall (1965:302) extended the definition: "Benthopelagic fishes (and other organisms) are those that swim freely and habitually near the ocean floor." This concept, for fishes however, was introduced earlier by Marshall (1960:97 et seq.). The term applies equally well to the cirrate octopods which are able to remain off the bottom by "hovering" or by normal swimming techniques.

DEPTH DISTRIBUTION

All known records of cirrates are from open nets except one closing net capture of *Grimptoteuthis* (Robson, 1924:682), and with only one known exception (Pereyra, 1965:429), these nets fished on the bottom.⁷ This, of course, does not preclude the possibility of capture higher up in the water column. Since our photographs indicate that the species of *Cirrotoeuthis* that we are concerned with is benthopelagic, we infer that at least some of the other cirrates share a similar habitat. If this is so, then depths of capture are assumed to approximate the recorded bottom depths. With these conditions in mind, the depth records for cirrate octopods in general range from 125 m to 2,251 m for *Opisthoteuthis* (Pereyra, 1965:429; Verrill, 1885:446)⁸ and from 339 m to 5,270 m for cirrates identified as species of *Grimptoteuthis* (Massy, 1916:186; Joubin, 1924:9).

Cirrothauma, originally known from about 1,500 m, is now recorded from the surface in the Arctic (in

Voss, 1967:527) to a maximum of 4,136 m in the Antarctic (see discussion and records in "Habitat" section). Specimens of *Cirrotoeuthis* species have been captured at depths that range from 2,342 m to 4,072 m (Apellöf, 1892:3; Hoyle, 1886:56). Therefore, the large majority of captures of cirrates (except *Opisthoteuthis*) have been at depths in excess of 1,000 m.

All of the specimens from the Virgin Islands Basin were photographed at a depth of 3,500 to 4,000 m. Other specimens were photographed in the *Thresher* search area at 2,500 m (Figures 8 and 11), in the Blake Basin at 5,000 m (Figures 12, 13, 21 and 29), SW of Bermuda at 4,250 m (Figure 10), in the Canaries Basin at greater than 3,000 m (Figure 24), and on the Sohm Abyssal Plain at 5,200 m (Figure 28). The majority of the specimens represented here, therefore, were photographed in depths that approach the deepest known records of cirrate octopods.

During the past several years a number of NRL photographic surveys have been made in depths of less than 2,500 m. No photographs of cirrate octopods have been noted from the extensive collections of photographs. The following table lists the area surveyed, the depth range, and the number of photographs taken:

Area	Depth Range (meters)	No. of Photos
Blake Plateau	400-800	7500
Tongue of the Ocean	1500	3000
Eleuthera	200-1500	2000
Western Mediterranean* (Toulon)	1000-2300	70,000
		82,500

* Warm water (>13°C) may account for the absence of cirrates here.

⁷ Robson (1932:21, 83) misinterpreted Chun's (1914) capture record of *G. umbellata* from *Michael Sars* Station 53. Robson thought that the specimen was caught in a trawl at 1,430 fms (2,615 m), 137 fms above the bottom depth of 1,567 fms (2,865 m). Actually, the *Michael Sars* station data indicate that Station 53 was a benthic tow that fished on the bottom over the depth range of 1,430-1,567 fms (2,615-2,865 m) (Murray and Hjort, 1912:xviii).

⁸ During our search of the literature we have noted an incorrect depth record which has been perpetuated since one of the earliest citations of the genus. Verrill (1885:408) reported and described the second-known specimen of *Opisthoteuthis agassizii* Verrill, 1883, which was captured in *Albatross* Station 2196 from 1,058 fms (1,934 m) off New Jersey. In the list of deep-sea species on p. 446, Verrill listed the depths for this species as 1,230 fms (2,251 m) without referring to a station number. The 1,058-fathom

depth subsequently has been recorded as the deepest record for *O. agassizii* (e.g., Robson, 1932:84, 167; Pereyra, 1965:430), while the 1,230-fathom record has been overlooked. (Robson, p. 167, had noted the 1,230-fathom record, but apparently discounted it because no station number was included by Verrill.) A check in the original dredging records of the *Albatross* (Townsend, 1901) indicates the source of the confusion: *Albatross* Station 2196 actually was taken at a depth of 1,230 fms (2,251 m), while the preceding station, 2195, was taken at a depth of 1,058 fms (1,934 m). Verrill had inadvertently recorded the wrong depth (and the wrong latitude) and introduced a 317-m error in the depth distribution of *O. agassizii*. The correct station data, from Townsend (1901:395), are as follows: *Albatross* Station 2196: 6 Aug. 1884, 39°35'N, 69°44'W, Bottom temperature 38°F, 1,230 fms, green mud, LBT (large Blake trawl).

On the basis of photographic data and capture records in the literature, it appears that these cirrate octopods are most abundant at depths in excess of about 2,300 to 2,500 m and that they range beyond 5,000 m.

SIZE

The cirrate octopods that have been recorded in the literature are, in general, rather small. Rarely have specimens been recorded greater than 30 cm in total length⁹ and most are around 20 cm total length or smaller (see Robson, 1932). The largest cirrate on record is the holotype of *Cirrotheuthis magna* Hoyle which measured 115.5 cm in total length (Hoyle, 1886:58). Robson (1932:154) mentioned a large specimen of *Grimptoteuthis* species taken by *Discovery* that "may have been 3-4 feet long" (91-122 cm), but it was "lost overboard."

Measurements of preserved specimens of the semi-gelatinous cirrate octopods are particularly suspect since, in time, specimens undergo a great amount of shrinkage in preservative (alcohol). This problem was mentioned by Verrill (1885:406-407) in comparing preserved with fresh specimens, and later by Robson (1932:159), who, after a period of several years, remeasured a specimen and noted up to about a 23% reduction in size. Observations by recent workers indicate that shrinkage can be more severe than that (R. Young, E. McSweeney, pers. comm.; C. F. E. Roper), and Voss (1967:522) claimed that it reaches 50% of its original size.

The size of the photographed specimens varies considerably. The shadow geometry technique for calculating size is discussed in an earlier section (p 7). Since it is not always possible to measure directly the total length of the specimens in the photographs, the calculated sizes (the greatest diameter across the outstretched web and arms) have been interpolated to a measurement of total length where feasible. From measurements in the literature and from certain photographs (Figures 8, 9, 11, 13, 14) it is estimated that the arms comprise about $\frac{2}{3}$ of the total length of the animal and the body (mantle and head) the remaining $\frac{1}{3}$. So, if one value is known, an ap-

proximation of the total length can be made. If the photographed specimen has the arms and web straightened out to its fullest extent normal to the body axis, the arm length is taken to equal one-half the calculated size less the body radius, and this value accounts for two-thirds of the total length. (Where arm tips are curled up, arm lengths are extrapolated by estimating the amount of curl and adding that to the measured diameter.) Table III shows the calculated size in the greatest dimension and the estimated or interpolated total length.

In the photographs where measurements are possible, the estimated total length of specimens ranges from 10 cm to 128 cm (4 to 50 inches). Four specimens are in the 90-103 cm (35-41 inch) range. The largest span across the arms is about 170 cm (67 inches). This specimen, at a total length of 128 cm, represents the largest known cirrate octopod to be recorded (Figure 24). The literature to date records predominantly small specimens, but the photographs indicate that specimens of a meter or longer in total length and with arm spans approaching a meter and one-half are relatively common. As larger nets are used in deep-sea benthic sampling, large specimens of cirrate octopods should become more common in collections.¹⁰

LOCOMOTION

Previous studies speculating on the mode of locomotion by cirrate octopods have assumed, on one hand, that cirrates are ineffectual swimmers owing to weak funnel development, gelatinous consistency of mantle and funnel tissues, and reduced or absent mantle opening. It has also been suggested that cirrates use their fins and webs for providing locomotion, or that the fins are merely balance organs, and the web is used as a net for securing food. The lack of observations on living specimens has hindered a satisfactory interpretation of the various adaptations that may have a locomotory function, e.g., the web and the fins, as well as the mantle and funnel. By 1932, at least, Robson (pp. 22, 28, 57) was of the opinion

⁹Total length is measured from the posterior tip of the body (mantle) to the tip of the longest arms, where the arms are extended straight anteriorly parallel to the body axis.

¹⁰It is suggested to potential collectors that cirrate octopods be fixed and preserved in a 7-8% solution of formalin (buffered fresh water or sea water). Alcohol should not be used if at all possible since it dehydrates the semi-gelatinous tissue, so that specimens rapidly become shrunken and distorted. Specimens can be frozen if formalin is unavailable.

TABLE III.—*Sizes of Cirrate Octopods (cm)*

Figure	Calculated Size ^a	Estimated Diameter Arms Normal to Axis	Estimated Total Length
7	50	—	50
8	103	—	103
9	—	—	—
10	26	—	26
11	64	—	64
12	17	—	17
13	43	—	43
14–15	—	—	—
16	25	35	24
17	13.3	19	12
18	—	—	—
19	13	17	10
20	98	129	90
21	25	35	26
22	125	146	102
23	53.5	59	39
24	170	170	128
25–26	111	120	90
27	36.6	46	32
28	—	—	75 ^b
29	48	64	48
30–33	—	30 ^c	22

^a The various techniques employed for determining size are discussed in the section on Photogrammetry (p. 6).

^b Estimate by C. D. Hollister.

^c Estimate by R. R. Hessler.

that the cirrate octopods use their large webs for swimming. Earlier, Verrill (1882:373) had mentioned that the deep-living non-cirrate octopod, *Bathypolypus arcticus*, swims by a pulsating or opening and closing motion of the arms and web. A similar mode was suggested for *Opisthoteuthis* by Ijima and Ikeda (1895:329) on the basis of their morphological studies and again by Berry (1952:184).

Direct observations on living material were reported for the first time by Pereyra (1965:430) who observed *Opisthoteuthis californiana* in a ship-board aquarium. Pereyra established that *Opisthoteuthis* does use the interbrachial web in locomotion by opening and closing the web in a manner analogous to the movement of a jellyfish. Ejections of water from the funnel are simultaneous with the contraction or closing of the web, but Pereyra felt that this aided little in the overall movement. The fins were very active primarily as balance and orientation structures, and secondarily they appeared to aid in movement (p. 437).

Swimming behavior in *Vampyroteuthis infernalis* also has been observed (R. E. Young, pers. comm.). Although *Vampyroteuthis* is not an octopod (it belongs to a separate order—Vampyromorpha), its general appearance is quite similar to that of cirrate octopods. It is entirely bathypelagic. According to Young, three methods of swimming have been observed in *Vampyroteuthis*: (1) moderate swimming with arms pointing forward in the direction of motion and propulsion provided by the fins; (2) rapid swimming or escape reaction with a medusoid action of the arms and web; (3) slow swimming with water ejection through funnel and fins spread as stabilizers. Young stated that the first is the primary method, while the second is rarely used; the third method needs verification.

When the series of photographs that are presented here were originally accumulated, little could be made of the several positions depicted. With the exception of Figures 14, 15 and 18, no sequential shots of octopods were made; therefore, each of the remaining photographs represents a different specimen. While the large number of specimens is interesting in itself, the near absence of sequential shots makes it difficult to determine the functional significance of the various individual positions represented in the photographs. Furthermore, in view of Pereyra's (1965:436) observations that *Opisthoteuthis* completes a stroke cycle once every four seconds or more rapidly, it is very unlikely that sequential shots taken once every 10 seconds would record parts of the same stroke cycle in cirrates. Since all specimens were photographed above the bottom and since no small organisms are visible in the photos showing specimens with outstretched arms and web, we assume that the octopods are not in the act of feeding per se but are swimming, hovering, or drifting above the bottom, perhaps in a "hunting" position.¹¹

A system of locomotion has been proposed on the basis of the photographs. We conclude that several

¹¹ A study of recently acquired WA photographs from the BLB (June 19, 1971) reveals two specimens each of which was photographed twice. In both instances the interval between exposures was 16 seconds. The cirrates remained in essentially the same umbrella attitude and position relative to the bottom as the towed "fish" approached and passed above. This observation lends additional support to our thesis that a hunting or drifting mode is utilized by cirrates in the open umbrella attitude and that the animals usually appear undisturbed by the "fish."

styles of locomotion are employed either singly or concurrently: (1) the water-ejection (jet propulsion) type typical of other octopods, (2) the pulsating type using the web and arms, and (3) the droguelike or umbrella phase utilizing outstretched web and arms.

Water-ejection style.—This type of locomotion, typical of other cephalopods, apparently occurs in the cirrate octopods as well. The propulsive stroke, as illustrated in Figures 7 and 8, is characterized by contraction of the mantle which forces water out of the mantle cavity through the funnel, and results in a true jetlike action that generally propels the animal body-end first. While the relatively small mantle cavity in these octopods probably does not exchange a large volume of water with each pumping action, a

large volume of flow would not be necessary to propel an animal that is neutrally buoyant or nearly so.

Simultaneous with the ejection, the fins are brought down (ventrally) in a stroke that terminates with the fins wrapped tightly around the ventral surface of the body. The arms are held tightly together to form a surface of favorably low hydrodynamic drag. The webs are completely concealed in the tightly held arms. In these figures, the body is noticeably contracted as water is expelled (particularly Figure 7) in contrast to the fuller, more rounded bodies in other figures (e.g., Figures 20, 25). This propulsive ejection stroke may occur following an initial pulsating stroke, and it probably is used when more rapid locomotion, such as an escape reaction, is required.

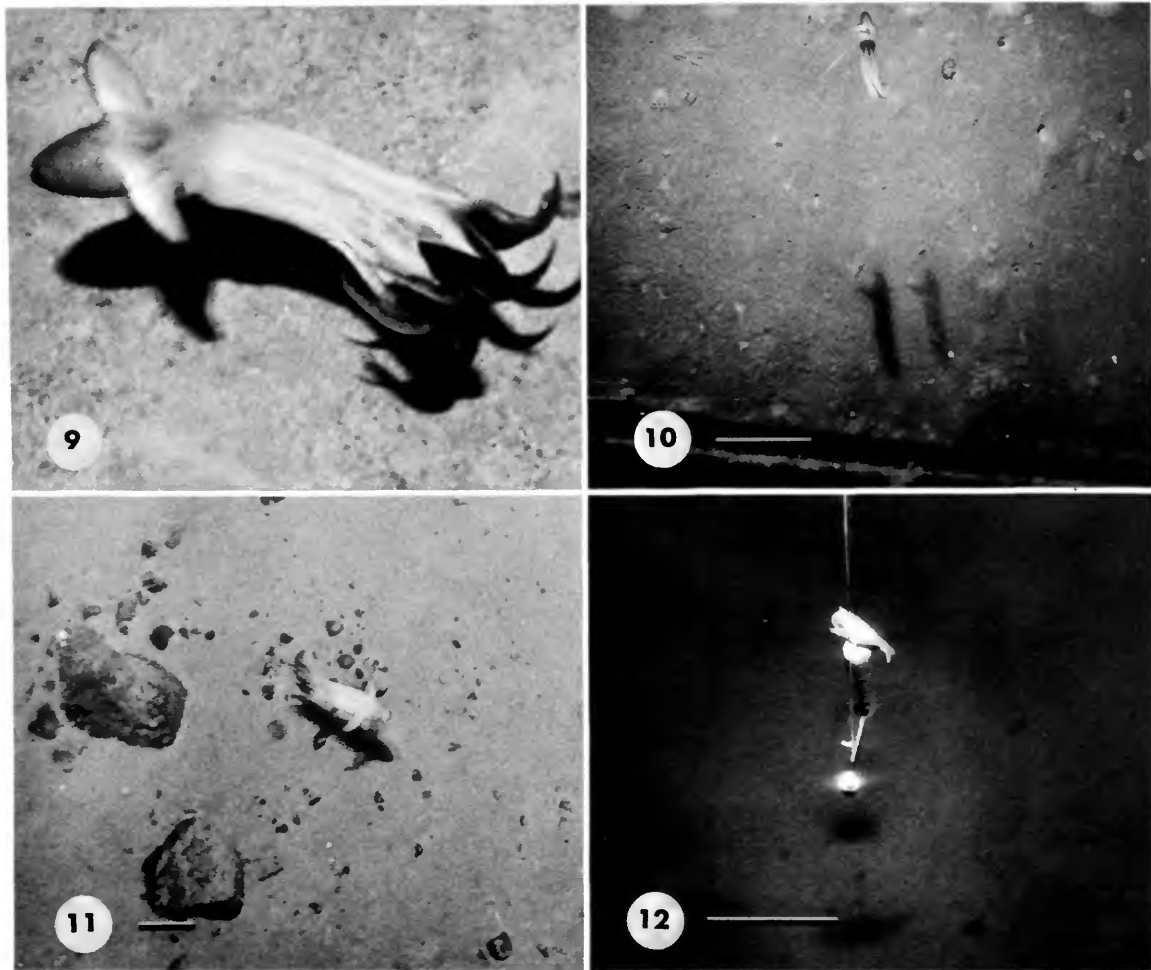
Between propulsive ejections, a short glide period occurs during which the arms are relaxed somewhat, particularly at the tips, and the fins straighten out perpendicular to the body. Figures 9, 10, 11, and 12 illustrate this glide mode. During the glide mode the mantle expands and draws water into the mantle



FIGURE 7.—Cirrate octopod in typical jet propulsion or water-ejection swimming mode with mantle contracted, arms in streamlined posture, and fins wrapped ventrally just posterior to left eye. An image of the photographic data partly overlaps primary image. Table II presents additional information on Figures 7–33. (NA.3480.VIB) (The legends to Figures 7–53 terminate with a parenthetical abbreviated code which signifies: type of camera, depth of bottom in m, and location. Length of scale mark on photographs equals 30 cm.)



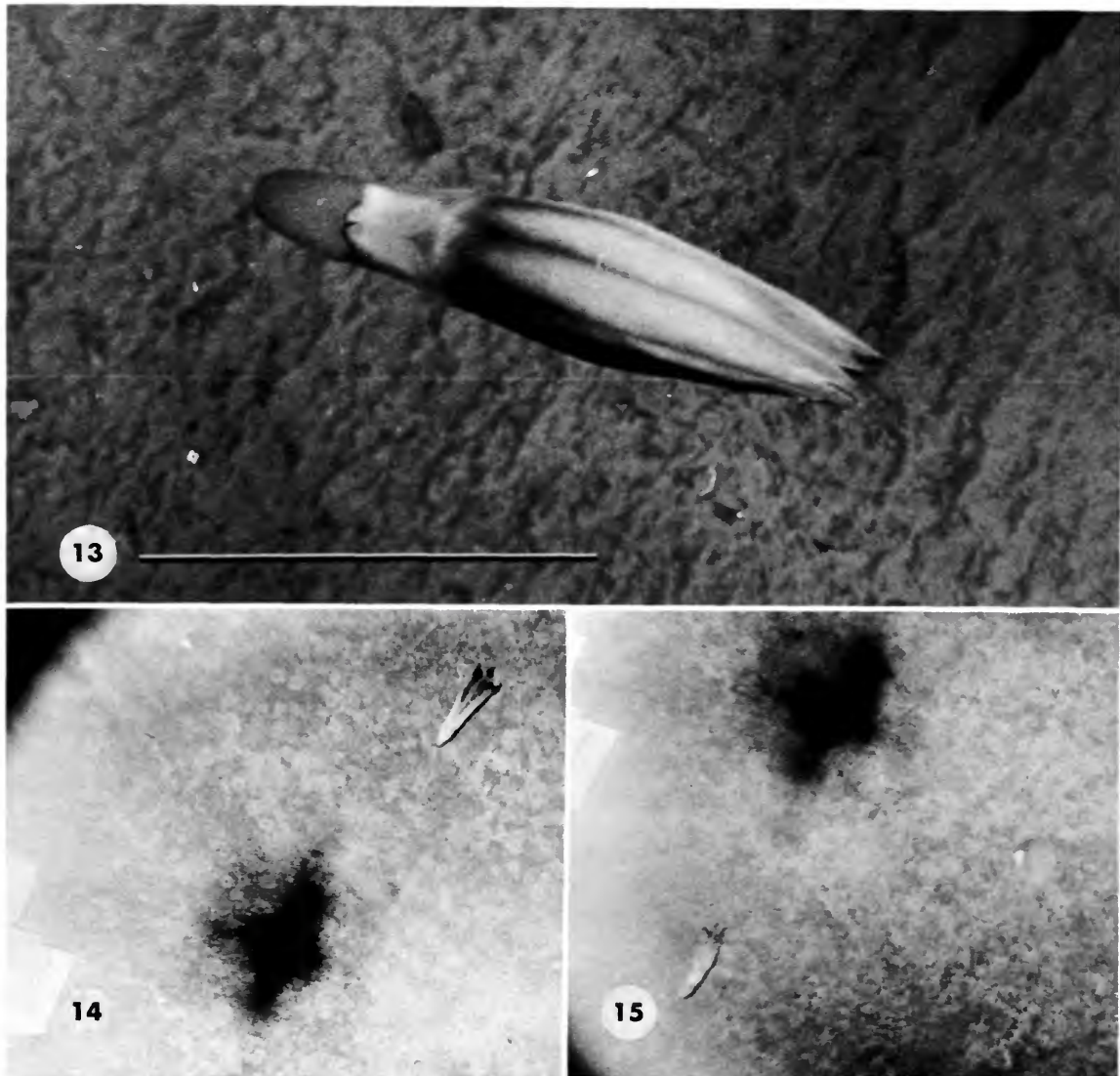
FIGURE 8.—Cirrate in water-ejection mode. Sea urchin in lower right provided a known size reference for determining size of octopod. (TH.2500.NEC) (Bottom photograph courtesy of J. Lamar Worzel)



FIGURES 9-12.—9, Swimming cirrate with fins extended probably as stabilizers during a glide. Specimen executing a “right-hand” turn. (NA.3620.VIB). 10, Photo of swimming cirrate from starboard-looking camera of a trimetregon arrangement. Center (vertical) camera photographed compass striking bottom at uniformly sized linear depression (bottom), providing a measure of the shadows of gliding cirrate and of camera altitude. Distance between shadows was used to determine camera-to-cephalopod range which permitted calculation of animal’s size. On the bottom are a clump of *Sargassum* sea weed (lower right near depression), numerous burrows and mounds, and fan-shaped radial lebensspuren (upper left). (NA.4250.BDA). 11, Attitude and shadow of cirrate with extended fins suggest an upward glide from a position close to the bottom. The rocks are characteristic of this site at the top of the continental rise off New England (see also Figure 8). (NA.2500.NEC). 12, Cirrate at uncommon altitude above bottom (2 m) and its position between instruments suspended from camera vehicle suggest a possible attraction to the equipment. (WA.5030.BLB)

cavity. Possibly minor, more gentle ejections occur during this period so that the animal can maintain course and altitude; the large fins may aid in this

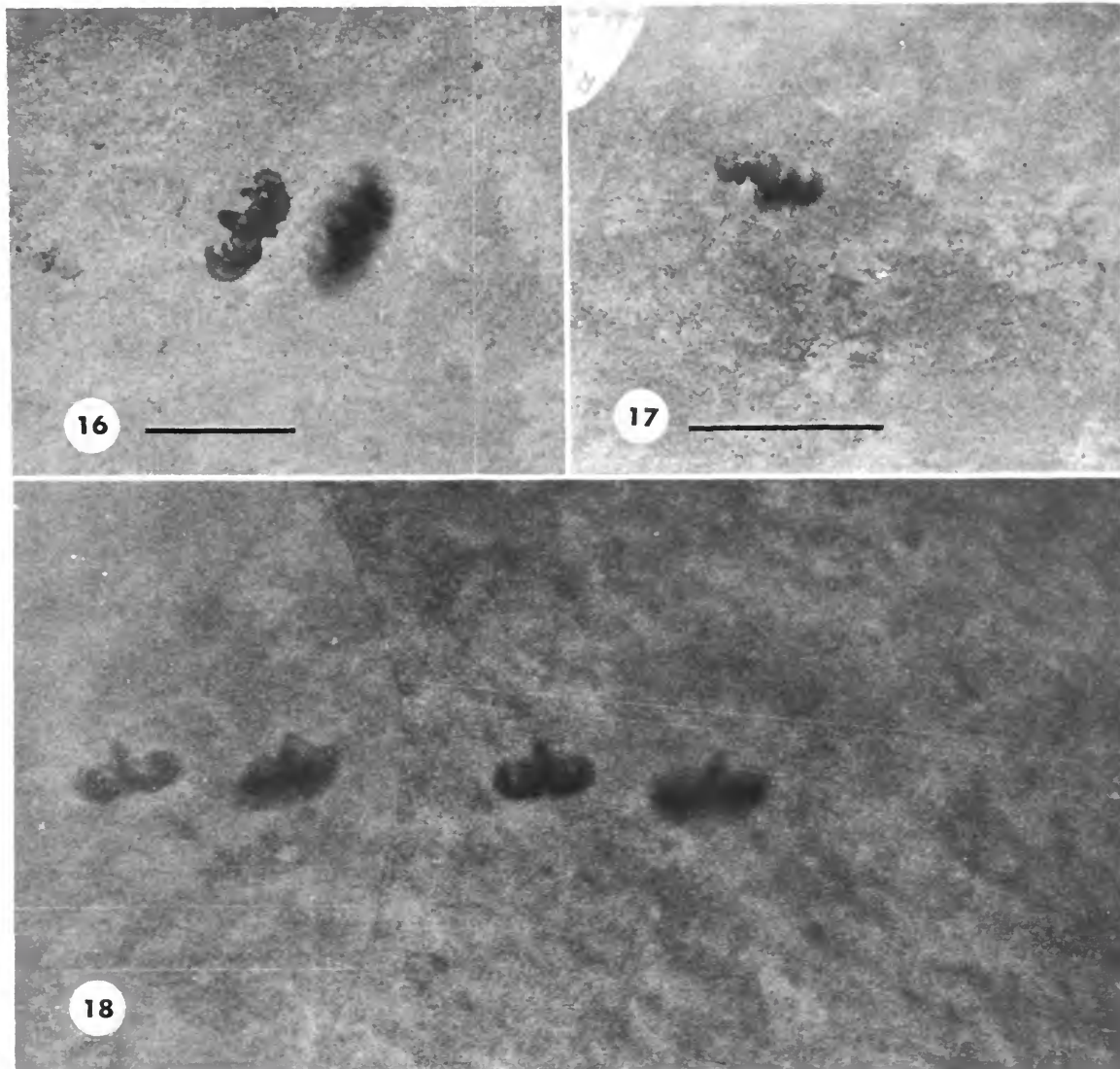
function. The specimen in Figure 9 with outstretched fins is arched as though it were making a right-hand turn.



FIGURES 13-15.—13, The dorsally extended fins on this cirrate may indicate the onset of a downward stroke or possibly completion of a recovery stroke. Note distinct coloration at base of the arms not accountable as shadows (see also Figure 10). (NA.5030.BLB). 14, The cirrate in this and the following photograph is believed to be employing a water-ejection mode of locomotion at a calculated speed of 1.2 knots. (WA.3990.VIB). 15, The light-colored object at left edge of this and preceding figure is a Shipek sediment sampler which was suspended from the lead end of the vehicle. (WA.3990.VIB)

The cirrate in Figure 13 is in the water-ejection phase with closed arms. The fins, however, are extended dorsally rather than ventrally, judging from the location of the bases of the fins (compare, e.g.,

Figure 7 and 9) and the absence of any indication of the funnel. The far-dorsal extension of the fins may represent the initiation of a downward fin stroke, or the completion of an upward stroke.



FIGURES 16-18.—16, Attitude of cirrates in this figure and in Figures 17 and 18 may represent initiation of or full recovery from a pulsating stroke (see text). This position with curled arms nearly perpendicular to the bottom is typical of the smaller specimens photographed (see Table III). (NA.3660.VIB). 17, This small cirrate may have gone unnoticed had it not been for its distinctive shadow (19 cm estimated diameter). The small (0.8 by 0.4 mm) size of the original image on the negative indicates the great clarity of the water in the Virgin Islands Basin. (NA.3770.VIB). 18, Montage of two photographs taken at a 12-second interval. The similar positions and apparent lateral progress suggest that the cirrate is in the same stage of the pulsating stroke cycle or is holding a fixed position. (NA.3790.VIB)

Neither the interbrachial nor the intermediate webs seems to play an active role in this dynamic, water-ejection mode of swimming.

Figures 14 and 15 are sequential shots that indicate the progress of a specimen across the bottom in the 30-second interval between shots. Using the distance

traveled and the known towing speed of the camera, the average speed of advance of the octopus across the bottom is calculated to be about 63 cm/sec, or about 1.2 knots. The arms are in nearly the same anteriorly directed position in both photographs, so that it is difficult to determine which method of propulsion is being employed. Unless both shots were taken at about the same position during the pulsating cycle, it seems probable that the water-ejection method is being employed, especially in view of the apparent speed of the animal.

Brundage et al. (1967, Figures 6–19 and 6–20) published photographs of two swimming organisms at 2,500 m in the vicinity of the *Thresher*. The specimens were tentatively identified as a “nektonic octopod,” but more precise identification was impossible at that time. Our present experience based on the several photos now available leads to the conclusion that both earlier specimens were the same type of cirrate octopod that occurs in the current series. Each specimen is in the water-ejection mode of swimming. An additional unpublished photograph of the specimen in Figure 6–20 permitted calculation of its speed across the bottom as about 0.25 knots.

Pulsating style.—The pulsating phase begins as the arms are curled or arched back aborally, so that the plane of the basal portion of the arms and the interbrachial web is perpendicular to the longitudinal axis of the body and the distal portion of the arms are arched posteriorly so that the tips are nearly in line with the posterior end of the body (Figure 16, 17, 18). The interbrachial web is contracted proximally along the arms and greatly reduced in surface area as the arms are curled back. The intermediate webs form a broad, tightly stretched membrane between the posteriorly arched arms and the contracted interbrachial web. The large fins, although not visible in photos 16, 17, and 18, probably are arched dorsally to the maximum extent of their recovery (as in Figure 13).

The propulsive stroke begins as the arms are brought anteriorly through an arc; the down-stroke is initiated from the base of the arms and is carried out smoothly to the tips. The arm tips arch and straighten laterally, thus reducing the intermediate webs. This action also pulls the interbrachial web distally along the arms and expands its surface area. The fins swing ventrally in their stroke, providing stability and balance.

The stroke continues as the arms pass through the perpendicular and curve anteriorly. The interbrachial web remains expanded to its maximum surface area so that only the tips of the arms are visible; the intermediate webs remain contracted. The fins have moved well ventrally in their power stroke.

The propulsive stroke ends as the arms swing together into a straight, anterior position, bringing the arm tips close to one another. The interbrachial web is relaxed, and the fins have completed their stroke and are wrapped ventrally around the body. During the pulsating stroke it seems probable that a simultaneous expulsion of water from the funnel would take place, although this cannot be detected in the photographs.

The arms arch posteriorly for the recovery stroke while the interbrachial web remains relaxed, so that as the arms and web sweep in the direction of motion of the animal—a minimum of surface area—a minimum resistance is offered. The fins move dorsally in their backstroke. All components return to the original positions.

Figure 19 may represent a stage of the return stroke since the interbrachial web is deeply billowed anteriorly (orally), a condition that would result as the arms are swept posteriorly. The same configuration could also occur during the transition between water-ejection and drogue modes.

No photographs are available that confirm the steps between the radial position of arms and web (i.e., arms and web perpendicular to the body axis) and the completed power stroke with the arms together. It is possible that the pulsating mode may consist of shorter strokes that begin with arms curled posteriorly and end with straightened arms and expanded interbrachial web perpendicular to the body; each pulse may be followed by a short period in the drogue position.

If the complete pulsating technique of swimming does occur in cirrates in the manner that has been observed in the related *Opisthoteuthis* and in *Vampyroteuthis*, complete photographic confirmation is lacking. With the exception of Figure 20, and to a lesser extent Figure 21, no photos show the interbrachial web strongly billowed in the posterior direction which would be expected during the powerstroke—especially as the extended arms pass anteriorly through a plane normal to the body axis. The interbrachial web in Figures 20 and 21 is billowed, but the



FIGURE 19.—A stage in the recovery portion of the pulsating stroke is suggested by the inward curve of the arm tips and orally billowed interbrachial web. (NA.3620.VIB)

arm tips are strongly curved posteriorly (prior to the horizontal position), and the intermediate webs are greatly expanded.

In the absence of the photographic evidence we have less confidence in the existence of a full-stroke pulsating mode than we do in a short-stroke pulsation and in the water-ejection and the droguelike modes.

Droguelike or umbrella style.—Several photographs show the arms stretched out perpendicular to the body axis and the web almost completely or fully expanded (Figures 22–27 and others in our files). The plane of the brachial crown in these specimens is parallel, or nearly so, to the bottom, and all specimens except the one in Figures 25 and 26 are within 1 meter of the bottom. The relatively large number of photos of specimens in this particular position, rather than in other possible positions to be expected during the pulsating phase, suggests that the cirrates are able to maintain a more passive attitude. The outstretched arms and expanded web certainly create a

large surface-area-to-weight ratio which would further enable a nearly neutrally buoyant animal to maintain a passive or drifting position above the sea floor with a minimum expenditure of energy.¹² Both the buoyancy and viscosity¹³ of cold water make a droguelike or umbrella style of locomotion more effective than in warm water.

As most specimens in the droguelike position are close to the bottom, this attitude probably represents a food-hunting mode. If the bottom were approached too closely, the animal could regain altitude by gently pulsing the arms and web or by use of the fins. The erect cirri on the outstretched arms, as in Figure 20, which may have a sensory function for food gathering, would most effectively cover a maximum area just above the bottom where small planktonic organisms may concentrate.

The hunting-drifting mode is further suggested by the absence of puffs of fine sediment which surely would be present if the animals in the photos had just left the bottom. The passive droguelike mode could begin with a short pulsating movement of the arms which serves to gain altitude for the succeeding drogue phase, or it could be integrated with the dynamic ejection mode.

Certainly a few feet of good quality motion picture footage of some of the specimens shown here would answer many questions about cirrate locomotion. The large number of still photographs, however, has enabled us to suggest a plausible explanation of attitudes in this cirroteuthid in terms of locomotion. We believe that the photographs demonstrate several points: (1) typical octopodan water-ejection locomotion occurs; (2) a pulsation mode of swimming occurs occasionally in these cirrate octopods (somewhat

¹² Cephalopods, in general, are negatively buoyant and must either swim continuously or possess a buoyancy mechanism if they are to remain at their level in the ocean. Several buoyancy mechanisms have evolved in the cephalopods including gas vessels, gelatinous tissues, light-weight ammonium ions (see Denton and Gilpin-Brown, in press) and oil reservoirs (Roper, personal observation). Cirrate octopods have no gas vessels or oil reservoirs, but they are very gelatinous. Whether they concentrate ammonium ions has not been established experimentally, but Percy (personal communication) has observed that freshly caught cirrates have gelatinous arms that appear similar to the NH_4Cl -filled ventral arms of *Chiroteuthis*.

¹³ Viscosity doubles during a temperature change (pressure effect negligible) from 30°C to 3°C (Dorsey, 1940: 182–188).

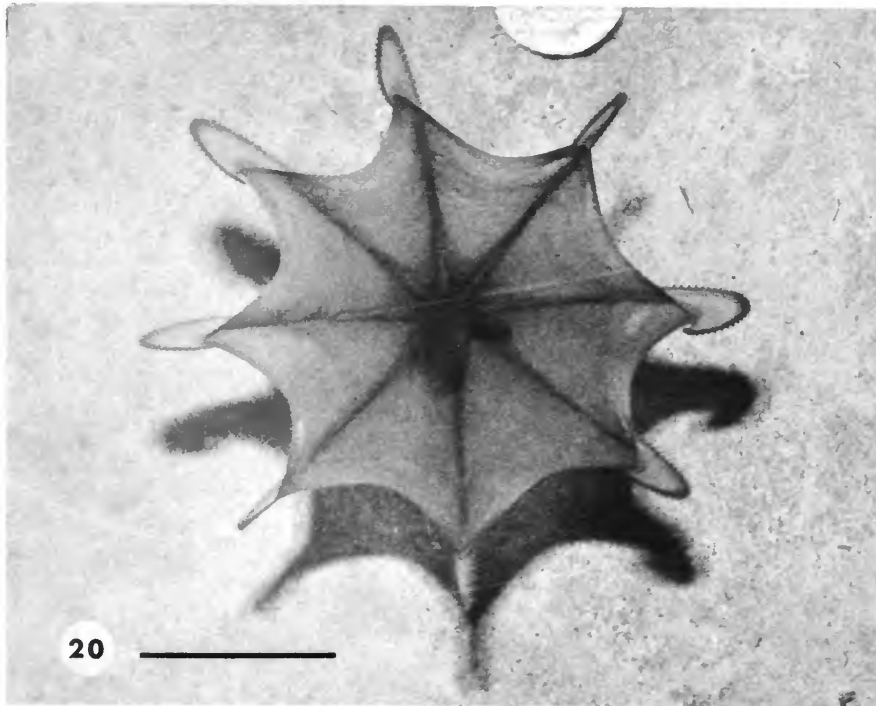


FIGURE 20.—The erect cirri, clearly visible on most arms, probably have a sensory function in hunting for prey. (NA.3970.VIB)

similar to that observed in *Opisthoteuthis*); (3) a passive droguelike attitude is common with outstretched arms and interbranchial web, probably with a hunting function—the umbrella is held in an open attitude such that any natural water movement might act to transport the animal just above the bottom; (4) the interbranchial web and the intermediate webs, in concert with the arms, function as the driving force of the pulsating movement and as the planing surface during the drogue phase.

CIRRI

The function of the papilla-like cirri on the arms of cirrate octopods has long been a topic of discussion among cephalopod workers. Suggestions in the literature for their function include: tactile or ciliary for setting up currents to carry food to the mouth (Hoyle, 1886:56); sensory (Meyer, 1906:201); tactile (Abel, 1916:27). Robson (1932:120) suggested, though not too strongly, that the cirri may be the homologues of the trabeculae or Seitenbrücke

that support the protective membranes in decapod cephalopods. Berry (1952:187) suggested that the cirri are used to sweep microplankton or detritus down the disk toward the mouth of *Opisthoteuthis*.

One photograph in the present series (Figure 20) shows the cirri. The distal position of the arms are curled back aborally and the cirri appear to stand erect and nearly perpendicular to the surface of the arms. Little else can be added, except that perhaps the erectness of the cirri may suggest a tactile-sensory role. The tips of the arms on the swimming specimen in Figure 9 are shown very clearly, but no cirri can be detected.

Since the cirri appear to be erect when the arms and web are expanded, perhaps they function as sensory probes during the search for prey. Possibly the cirri act as receptors to detect movement of water displaced by potential prey organisms. As such, the cirri would have the maximum sensitivity when the octopod was not moving, that is when it was drifting with outstretched arms. If prey were detected in this manner, it could be effectively enveloped by the out-



FIGURE 21.—Light-colored aboral surface on interbrachial web and dark arms seen here was noted on five of the six specimens photographed with open umbrellas in the Blake Basin. Dark banding on web sectors nearest top and bottom of photo is apparently an effect of light and shadow rather than true coloration (NA.5110.BLB)

stretched arms and web in a fashion similar to prey-capturing by shallow-water octopods.

Again, more observations, including histological studies, are needed to determine the function of the cirri.

COLORATION

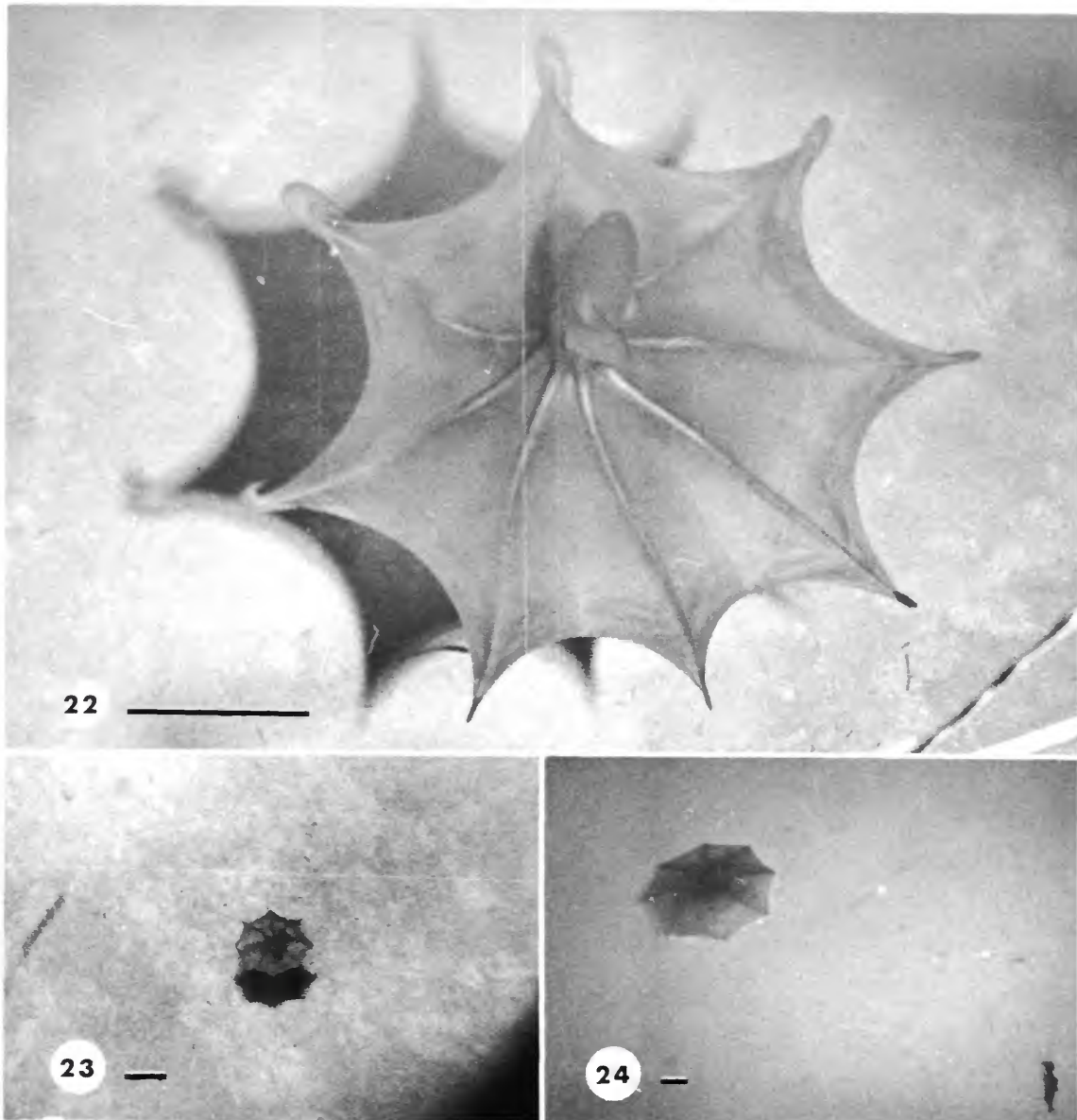
The coloration of preserved specimens of cirrates has been described variously as being from cream white to black, but mostly in hues of red, purple, and brown (see Robson, 1932). While specimens preserved in alcohol and even in formalin lose their true lifelike colors, some coloration does remain and the relative intensities of the coloration on different parts of the body generally persist. Where color is recorded, for instance, most cirrates have a much more darkly pigmented oral surface of the web and arms.

The photos presented here also indicate variation in shading, some of which may be attributable to the distance the specimen is from the light sources, to the angle of the specimen in relation to the light rays, and to differences caused by backscattering from the water column and reflection from the bottom. Other differences may well be natural, but we will restrict our discussion to gross differences that persist regardless of the size of the organism and location of the specimens relative to light, camera and bottom.

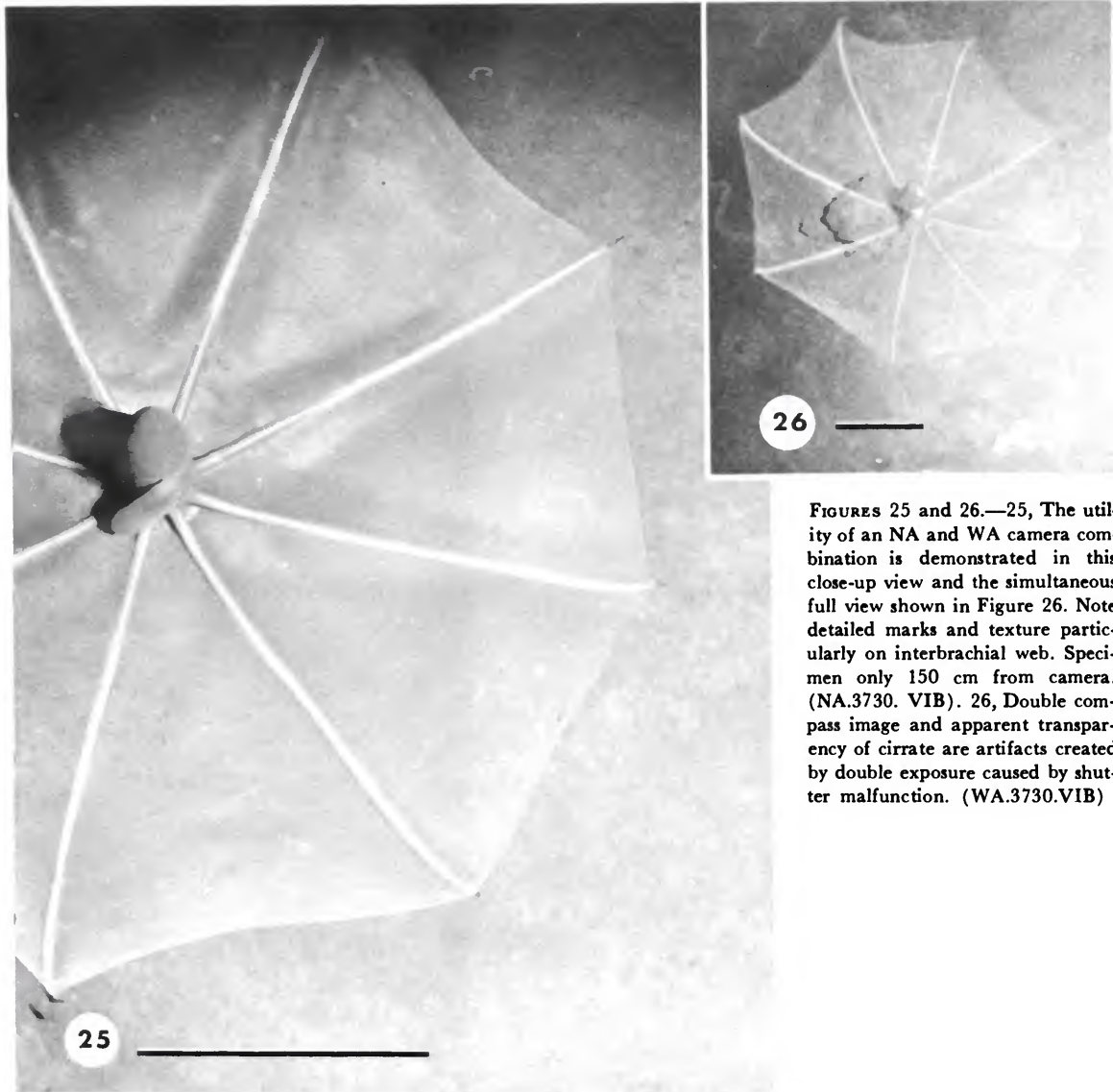
Deep-sea octopods apparently are not as well supplied with chromatophores as their shallow-water counterparts, and they may lack them altogether. Deep-sea cephalopods in general, however, tend to have a basic nearly continuous covering of pigment that may vary in intensity on different parts of the animal. Meyer (1906:188–189) stated that *Opisthoteuthis* has no true chromatophores on the outer surfaces of the animal. The large pigment cells present are not expandable and contractile. True chromatophores occur interiorly only on the intestine, gonads and mantle cavity.

Differences in coloration¹⁴ are apparent in the photographs. In this discussion of coloration we have attempted to eliminate differences due to light and shadow on the basis of our knowledge of the location of the light source in relation to the location of the specimen. In Figures 20, 23, 24, and 27 the body, head, fins and arms are dark and the aboral surface of the web is lighter, probably as a result of light reflected off the light-colored bottom passing through the thin membranous web. The arms appear dark because of their thickness and opaqueness in relation to the web. The specimen in Figure 25 is well off the bottom and close to the camera vehicle. The body and fins, which appear to have an almost velvety texture, are dark; the arms are highlighted by the strobe light; the web is lighter than the body but appears to be pigmented nonetheless (this is true of Figure 22 also). Figure 26 shows the same specimen as does Figure 25, but it is a double exposure and makes the specimen look transparent. In Figures 14 and 15, the body, head, and basal portion of the arms are light, while the arm tips are dark.

¹⁴ In a strict sense the use of "color" and "coloration" in this discussion is inaccurate because all photos are black and white prints. We assume, however, that the photos register grades of shading in proportion to (intensities of) the pigmentation known to exist in cirrates.



FIGURES 22-24.—22, Open umbrella-like posture of cirrate in Figures 20-27 occurs in nearly half of the cirrate octopod photos in our files. This posture is interpreted as a passive drifting-hunting mode that requires little energy expenditure. (NA.3770.VIB). 23, Cirrate in droguelike mode with outstretched arms and web. Lack of resolution in this and other WA photographs from the Virgin Islands Basin is due to use of an aerial lens mounted behind a transparent hemisphere and not to unclear water. (WA.3710.VIB). 24, Largest cirrate octopod known to date is seen in this photograph from Canaries Basin (170 cm estimated diameter). Dark object (lower left) is probably a fragment of sunken algae (possibly *Sargassum*). (WA.3500.CAB)



FIGURES 25 and 26.—25, The utility of an NA and WA camera combination is demonstrated in this close-up view and the simultaneous full view shown in Figure 26. Note detailed marks and texture particularly on interbrachial web. Specimen only 150 cm from camera. (NA.3730. VIB). 26, Double compass image and apparent transparency of cirrate are artifacts created by double exposure caused by shutter malfunction. (WA.3730.VIB)

The specimens in typical swimming position (Figures 7 and 8) are very light; the arm tips in both are pigmented and the body in Figure 8 shows dark shading. The swimming specimen in Figure 9 has a moderately to lightly pigmented body and head; the fins appear pigmented around the edges but lighter

toward the bases. The aboral surface of the arms and interbrachial web proximally are quite light, whereas the surfaces of the arm tips and the border and oral surface of the web are pigmented. The specimen in Figure 11, although far less distinct, shows a similar coloration. The body, head and proximal portion of



FIGURE 27.—Smallest cirrate photographed in the drogue-like posture (46 cm estimated diameter). It has a translucent web through which details of its own shadow can be seen. (NA.3770.VIB)

the arms of the specimens in Figures 10 and 13 are darkly pigmented; the distal tips of the arms are lightly pigmented; the fins are light, with slightly pigmented borders in Figure 13. The relatively small specimens in Figures 16–18 appear to be heavily pigmented.

In Figure 21 the body, fins and arms are darkly pigmented; the web is very light and apparently opaque.

The specimen in Figure 28 has a dark pigmentation over the entire body with an elongate light patch on the dorsal surface of the mantle at the base of each fin. Similar light patches appear to be present also in Figures 9, 10, possibly 16, 29 and others in our files. The distal edge of the interbrachial web also appears to be very lightly pigmented in Figure 28. Other light patches on the left side of the specimen at the posterior end and along the head may be explained as



FIGURE 28.—This cirrate apparently had been injured, judging from its torn interbrachial web and unusual markings along its left side. Photo from Heezen and Hollister, 1971, fig. 2.64 [specimen misidentified in figure and in text, p. 86, as "vampire squid"], by permission of Oxford University Press (scale estimated by Hollister, pers. comm.). (TH.5202.SAP)

damaged areas, since the web has a large tear distally between left arms I and II.

Figure 29 shows a specimen in an unfamiliar attitude in that its oral surface is directed diagonally

away from the bottom; this represents the only photograph we have showing the oral surface of the brachial crown complex. The dorsal surface of the mantle, head, tips of arms and oral surface of arms and web are darkly pigmented. The distal edge of the interbrachial web is lightly pigmented. The proximal suckers, where visible on four of the arms, also are lightly pigmented in comparison with the surrounding tissues. Distal suckers are not visible so apparently they match the pigmentation of the darker arms and web.

The dark pigmentation in the photographed specimens probably includes several shades of reddish or purplish-brown if it resembles that of most described material (see p. 26. Live *Opisthoteuthis californiana* are a dark reddish-brown (Pereyra, 1965).

"Reverse coloration" has been described in some animal groups. For instance, Hansen and Madsen (1956:57 et seq.) discussed deep-sea holothurians

that are a darker brown or purple ventrally than dorsally. Hansen and Madsen (p. 56) present a translated quote from Ostergren (1938:89) which advances the theory for deep-living (benthopelagic and pelagic) holothurians that the dark ventral surface absorbs light and gives protection from below, while the same holds true for the light dorsal surface against the bottom when viewed from above. According to Hansen and Madsen (1956:56), "Most psychropodids and species of *Paelopatides* are of a violet color and often with the ventral side the darker."

Forster (1967) described a new species of deep-sea ray, *Breviraja pallida*, which is characterized in part by a very pale brown dorsal surface and a dark brown ventral surface (p. 284). At least three other species of ray from deep water have the ventral surface more darkly pigmented than the dorsal surface, although they are not as pale dorsally as *B. pallida* (Forster, p. 286).

While it is difficult to interpret the large variety of color patterns shown in the photographs, the following discussion presents an interpretation that seems to parallel the observations concerning reverse coloration in some other animals cited above.

In most cirrates the oral surface of the web is more heavily pigmented than the aboral surface. The oral surface would face the bottom if the animal spread open its arms and web while in the pulsating or drogue modes of swimming, or preparatory to pouncing on prey. If viewed from below by bioluminescent light, the only source of light at great depths, the dark oral surface would not reflect light but instead would absorb it and blend into the black background overhead. Similarly, if the animal were being approached by a luminescing predator, either from below or horizontally, the outspread arms and web with very dark oral surface, which would face the predator, would blend with the dark background. The cirrate could either splay the arms and web initially when perceiving an attack, then undergo the typical octopodan escape reaction, or it could escape and then hang unseen in the water with dark oral surface of arms and web spread out facing in the direction of the attacker.

Furthermore, cirrates entirely lack an ink-sac which functions effectively as a defense mechanism in shallower dwelling incirrate octopods. The splaying of the arms and blending into the dark background by a cirrate would be the analog of the ink-ejection and



FIGURE 29.—Cirrate at calculated height of 4.5 m above the bottom (see Table II) and only 10 cm below approaching compass. Note light colored suckers on oral surface of brachial crown. (NA.5110.BLB)

blanching out of chromatophores to blend with the light background of the shallow-water octopods. The survival value of each technique seems well suited to the particular habitat.

If these cirrates are lightly pigmented aborally or dorsally, as indicated in some photos (Figures 7-9, 11, 14, 15, 21 and others on file), the light coloration would also provide survival advantage when viewed from above. The animal would reflect bioluminescent light from above and would blend in with a light-colored sediment in the background.

Functional coloration in deep-sea animals is an interesting subject and one in which further investigation may shed light on other aspects of the biology of these organisms.¹⁵

RELATIVE ABUNDANCE

Although it is difficult to derive a picture of true abundance of a mobile benthopelagic deep-sea species, it is possible to get an idea of relative abundance or population density of a species on the basis of a large series of photographs from different localities (Marshall and Bourne, 1964:226, 237, 240).

The technique of assessing deep-sea populations by towing a camera about 5 m above the bottom may provide more accurate estimates than deep benthic sampling devices such as dredges, Blake trawls and otter trawls. This would be particularly true of some of the more mobile benthic and benthopelagic spe-

cies, e.g. fishes, cephalopods and prawns, which may be able to detect and avoid the nets. In addition, firmly attached forms such as some sponges, crinoids and anemones for example, may not get scraped off the substrate. The camera tends to be indiscriminate while nets are selective.

When the "fish" operates 5 m above the bottom taking pictures at 10-second intervals, the photographs represent a discontinuous 4.5 meter-wide swath across the bottom (each photo covers an area of 3.1×4.5 meters). The areal coverage is similar to that expected from a sampling device of equivalent width, e.g. a 15-foot (4.5 m) Blake or otter trawl, but the photographs are undoubtedly more representative; in addition to the losses due to net avoidance by swimmers and to firmly attached organisms, it has been shown that deep benthic sampling devices move very erratically across the bottom (Aumento and Lawrence, 1968:11).

We recognize, of course, the possibility that the flashing light source, clicking sonars and other disturbances of the towed "fish," may attract or repel some organisms. In the case of the octopods some were photographed in the hovering position, apparently undisturbed; others were photographed in typical jetting attitudes, possibly having been disturbed or attracted. If the instrument vehicle does have a disturbing effect on the octopods, it is possible that some escaped detection by the camera. The lack of multiple photographs of the same specimen indicates that the octopods are not strongly attracted to the camera vehicle.

We have series of photographs from four different localities that can be used to estimate relative abundance. Only NA camera photographs were used in this comparison. Although several WA photographs show cirrates, these have been excluded from the calculation of abundance, because this WA camera does not resolve sharply enough in the peripheral area to assure an accurate count. Areal coverage per unit photograph differed greatly throughout the series because of different camera altitudes and angles of bottom view. The Virgin Islands Basin and Blake Basin series are almost entirely vertical views. Those from Bermuda and Northeast Channel areas comprised about two-thirds oblique and one-third vertical views arranged in an overlapping format. The resulting bottom area covered resembled a bow tie in outline (see Figure 6-2 in Brundage et al., 1967). In calculating

¹⁵ This speculation concerning the observed coloration pattern in cirrates, which is included here to stimulate interest and discussion about this phenomenon in some deep-living animals, must assume several points. First, sufficient bioluminescent light must be available to make the counter-shading of value. To our knowledge no detailed studies exist that give information about the quantity or quality of bioluminescent light on and just above the bottom of the deep sea. Second, a predator, or predators, presumably fish, should be large enough to be able to capture the octopods which may exceed one meter in length, and should have eyes functional enough to utilize the available light to detect potential prey (image formation is not necessarily required). While the largest known deep-sea benthopelagic fish, brotulids of the genus *Parabassogigas*, grow to a length in excess of 1 meter and have functional eyes, their weak tooth structures indicate that they are scavengers rather than predators (D. Cohen, pers. comm.). (Highly developed teeth, however, would seem not to be requisite for ingesting the soft-bodied, semi-gelatinous cirrates.)

the area the assumption was made that the towed instrument vehicle remained horizontal and that the bottom was flat. The following table presents com-

parative data from only those NA films which were of sufficient quality for examination for the presence of cirrate octopods:

Locality	Average Depth (meters)	No. Photos	Total Area Covered (km ²)	No. of Cirrate Octopods	Abundance Value ^a
Virgin Islands Basin	3900	5300	.061	6	98
Blake Basin	5000	10,000	.187	6	32
Bermuda	4300	10,300	.896	1	1.1
Northeast Channel	2500	38,400	2.36	3	1.3

^a Abundance value = No. cirrate octopods/km².

The Virgin Islands Basin and the Blake Basin have abundance values at least one order of magnitude greater than the other two areas where sufficient numbers of photographs are available for study. The Virgin Islands Basin area is unique among the four in being quite close to land (islands) and being an enclosed, steep-sided basin with a relatively shallow sill depth. The basin appears to have an internal anti-cyclonic circulation. Erosion channels produced by turbidity currents and subsequent density flows are evident in some photographs (e.g., Figure 51). Perhaps a combination of these factors contributes to an unusual enrichment of the basin from shoal water by organic material such as sea grasses (*Thalassia* and *Syringodium*), mangrove leaves and other debris, as seen in a number of photographs (Figure 39, 43, 49, 52, 53) (see discussion on p. 42).

The Blake Basin is also enclosed, but the maximum relief of the sill above the 5,000-m deep basin is less than 300 m (Pratt, 1968, pl. I). While this readily distinguishes the Blake Basin from the Virgin Islands Basin there are similarities which may account for the relatively high abundance value. Contour currents in the area north of the basin would tend to transport plant debris southward into the basin. Menzies and Rowe (1969:219) have suggested that such currents transport algae southward on the slopes north of the Blake Outer Ridge. Bathymetric contours directly north of the Blake Basin indicate that a similar mechanism occurs in the basin. We have a number of photographs in our files which show both grass blades and *Sargassum* clumps on the floor of the basin. We also have photographs of an erosion channel along which there is a

broad accumulation of plant debris, primarily *Sargassum*.

Finally, there is an apparent northward decrease in the abundance value of cirrate octopods. Whether this reflects geographic, topographic, trophic or some other factors cannot be determined at this time.

ADDITIONAL CIRRATE PHOTOGRAPHS

After this manuscript was completed, we received a set of very fine photographs of a single cirrate from R. R. Hessler, Scripps Institution of Oceanography. The photos were taken during a dive of the Woods Hole Oceanographic Institution's submersible *Alvin* at about 39°46'N 70°32'W (90 miles south of Martha's Vineyard) at a depth of 1,300 m. We are most grateful to Dr. Hessler for supplying us with the photos and his observations, and we acknowledge the WHOI deep submersible program.

The photographs were taken with an externally mounted EG&G camera/strobe combination. Locality data are:

Alvin Dive No. 225, 26.IX.1967

Start of dive: 39°47.4'N 70°31.9'W

End of dive: 39°43.8'N 70°32.9'W

Depth: 1300 m

Pilot: Val Wilson

Scientists: Robert R. Hessler, George R. Hampson

Although the specimen appears to be a different species than that shown in our other figures, the photographs are included here because they show features not observed previously and because of Hessler's informative direct observations of the octopod.

Observations.—The following is based on the ob-

servations made by R. R. Hessler (pers. comm.). The octopus apparently had perceived the submersible before the observers sighted the specimen. When first observed out of a side port, the cirrate was hanging motionless in the water about 2 m above the smooth sedimentary bottom with its tentacles and web spread out so that the oral surface faced the vehicle. The plane of the arms and web was oriented normal to the bottom, so the body was not visible to the observers. The submersible was turned so the specimen could be photographed with the forwardpointing cameras. The first photographs show the cirrate with arms still in the spread-out position (Figure 30); in later shots the arms are closed (Figures 31–33). Once the submersible was turned toward the octopus, the specimen could no longer be seen by the observers, so direct observations of its locomotion and behavior from that point on could not be made.

Hessler estimated that the specimen was about one foot in diameter across the outstretched arms, although size determination is difficult from a submersible without a scale reference.

The color of the cirrate was a "deep brownish-red" over the entire surface of the animal. The suckers, as shown in Figure 30, were very light, almost white—"actually a light cream color" (quoted from Hessler). The photographs indicate that the color intensity was nearly uniform over the entire animal.

The bottom depth of 1,300 m is considerably shallower than that of our other photographs, but it is well within the range recorded in the literature for cirrates in general.

Photographs (Figures 30–33).—In Figure 31 the animal appears very long and slender with a short, conical mantle. The fins are not visible as they are tightly wrapped ventrally around the mantle. The head is broader than the mantle, and the large right eye protrudes from the surface so that the whitish lens is clearly visible. The arms are very long and held together so that the web is relaxed.

In Figure 32 the specimen is in much the same position as in Figure 31, but this is a ventral aspect that shows the fins wrapped ventrally around the mantle with the right fin overlying the left. The tips of the arms extend beyond the margin of the interbrachial web, and cirri are lacking from the visible portions of the arm tips.

The funnel can be seen in the ventral view of the specimen in Figure 33; it appears as a dark spot on

the ventral surface of the head nearly in line with the anterior borders of the fins. The fins appear to be in different positions: the right fin looks to be nearly perpendicular to the body while the left fin is swept further ventrally and appears to be rotated slightly on its axis. This indicates the capacity for independent movement of the fins and that the fins may serve as stabilizers in position-holding as well as driving oars in swimming.

In Figures 31, 32, 33, the specimen appears to be in the more or less typical cephalopoden swimming mode with arms held together in line with the body axis and with fin action, and possibly water ejection, used to hold position or to move slowly.

Figure 30 is an unusual shot of the entire oral surface of the outstretched arms and interbrachial web directed at the camera. The suckers in a single row along each arm appear very light-colored in contrast to the dark background of the web. The location of the mouth can be seen at the confluence of the bases of the arms. The long cirri are clearly visible along each side of the arms. They appear to originate very near the proximal end of the arms and continue nearly to the level of the margin of the web where they terminate, leaving the free distal tips of the arms devoid of cirri.

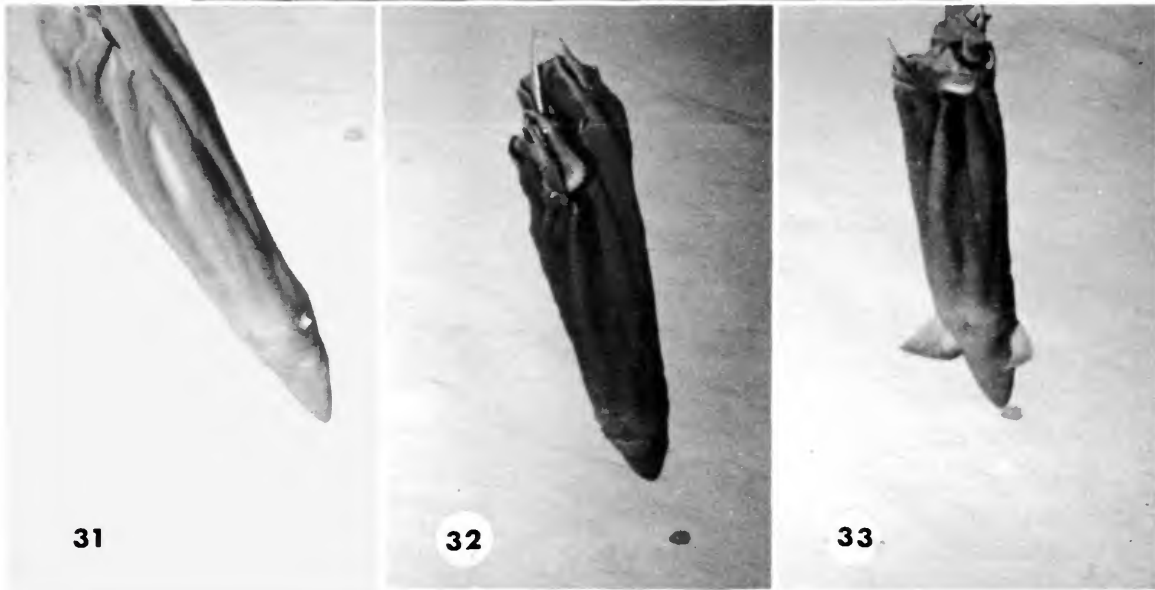
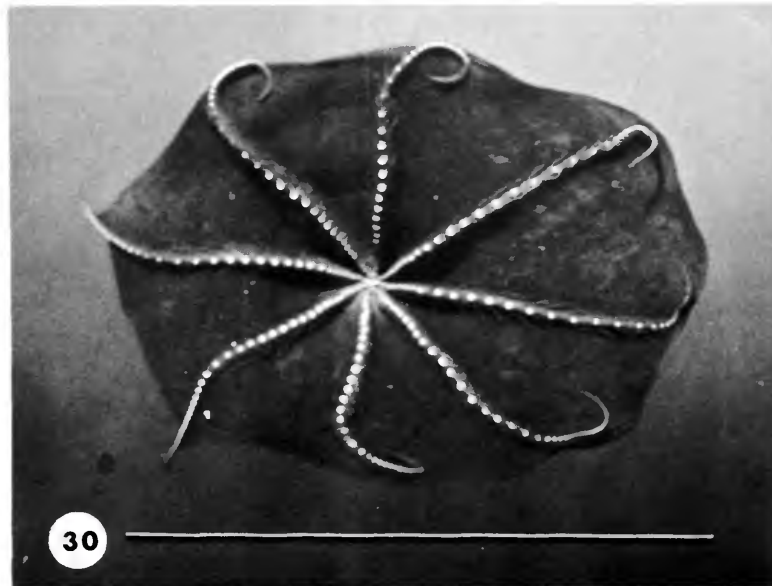
The intermediate or secondary web, so frequently visible in our other photographs, appears to be entirely lacking on the specimen in this set of photographs (4 published here, and 4 unpublished).

Initial observations and subsequent photographs (Figure 30, plus one other in the series) reveal the animal with arms and web outstretched so that the plane of the oral crown is facing the vehicle and camera. This may be a defensive attitude, as suggested in an earlier section. Subsequent photographs (Figures 31–33 plus others in the series), taken when the vehicle and camera were very close to the specimen, show the specimen in a jetting attitude heading away from the camera, but making very slow progress.

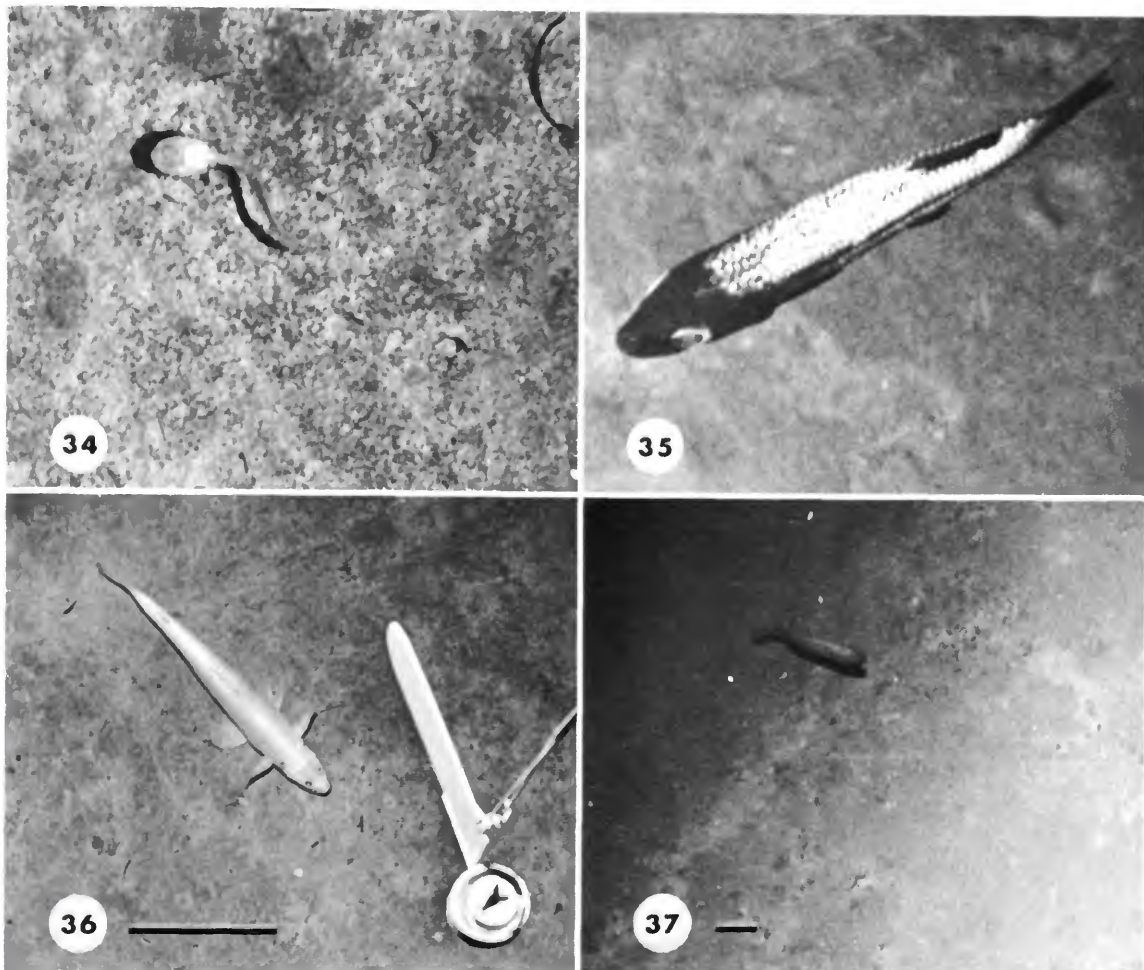
Associated Organisms

ANIMALS

The series of photographs from the Virgin Islands Basin contains a number of shots of organisms other than cirrate octopods. During the operations the bottom structure ranged from a smooth, relatively finely



FIGURES 30-33.—30, View of oral surface of arms and interbrachial web of cirrate showing suckers (white dots) and cirri along arms. (Photo and estimated scale from submersible *Alvin*; R. R. Hessler) (NA.1300.MVS). 31, Swimming cirrate with fins folded ventrally. Note bulging eye and lens. (*Alvin* photo; R. R. Hessler) (NA.1300.MVS). 32, Ventral view of swimming cirrate showing folded fins and location of funnel (dark spot immediately anterior to fin). (*Alvin* photo; R. R. Hessler) (NA.1300.MVS). 33, Ventral view showing fins expanded and location of funnel (dark spot on ventral surface of head between bases of fins) (*Alvin* photo; R. R. Hessler) (NA.1300.MVS)

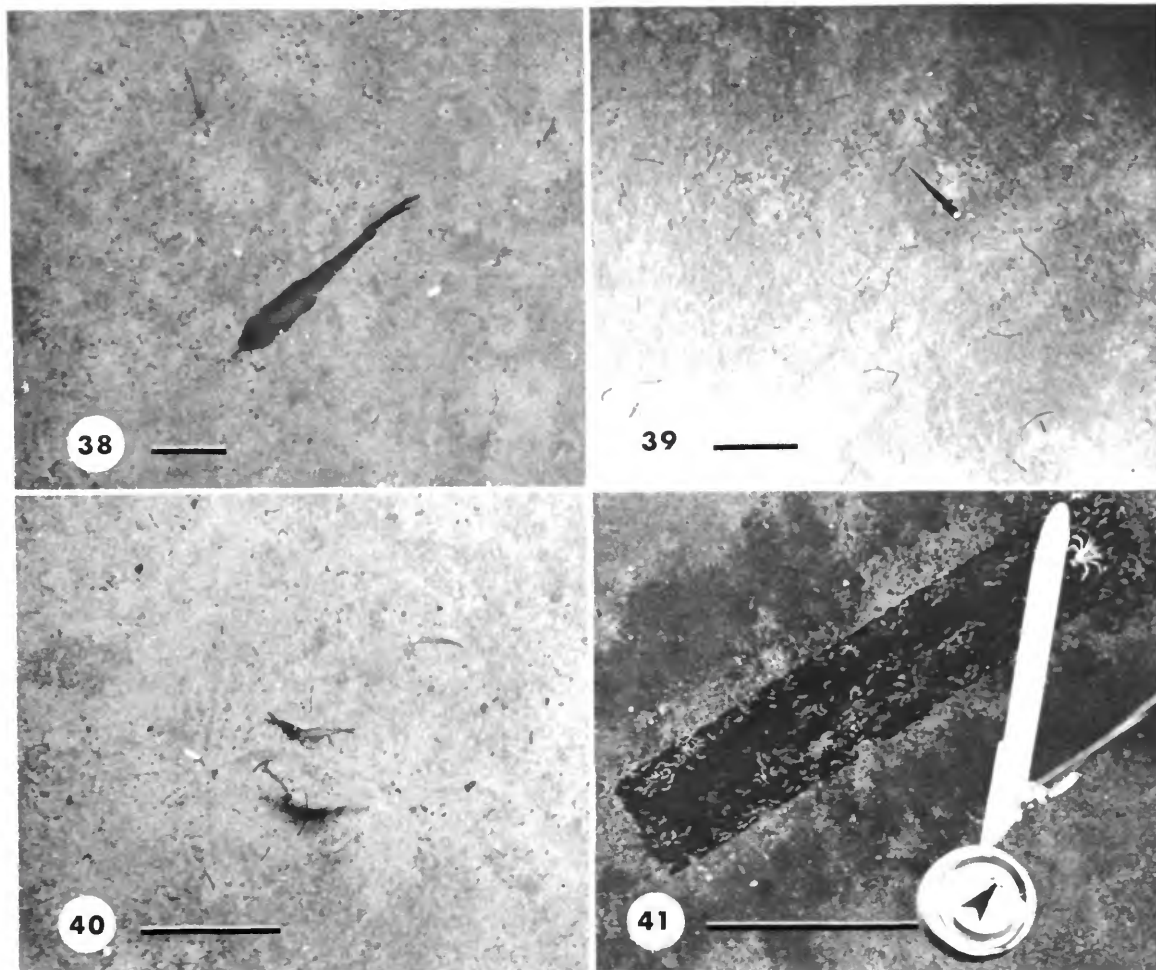


FIGURES 34-37.—34, The large-headed, slender-bodied, unidentified fish was the most common fish photographed in the Virgin Islands Basin. (NA.3950.VIB). 35, An unidentified species of the fish family Alepocephalidae. (NA.3810.VIB). 36, A species of *Bathysaurus*. (NA.3870.VIB). 37, A brotulid near the edge of the field of view. (NA.3790.VIB)

sedimented bottom, to a coarse gravel and boulder bottom, to deeply cut turbidity channels in compact sediment, to undercut and exposed rock outcroppings¹⁶ along the steeply sloping portions of the bottom. Photographs of the various habitats show a variety of organisms—both attached and mobile benthic forms, benthopelagic species, and lebensspuren.

¹⁶ We define outcroppings as rocks that appear to be uncovered portions of larger rock masses as distinguished from boulders that appear as isolated, unattached rocks.

Several different species of fishes were photographed. A common hindrance to the identification of deep-sea fishes from photographs is that the majority of photos view the fish from the dorsal surface, an aspect from which ichthyologists seldom examine their material. The most commonly photographed fish from the Virgin Islands Basin (Figure 34) is unidentifiable because it is always seen in dorsal aspect, from which it looks like any of several different groups. (In tabulations we refer to this as "Big head", realizing that several species may be represented.) The unusual dorsolateral view in Figure



FIGURES 38-41.—38, A morid or deep-sea cod. (NA.3880.VIB). 39, A species of *Ipnoys*. The brilliant spot on the head is a reflection from the highly modified, nearly fused eyes. Note accumulation of sea grasses on bottom. (NA.3780.VIB). 40, This unidentified species of penaeid (or caridean) decapod crustacean was often photographed close to the bottom. (NA.3880.VIB). 41, The galatheid crustacean to the right of compass vane is a species of *Munidopsis*. The dark rectangular shape is evidently a piece of waterlogged wood encrusted with serpulid polychaete worms. (NA.3880.VIB)

35 shows a species of the family Alepocephalidae. Other identifiable fishes include a bathysaurid (cf. *Bathysaurus*) (Figure 36), a brotulid (Figure 37), a morid (Figure 38) and an unidentified species of *Ipnoys*, a genus characterized by highly modified, nearly fused, dorsally located "eyes" (Figure 39) (Authority: R. H. Gibbs, Jr., G. Mead, N. B. Marshall, D. Cohen, J. Nielsen, pers. comm.). Most fish

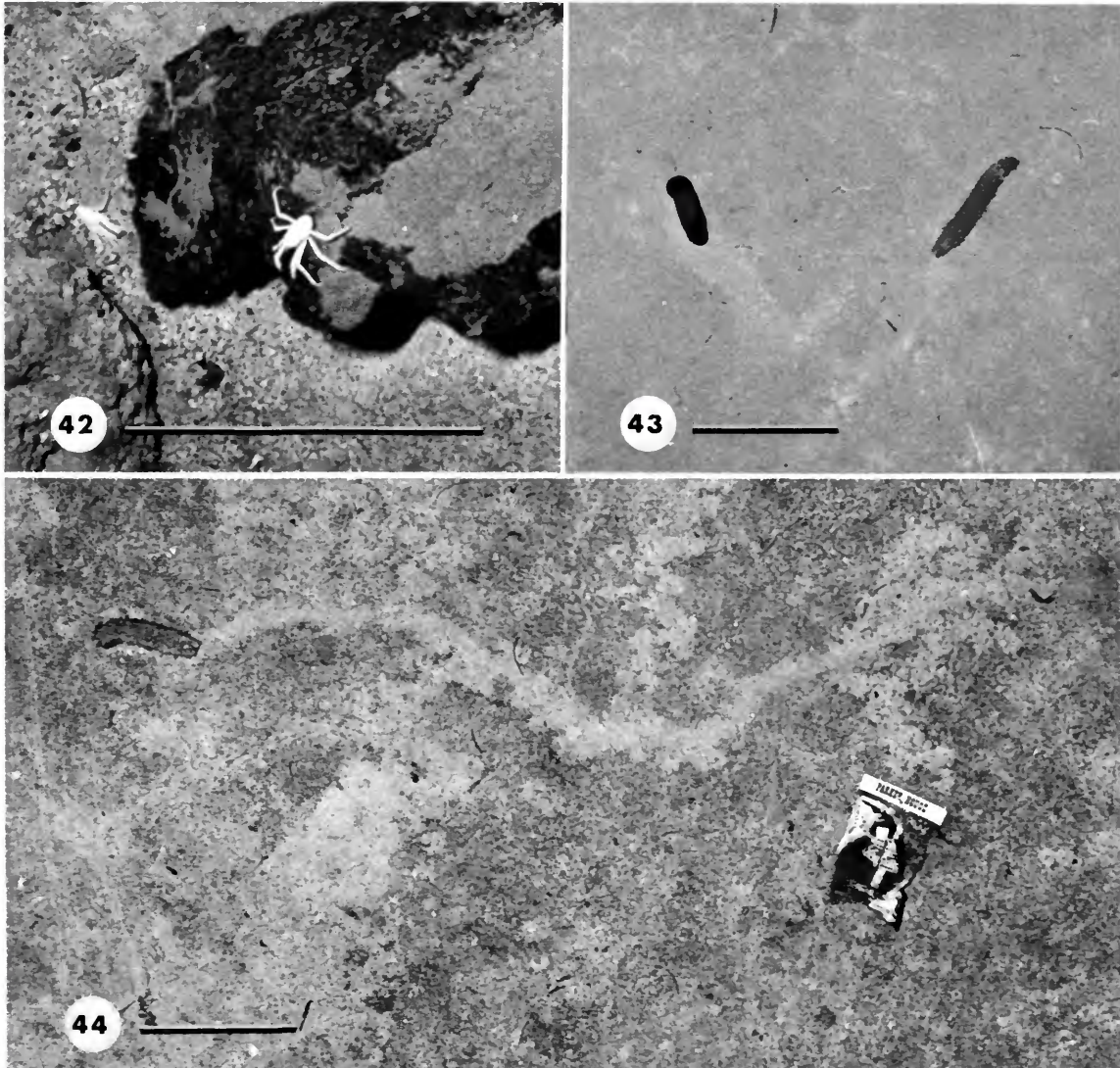
were photographed swimming within a few centimeters of the bottom

Several photos of a species of penaeid or caridean decapod crustacean are available (Figure 40; I. Canet, pers. comm.). This species appears to be benthopelagic since all specimens (more than 50 in two camera runs) were photographed just above the smooth sediment of the open bottom. A commonly

seen crustacean was the galatheid *Munidopsis* (Figure 41; F. Chase, R. Manning, pers. comm.). This photograph also shows what appears to be a piece of water-logged wood settled on the sediment, heavily encrusted with serpulid polychaete worm tubes (M. Jones, pers. comm.). Galatheids are abundant

in some portions of the area (Figure 42) (not all are verifiable as *Munidopsis*) and generally seem to be associated with a solid substrate such as rock, small boulders or wood; few photos show them on the open bottom.

At least two species of elaspod holothurians were

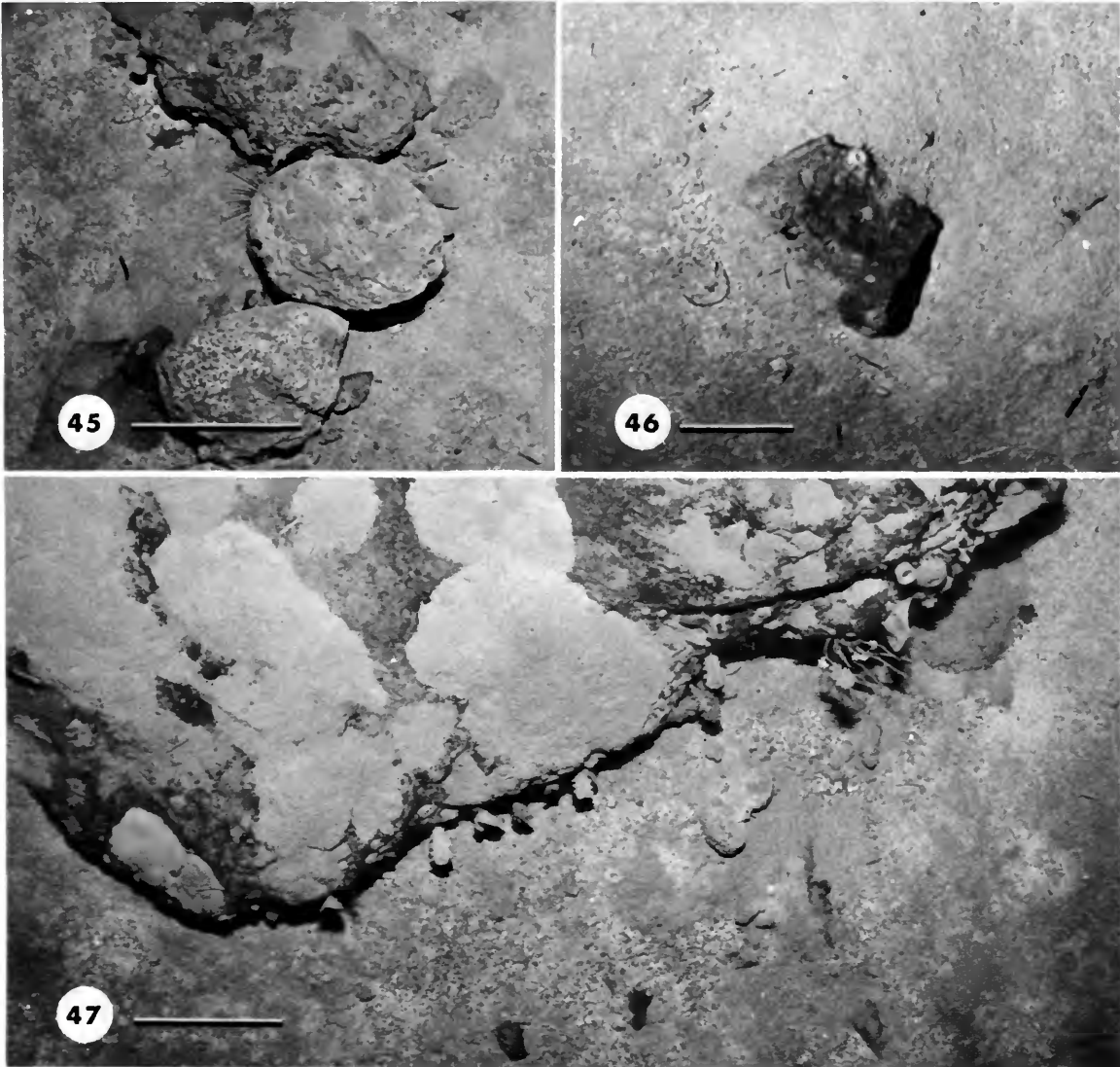


FIGURES 42-44.—42, Galatheids were photographed primarily on or near firm substrates. (NA.3850.VIB). 43, Holothurians common to the area were *Psychropotes* species (left) and a laetmogonid (right). Note the density of sea grass fragments. (NA.3860.VIB). 44, A laetmogonid cuts a trail near a polyethylene wrapper. Animal trails have been traced on a series of photographs over distances of several hundred meters. (NA.3880.VIB)

commonly photographed on the finely sedimented open bottom generally devoid of rocks. *Psychropotes* species and a species of Laetmogonidae (D. Pawson, pers. comm.) occur together in an area of concentration of organic debris, consisting of sea grasses (*Thalassia* and *Syringodium* [*Cymodocea*]) (Figure 43). Figure 44 shows a laetmogonid and its lebens-

spur across the sediment; evidence of man's contribution to the deep benthic environment also is present in this figure.

Several photos show what appear to be anemones (Figure 45), although a species of curved- and long-spined echinoid cannot be entirely ruled out because only appendages and no bodies are visible. Figure 46



FIGURES 45-47.—45, Tentacles of a sea anemone (or possibly a curved-spined urchin) protrude from behind the center boulder in this varied cluster of rocks. (NA.3920.VIB). 46, A light-colored anemone is attached to the upper edge of the dark boulder. (NA.3860.VIB). 47, Four species of sponges are affixed to vertical edge of outcrop. Scale is for level area at bottom of photo. (NA.3920.VIB)

shows another species of anemone or possibly a solitary coral.

In some photographs showing rock outcrops and boulders, attached organisms are very numerous, e.g., sponges, coelenterates and brachiopods. Figure 47 shows a partially scoured rock outcrop with four different species of sponge attached along the vertical face (K. Ruetzler, pers. comm.). Most sessile organisms seen in numerous similar photographs are located on the vertical face of the outcrops or boulders; seldom are organisms seen on the horizontal surface. This common orientation may be a response to more favorable position in the slight currents or to avoid sedimentation.

Many photographs (about 40 on a single camera lowering) were taken showing one or more irregularly shaped, debris-covered organisms at the end of a lebensspur (Figure 48). The organism appears to be a mollusk (J. Rosewater, J. Allen, pers. comm.), but photos do not reveal sufficient detail to settle the question of whether it is a gastropod or a bivalve. A small portion of light-colored material (shell?) is seen beneath or surrounded by each clump of plant debris; the photo shows small tendril-like appendages extending from the periphery of the light material. Each specimen and its accumulated "trappings" left a distinct meandering trail through the soft, sedimented bottom. Some photographs show accumulated clumps of plant debris, probably *Sargassum*, around which are gathered numbers of these curious organisms and their lebensspuren (Figure 49).

We have attempted to make an estimate of the relative abundance of some of the more commonly photographed motile, epibenthic and benthopelagic macroorganisms. The count estimate is based upon 2,500 photographs taken on a single run by the same camera on 27 November 1969 with an average altitude of the camera of 4 m. The total area surveyed by these 2,500 photographs was approximately 26,000 m². The photographs were all located in the SW hachured area of Figure 2. The following counts were obtained:

Sea Cucumbers	
Laetmogonidae—50	
<i>Psychropotes</i> —54	
Crustaceans	
Shrimp—34	
Galatheididae (including <i>Munidopsis</i>)—13	
Fish	
<i>Ipnopts</i> —3	

"Big Head"—5
Others—9
Other organisms¹⁷—7.

LEBENSSPUREN

The term "lebensspuren" is defined in its simplest sense as "... structures in the sediment left by living organisms" (Häntzschel, 1962:W178). The term applies equally to fossil and recent tracks, burrows, and other marks made by animals and plants on or in the sediment. Although "lebensspuren" has been utilized primarily by paleontologists, it is a convenient, descriptive word that can apply to numerous features seen in deep-sea photographs.

The surface sediment in the Virgin Islands Basin appears ideally composed for revealing trails and impressions made by the benthos. The coarse, light-colored and easily moved constituents of the sediment settle readily into depressions in the contrasting darker background composed of finer sediment. Holothurians were frequently photographed at the end of plainly marked meandering trails (Figures 39, 40), which form complicated patterns extending hundreds of meters over the flatter parts of the area. Other trails made by less easily identified organisms are also common, e.g., Figures 48, 49.

Another common type of lebensspuren consists of a radial arrangement of straight lines or grooves extending out from a shallow, round, central depression (Figure 50). The radial pattern frequently encompasses a full 360°, but occasionally lesser arcs occur (Figure 27). Invariably a smooth, widely conical mound is located close to or within the radial pattern of grooves. An indistinct depression generally can be detected at the summit of the mound of sediment. These lebensspuren are very abundant along the edges of erosion channels, generally in rock-free areas (Figure 51). Some, however, have been noticed on large rock surfaces that have been mantled with a layer of sediment.

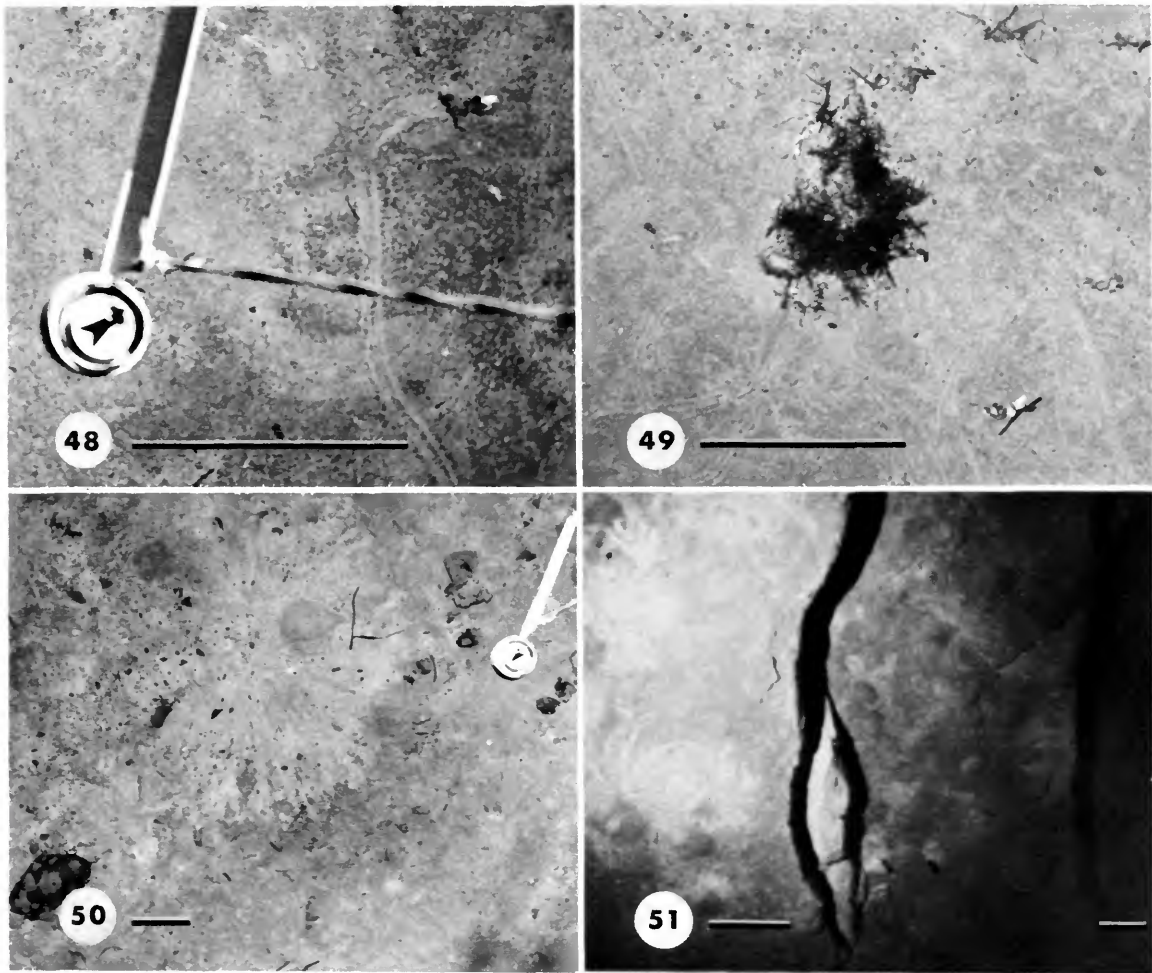
Despite the abundance of the radial patterns in bottom photographs, no organism or part of an organism responsible for the marks has been detected. It seems likely, however, that they mark the location of burrows, possibly of polychaete worms. The cen-

¹⁷ Other organisms include 3 asteroid starfish, a light-colored holothurian, and 3 unidentified dark animals that may have been echinoids or sea anemones.

tral depression and mound arrangement in deep-sea photographs, but not necessarily the radial patterns, are reminiscent of some polychaete burrows found on sedimented bottoms in undisturbed shallow waters. If this is so, then the central depression is the entrance of the U-shaped burrows; the radial lines (grooves) are made as the organism extends part of its body and drags it back across the sediment,

presumably collecting food; the mound is the effluent pile where ingested silt and wastes are deposited.

The large number of photographs that contain these radial lebensspuren indicates that several different kinds occur. The radial lebensspuren photographed in the Virgin Islands Basin seemed to be much more abundant than is indicated in the summary of such benthic features reported by Ewing



FIGURES 48-51.—48, White object (upper right) with light tendril-like appendages is part of an unidentified animal, probably a mollusk, which drags accumulated bits of debris across the bottom. (NA.3890.VIB). 49, Accumulations of plant debris were often photographed surrounded by lebensspuren (life-trails) and trailmakers (as that seen in Figure 48). This large clump probably is *Sargassum*. (NA.3920.VIB). 50, Radial grooves extending out from a central depression (light fan-shaped patch) were a type of commonly photographed lebensspuren (life-trail). (NA.3880.VIB). 51, Several radial lebensspuren on terraced side of erosion channel. Note block of compact sediment recently calved from edge of upper terrace. Scale mark to left is for uppermost terrace, to right for lowest level. (NA.3970.VIB)

and Davis from the deep sea floor more remote from land (1967, see especially Figures 24–53 through 24–63). These authors proposed a scheme of classification for lebensspuren.

PLANT DETRITUS

Several types of detrital plant material occur in the photographs. Two different sizes of long, thin, grass-like fragments can be seen in nearly every bottom photograph. The most common fragments are those with an average width of 1.5 mm, while others between 6 and 12 mm in width are present in much smaller numbers (Figure 52). The latter closely resemble the foliage leaves of the turtle grass, *Thalassia testudinum*, which at maturity has a tendency to break off just above the sheathed portion at the base (see Tomlinson and Vargo, 1966:758 and Figures 9, 10, 11). The broad fragments are decidedly blade-like, while the thin detritus is usually curved and ap-

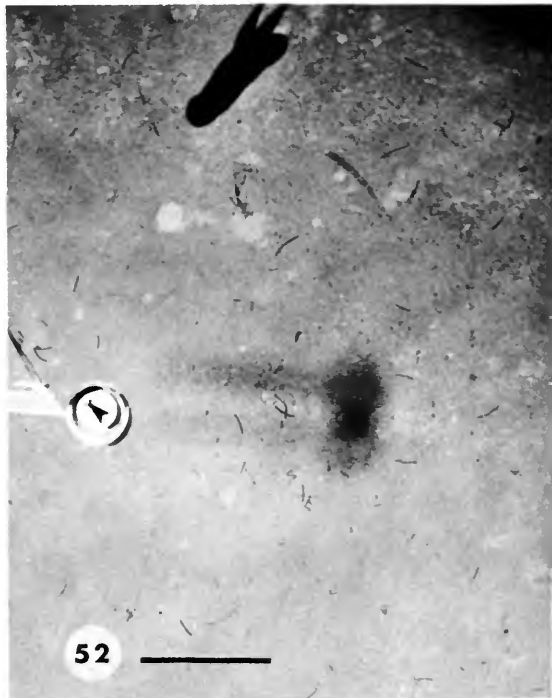


FIGURE 52.—Wide grass fragment (upper right center) is blade of *Thalassia*, while thin fragments are more abundant *Syringodium*. A psychropotid holothurian lies at top of photo. (NA.3850.VIB)

pears uniform in cross section throughout its length. These thin fragments probably are pieces of manatee grass, *Syringodium filiforme*, rather than the similarly sized but flat shoal grass, *Diplanthera wrightii*. Both of these grasses grow in the same shallow-water habitat as *Thalassia* (Stephens, 1966:265; Welch, 1963). A survey of the shallow waters of the nearby island of St. John revealed extensive areas of both turtle grass and manatee grass with the latter dominant at greater depths, some even to more than 20 m (Kumpf and Randall, 1961:548). H. J. Humm (pers. comm.) has confirmed the identification of both *Thalassia* and *Syringodium* fragments in our photographs (e.g.: Figures 39, 52, 53 and others on file).

No closely examined photograph from the Virgin Islands Basin was found devoid of these detrital grasses and a count of greater than 10 fragments per square meter was typical in hundreds of photographs.

The large number of sea grass fragments in our Virgin Islands Basin photographs is an order of magnitude greater than those recorded from similar depths in other works. Pratt (1962:495) presented a photograph from the Puerto Rico Trench showing two blades, and Menzies and Rowe (1969:219) reported highest concentrations of $\frac{3}{4}$ to 1 blade per photo at abyssal depths off North Carolina.

Clumps of a fucoid-type seaweed, probably *Sargassum*, were noted in several photographs (see Figure 49 and p. 32). Humm (pers. comm.) has concurred with the identity of *Sargassum* and also has suggested that possibly some of the clumps may consist entirely or in part of some of the common large red algae from seagrass beds, especially *Laurencia*.

Fragments and entire leaves, apparently of terrestrial origin also were photographed on several occasions. At least one of these is identifiable as a mangrove leaf (Figure 53), possibly from one of the three common tropical species found on the nearby island of St. John (Kumpf and Randall, 1961:551).

Plant debris also was noted in photographs from the Blake Basin, particularly along an erosion channel. This consisted primarily of *Sargassum* clumps, and, less commonly, of single blades of *Thalassia*.

The importance of shallow-water plant debris as a source of food for the abyssal benthos has been suggested by a number of investigators (see Menzies, et al., 1967:111). Mortensen (1938:225 et seq.) listed a number of species of deep-sea echinoids collected from as deep as 3,000 m that had gut contents consisting of plant material, some of terrestrial origin

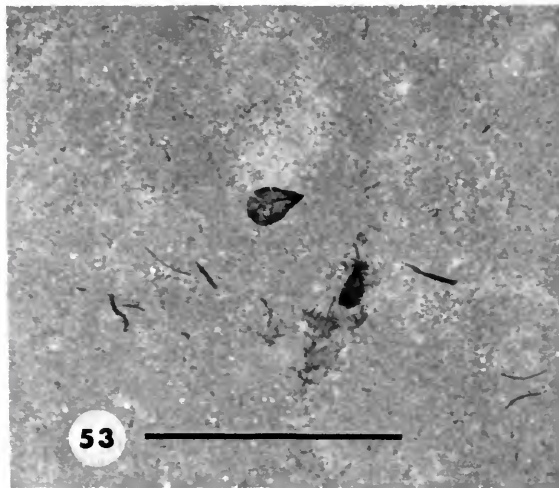


FIGURE 53.—One mangrove leaf and probably a fragment of a second can be seen in center of this view along with many sea grass fragments. (NA.3770.VIB)

and some marine, such as fucacean algae. Mortensen (p. 228) concluded that many deep-sea echinoids are "facultative vegetarians" in regions where rich plant material is available to be carried out to sea.

Moore (1963:1234) has pointed out the probable significant importance of sea grass as a source of energy for West Indian deep-sea organisms. The deposition of grass probably occurs continuously, but it is expected to be especially heavy following storms and hurricanes during which time great quantities of grass are broken off or uprooted. Further indication that deep-sea organisms ingest algae of shallow-water origin was given by Okutani (1969:34) who discovered quantities of littoral and sublittoral "kelp" in the stomachs of the deep-sea urchin, *Hygrosoma*, from Sagami Bay and Oshima-Miyake Region, Japan.

Our photographs indicate that at least two species of holothurians, a laetmogonid and *Psychropotes* species, are relatively more abundant in those areas where plant fragments are most numerous (Figures 43, 52). Another species, possibly an unidentified mollusk, visibly utilizes plant material from the surface by gathering and transporting fragments. The animal leaves a distinct trail in the soft sediment (Figures 48, 49).

Several photos show clumps of seaweed, probably mainly *Sargassum*, which are surrounded by conspicuous lebensspuren (Figure 49). Similar observations have been made from photographs taken in the

open Hatteras Abyssal Plain (Rowe and Menzies, 1969:536). Such clumps probably provide a concentrated source of organic material for foraging benthic organisms in the enclosed Virgin Islands Basin, either from the alga itself or from the organisms attached to it.

The point that we wish to emphasize is that there seems little doubt that plant materials of shallow-water origin are utilized by deep-sea organisms, and that the degree of utilization and the overall importance of this material in deep benthic food webs previously may not have been properly appreciated or emphasized.

BIOMASS

The Virgin Islands Basin appears to be a relatively organically rich area judging from the photographs available. Cirrate octopods are significantly more abundant than in other areas sampled, and a high incidence of other benthopelagic and benthic macroorganisms has been noted above.¹⁸

It is perhaps more significant that fragments of plant material, especially sea grasses, were identified in each one of the thousands of closely examined photos from the Basin. Counts of up to 10 pieces per square meter were recorded; this value is an order of magnitude greater than previously recorded in photos from other areas at comparable depths.

Certainly there appears to be a positive correlation between abundance of plant material and abundance of organisms in the deep sea. This correlation has been discussed by, among others, Heezen, Ewing and Menzies (1955:174) and Schoener and Rowe

¹⁸ Several attempts were made to arrange to sample the Virgin Islands Basin with deep benthic trawls in an effort to capture specimens of cirrate octopods and other benthic organisms. After our own efforts to secure a vessel with adequate trawling capabilities met with little success, G. L. Voss, Institute of Marine Sciences, Miami, kindly agreed to divert the R/V *Pillsbury* to the Basin during a cruise to the Caribbean Sea in June 1970. Adverse circumstances prevented trawling in the bottom of the basin at 4,000 m. One tow, however, was made along the steep southern slope of the basin. The net fished between about 400–2,000 m, and while it caught no finned octopods, other forms of benthic life were extremely abundant. Although the analysis of the sample is incomplete, Voss (pers. comm.) has the impression that the basin has a very rich benthic fauna that surpasses the faunas from the same depth stratum in other areas sampled by the *Pillsbury* during the current deep-sea biology program aboard this ship.

(1970:923) (see their references). Numerous observations are recorded in the literature, and more have been made during deep-sea trawling activities that strongly support the concept of the relationship between plant debris and animal abundance.¹⁹

Our Virgin Islands Basin photographs indicate that holothurians, for instance, are most numerous where sea grass is abundant (Figures 43, 44, 52), and that organisms and lebensspuren are abundant around clumps of *Sargassum* (Figure 49).

The question of the nutritive value of sunken sea grasses and weeds to benthic organisms and, indeed, the question of whether these animals can utilize plant material are important points that need answering. Some protoplasm remained in ectoproct tests attached to *Sargassum* retrieved from stomachs of deep-sea brittlestars (ophiuroids). This point led Schoener and Rowe (1970:923) to suggest that the nutritive value of *Sargassum* to the deep benthos may derive from the attached fauna rather than from the alga itself. On the contrary, Vinogradov (1961:1441) presented data indicating the degree of decomposition in pteropods at increasing depths; below 2,000–3,000 m little or no protoplasm remained in the tests as a source of food to benthic organisms. Although pteropod tests were noted in the sediments of the Virgin Islands Basin (see Table I), they probably do not contribute food to the benthos. The situation with other small organisms may be similar if the transport is by passive sinking, commonly termed the "rain" of dead organisms.

More rapid means of transport of organic material to the deep sea do exist: (1) terrigenous material that is rafted or current carried, and (2) near-shore, estuarine, or terrestrial material transported by turbidity currents (Heezen, et al., 1955:176), or by migrations of animals.

It is possible that both of these active transport mechanisms function in the Virgin Islands Basin, but

¹⁹ Neither plant debris nor organisms (visible in photographs) were found to be nearly as abundant in the Blake Basin as in the Virgin Islands Basin. It is interesting, however, that out of a recent series of five camera runs, all eight cirrates that were photographed occurred during the single run which traversed an erosion channel along which was deposited a broad band of plant debris, primarily *Sargassum*. This run took place about a mile south of the area covered by the other four runs, where no erosion channels were photographed. We are not suggesting a direct correlation between abundance of plant debris and cirrate octopods.

the broad distribution of plants suggests that the rafting or current-carried method is more important. As pointed out on p. 9 there are data to suggest that a cyclonic circulation occurs beneath sill level in the basin. On the south side of the basin this circulation would appear as a reversal of the westerly surface flow. Sea-grass debris from the shallows on the north coast of St. Croix would first be carried westward until it sank beneath about 2,000 m, after which it would be transported back towards the east, where the relatively rich fauna was photographed. In addition, sinking organic matter, e.g., *Sargassum* and sea grasses, from the north and east would tend to be trapped by the relatively shallow sill at the western end of the basin.

Many photographs taken at the base of the slope show distinct erosion channels that probably are the result of turbidity currents. Small-scale density flows down the slope probably follow the channels and carry in shallow-water materials. Several photographs show small down-slope lineations of plant debris, primarily sea grasses, accumulated along the edges of rock outcroppings. Furthermore, the detailed acoustic records show that a ridge approximately 200 meters in relief, occurs along the base of the steeply sloping south side of the basin (Figure 6). The ridge may act as a dam to trap organic materials carried down the slope.

In general the productivity in the surface waters of the Caribbean Sea is regarded as relatively low (Fleming and Laevastu, 1956:183), and this is reflected in the midwater fauna. The benthic fauna is rich in near-shore areas along the continental margins where enrichment from river runoff occurs. We suggest that the Virgin Islands Basin, isolated from continental enrichment but exposed to Atlantic water intrusion through the Anegada Passage and to sea grasses and organic materials from the neighboring islands and reef flats, serves as a bowl of concentration of organic materials with a resultant unusual abundance of deep-sea benthic and benthopelagic organisms.

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